

# The use of resighting data to estimate the rate of population growth of the snail kite in Florida

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**ABSTRACT** *The rate of population growth ( $\lambda$ ) is an important demographic parameter used to assess the viability of a population and to develop management and conservation agendas. We examined the use of resighting data to estimate  $\lambda$  for the snail kite population in Florida from 1997-2000. The analyses consisted of (1) a robust design approach that derives an estimate of  $\lambda$  from estimates of population size and (2) the Pradel (1996) temporal symmetry (TSM) approach that directly estimates  $\lambda$  using an open-population capture-recapture model. Besides resighting data, both approaches required information on the number of unmarked individuals that were sighted during the sampling periods. The point estimates of  $\lambda$  differed between the robust design and TSM approaches, but the 95% confidence intervals overlapped substantially. We believe the differences may be the result of sparse data and do not indicate the inappropriateness of either modelling technique. We focused on the results of the robust design because this approach provided estimates for all study years. Variation among these estimates was smaller than levels of variation among ad hoc estimates based on previously reported index statistics. We recommend that  $\lambda$  of snail kites be estimated using capture-resighting methods rather than ad hoc counts.*

## 1 Introduction

Understanding the biological and physical factors that regulate a population is a fundamental challenge in population ecology (Hastings, 1997). In fluctuating

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environments, individuals in a population may shift metabolic resources normally allocated for reproduction to survival when environmental conditions are unfavourable. Thus, a species' life-history strategy should, in theory, reflect the nature of the environment occupied (Lack, 1954; Stearns, 1976, 1992). How the variability in the environment influences the evolution of a life-history trait depends on several factors, including the magnitude of environmental variation, the covariation among life-history traits, the life-history trait being considered, and how the variability in life-history traits influences the rate of population change (Franklin, 1997).

The snail kite (*Rostrhamus sociabilis*) is an endangered species that resides in the central and southern Florida wetland ecosystem. For the snail kite, this ecosystem is highly fluctuating as a result of natural and anthropogenic hydrological modifications. Many of the life-history parameters of the snail-kite, such as rates of survival and reproduction, are thought to vary both temporally and spatially (Sykes, 1987; Snyder *et al.*, 1989; Sykes *et al.*, 1995). Various approaches have been used to estimate the rate of population growth ( $\lambda$ ) of the Florida population of snail kites. A deterministic population model employing Lotka-Leslie matrix models produced an estimate of  $\lambda = 1.054$  from 1969-1979 (Nichols *et al.*, 1980). Population projection models permit computation of the rate of population increase approached asymptotically when the population is exposed to the same vital rates over many time steps. However, for populations that reside in highly fluctuating environments, such as the snail kite, the constant-parameter nature of deterministic matrix projection models make these models of questionable value for the purpose of estimation because the population experiences substantial temporal variation in vital rates (Nichols *et al.*, 2000; Nichols & Hines, this issue).

A second approach examined the effects of environmental states on  $\lambda$  to predict the viability of the Florida population of snail kites. This population viability analysis suggested the population increased annually, on average, by 13% from 1968-1988 based on the Annual Survey (Beissinger, 1995). The Annual Survey is a data set consisting of the number of snail kites counted annually in November-December from 1969 through 1994 (Sykes, 1979, 1982; Rodgers *et al.*, 1988; Bennetts *et al.*, 1994), which has been assumed to be a count of the total population (i.e. a census). The treatment of count data as censuses to estimate  $\lambda$  of any population is generally invalid (Burnham, 1981; Nichols, 1992; Link & Sauer, 1997, 1999; Sauer *et al.*, 1994). Nichols (1992) provides reasons as to why a complete census is seldom achieved in animal populations because of incomplete detectability and the variation in detectability of animals over time. In particular, Bennetts *et al.* (1999a) showed that not taking into account the inherent sources of error associated with the Annual Survey on snail kites results in misinterpretation of most demographic parameters derived from this data set.

For the snail kite, assessing  $\lambda$  and estimating how life history parameters (i.e. survival and recruitment) influence  $\lambda$  are critical for identifying and evaluating the effectiveness of management actions and conservation strategies. Here we use two different approaches to estimate the annual rate of population change ( $\lambda_t$ ) for the Florida population of snail kites. Although the approaches are not completely independent, they are quite different. One approach takes advantage of the robust design (Pollock, 1982), whereas the other uses the direct estimation approach of Pradel (1996) for open population models.

## 2 Methods

### 2.1 Study area

The Florida snail kite population is best viewed as one continuous population that is distributed among a network of heterogeneous wetland units in central and southern Florida (Bennetts & Kitchens, 1997a, b). Snail kites use the entire spatial extent of their range, exhibiting considerable interchange among wetland units in Florida, suggesting a panmictic population rather than a metapopulation consisting of distinct subpopulations (Rodgers & Stangel, 1996; Bennetts & Kitchens, 1997a, b). Therefore, the geographic scope of this study encompassed a large proportion of the wetland units utilized by snail kites in central and southern Florida (Fig. 1).

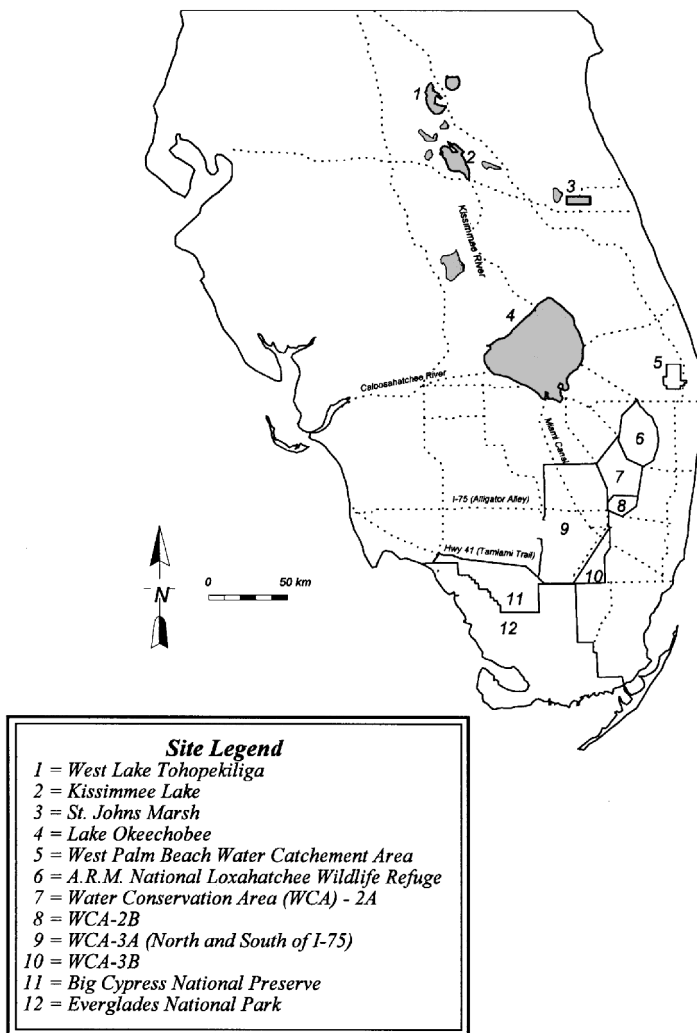


FIG. 1. The study area showing the wetland units in central and southern Florida that were sampled every 2 to 3-weeks for snail kites to estimate the rate of population change.

## 2.2 Sampling methods

Mark-resighting data were collected from March 1 to June 30 of each year starting in 1997 and continuing through 2000. This sampling period was chosen because it coincides with the major period of breeding activity (Sykes *et al.*, 1995; Bennetts & Kitchens, 1997a). During the breeding season, adults remain in close proximity to their nest, increasing our ability to read the band (i.e. a resighting). Sampling during this period also coincides with our banding of juveniles at the time of fledging (24–30 d) (Sykes *et al.*, 1995). Prior to 1997, over 1000 snail kites had been banded as either adults or juveniles. Juvenile snail kites have the potential to breed at nine months (Snyder *et al.*, 1989); thus, they advance to the adult age class the following breeding season.

During the sampling period, the entire study area was surveyed on six separate 2 to 3-week sampling occasions. Except for temporal replication, the format of the surveys was similar to the quasi-systematic transects conducted by airboat for the Annual Survey (Sykes, 1979, 1982; Rodgers *et al.*, 1988; Bennetts *et al.*, 1994). During each sampling occasion, we categorized and recorded an individual as (1) 'marked' if the sighted bird had a coloured leg band with a distinct letter/number combination so that individuals could be identified; (2) 'unmarked' if no leg bands were present or if birds were banded with a colour band without a letter/number combination, or (3) 'unknown' if the banding status was not determined.

## 2.3 Analysis

**2.3.1 Robust design approach.** Our first method used the robust design approach to estimate  $\lambda$  indirectly. Initially, we had hoped to follow the original robust design approach of Pollock (1982) and to use resighting data with capture-recapture models for closed populations because of the ability to model sources of variation in capture probability with these models (e.g. Otis *et al.*, 1978; White *et al.*, 1982). Therefore, we first tested the assumption of demographic closure of the sampled population using programs CAPTURE (Otis *et al.*, 1978) and CLOTEST (Stanley & Burnham, 1999) in conjunction with the resighting data for marked birds only (data on unmarked birds were not used in the closure tests). The closure test in CAPTURE is unaffected by heterogeneity in resighting probabilities; however, it can be influenced by certain patterns of temporal variation in capture probabilities (Otis *et al.*, 1978). Program CLOTEST is more robust to time-specific variation in resighting probabilities in the absence of behavioural response or individual heterogeneity in resighting probabilities, and its use is recommended in conjunction with the closure test in program CAPTURE in order to detect better closure violations in resighting data sets (Stanley & Burnham, 1999).

The results from the closure analyses (Table 1) suggested that open-population models were needed for use over the secondary periods within each year to estimate  $\lambda_t$ . The snail kite is a highly nomadic species with approximately 25% of the population moving at least once during any given month to a different wetland (Bennetts & Kitchens, 2001). Thus, temporary emigration to un-surveyed wetlands could account for the apparent violation of the geographic closure assumption. This species exhibits temporary emigration in and out of the wetland units in the study area for foraging even during the breeding season, when birds may have committed to breeding activity (Bennetts & Kitchens, 1997b). Thus, we believe that the area sampled during the spring and summer covers the majority of snail

TABLE 1. Test statistics computed by programs CAPTURE and CLOSTEST to test the assumption of demographic closure for the secondary sampling periods within each year. Test results were used to determine whether closed- or open-population models should be used for estimating demographic parameters of snail kites over secondary sampling periods

Year	Program CAPTURE ( $H_0$ : Closed model $M_h$ )		Program CLOSTEST ( $H_0$ : Closed model $M_c$ )		
	$z$ -test	$P$	$\chi^2$	df	$P$
1997	-3.90830	< 0.001	59.38645	8	< 0.001
1998	-2.49569	0.006	66.44865	8	< 0.001
1999	-5.06722	< 0.001	103.59770	8	< 0.001
2000	-3.73400	< 0.001	70.71698	8	< 0.001

kite habitat, but that birds may be absent from this area for certain sampling periods during each breeding season. However, we also believe that it is unlikely for many birds to spend the entire spring-summer sampling season outside the sampled area.

The estimation task is thus to estimate the total number of birds that use the sampled area during at least some portion of the spring-summer sampling period. We followed the superpopulation approach of Crosbie & Manly (1985) and Schwarz & Arnason (1996) for modelling and estimation. This approach has been generalized by Schwarz & Stobo (1997) in a robust design framework to account for migration during secondary sampling or, in our instance, among the six sampling occasions. We denote the annual parameter of interest as  $N_j^*$ , the size of the snail kite superpopulation in year  $j$ . Specifically, the superpopulation size is the total number of birds that were ever available for capture in the population of interest over the course of the sampling year (i.e. it includes any bird available for sighting at any sampling occasion,  $i = 1, \dots, 6$ , within year  $j$ ). Superpopulation size for any year can be estimated as:

$$\hat{N}_j^* = \sum_{i=0}^5 \hat{B}_{ij}$$

where  $B_{ij}$  is defined as the number of new animals in the population at sampling occasion  $i + 1$  of year  $j$  that were not present in the population at  $i$ , where  $B_{0j} = N_{1j}$ , the abundance in the first sampling period of year  $j$  (i.e. all animals in the population in the first sampling period are 'new' with respect to sampling).

The robust design approach requires not only the sightings of previously marked individuals, but also information on the unmarked individuals that are caught during the study. Resighting data were used to develop capture histories over the six sampling occasions to estimate survival probabilities,  $\phi_{ij}$ , and resighting probabilities,  $p_{ij}$ . The basic Cormack-Jolly-Seber (CJS) (Cormack, 1964; Jolly, 1965; Seber, 1965) approach, implemented in program MARK (White & Burnham, 1999), was used to produce estimates of  $\phi_{ij}$ , defined as the probability of not dying and not permanently emigrating to an area not sampled between periods  $i$  and  $i + 1$  of year  $j$ , and of  $p_{ij}$ , defined as the probability of sighting an individual, given that it was present in period  $i$  of year  $j$ .

A suite of biologically relevant candidate models was developed. We did not model survival between years and thus treated the modelling as a multi-group

problem with four annual capture-recapture data sets. Bennetts *et al.* (1999a) estimated annual survival of adult snail kites to be constant. Within-year survival estimates further showed that most adult mortality in this species occurs during the winter or prior to the spring breeding season (Bennetts & Kitchens, 1999). Thus, we only allowed  $\phi_{ij}$  to vary by year or to remain constant (i.e.  $\phi_{ij} = \phi_j, \phi$ ), but not to vary over the six sampling occasions. Resighting probability was modelled as varying by year, varying among the six sampling occasions, or remaining constant. During the 1999 sampling period the number of breeding individuals was relatively low (Dreitz, unpublished data). Since non-breeding individuals were less likely to stay in the immediate vicinity of where they were initially observed (i.e. they had no nest to defend), the ability of the observers to determine the banding status and/or read the band identification of an individual may have been hindered. Therefore, we also developed models in which the resighting probability was constant for all years except 1999.

Model selection was based on Akaike's Information Criterion (AIC) (Akaike, 1973; Shibata, 1989; Burnham & Anderson, 1998) corrected for small sample sizes (AIC<sub>c</sub>) (Hurvich & Tsai, 1989) and extra-binomial variation (QAIC<sub>c</sub>) (Burnham & Anderson, 1998). The extra-binomial factor ( $\hat{c}$ ) was obtained by bootstrapping on the global model (i.e. the model with the largest number of parameters) (Cooch & White, 2001). Models with  $\Delta\text{QAIC}_c$  scores of  $\leq 4$  were all considered as plausible models (Burnham & Anderson, 1998, p. 123). Estimates of survival,  $\phi_j$ , and resighting,  $p_{ij}$ , probabilities were obtained using program MARK (White & Burnham, 1999; White *et al.*, 2000).

In order to estimate superpopulation size, first we estimated the abundance at each sample occasion as

$$\hat{N}_{ij} = \frac{m_{ij} + u_{ij}}{\hat{p}_{ij}} \quad (1)$$

where  $m_{ij}$  and  $u_{ij}$  are the numbers of marked and unmarked animals, respectively, seen at each sampling period,  $i$ , in year  $j$ . Given the constraint,  $p_{1j} = p_{2j}$ , abundance can be estimated for all  $K = 6$  sampling occasions in the season. The new birds entering the sampled area from areas not sampled on each occasion were then estimated as:

$$\hat{B}_{ij} = \hat{N}_{i+1,j} - \hat{N}_{ij}\hat{\phi}_{ij}, i > 0 \quad (2)$$

where  $B_{ij}$  is the number of birds entering the population between periods  $i$  and  $i + 1$ , and available to be sighted at  $i + 1$ . Given the constraints,  $p_{1j} = p_{2j}$  and  $p_{5j} = p_{6j}$ ,  $B_{ij}$  can be estimated for periods  $i = 1, \dots, 5$ . Finally, the superpopulation size was then estimated for each year as:

$$\hat{N}_j^* = \hat{N}_{1j} + \sum_{i=1}^5 \hat{B}_{ij} \quad (3)$$

The above expression provides the best estimate of snail kite abundance each year. The rate of population growth,  $\lambda_j$ , is then estimated as:

$$\hat{\lambda}_j = \frac{\hat{N}_{j+1}^*}{\hat{N}_j^*} \quad (4)$$

Variance and 95% confidence intervals for  $\hat{\lambda}_j$  were obtained using a parametric bootstrap (500 simulations). This approach involved simulating the population-

dynamic and sampling processes, treating the following estimates as the true values governing these processes:  $\hat{\phi}_{ij}$ ,  $\hat{p}_{ij}$ ,  $\hat{N}_{1j}$ ,  $\hat{B}_{ij}$ . The approach was complicated by the necessity of simulating the marked and unmarked components of the population separately. We assumed that the survival and sighting probabilities of the marked group of birds applied similarly to the unmarked group, and we allowed new marked birds to enter the marked population in proportion to the entry of new birds to the entire population. We subjected the capture history data and data of the number of unmarked birds to an overall model with constant period-specific survival within each year and time-varying capture probabilities ( $\phi_j, p_{ij}$ ). The resulting estimates were used in conjunction with simulated numbers of marked and unmarked birds to estimate annual abundance (equations (1)-(3)) and the corresponding  $\hat{\lambda}_j$  (equation (4)). The standard deviation of the resulting estimates was then used to estimate  $\hat{SE}(\hat{\lambda}_j)$ , and the 95% confidence interval was taken directly from the empirical distribution of  $\hat{\lambda}_j$ .

*2.3.2 Pradel's temporal symmetry approach.* Our second method followed Pradel's (1996) approach, which simultaneously incorporates survival and recruitment parameters in an open population model and thus permits the direct estimation of  $\lambda_i$  as a model parameter (Pradel, 1996; Nichols *et al.*, 2000; Williams *et al.*, in press). This approach has been referred to as temporal symmetry modelling (hereafter TSM) (Williams *et al.*, in press; Nichols & Hines, this issue), because it simultaneously uses the temporal symmetry of capture history data for both forward- and reverse-time modelling. The survival probability ( $\phi_j$ ) is the probability that an animal present just **after** time  $j$  will still be present just **before** time  $j + 1$ . The 'backward survival probability', called the seniority probability ( $\gamma_j$ ), is the probability that an animal present just **before**  $j$  was already present just **after**  $j - 1$  (Pradel, 1996). In the TSM approach, the rate of population growth is computed as:

$$\lambda_j = \frac{\phi_j}{\gamma_{j+1}} \quad (5)$$

Our sample included only resightings of adult birds, and this required modification of the standard TSM approach to estimation of  $\lambda_j$ . For example, if we had used reverse-time modelling with these data,  $\gamma_j$  would have been estimated as 1 for all periods that included no releases of previously unmarked individuals. That is, all marked animals seen at period  $i + 1$  must have been present in the previous sampling period. Even though estimation of sighting probability must be based on marked birds, estimation of  $\gamma_j$ , and thus  $\lambda_j$ , under the TSM approach also requires the information on unmarked animals that are sighted.

Estimation under the Pradel (1996) TSM modelling approach treats the counts of unmarked birds as though these are 'losses on capture' (because the birds are not 'released' with marks following sighting). The usual parameter denoting the probability that a captured bird survives the capture process,  $\eta_j$  (see Pradel, 1996), now denotes the probability that a randomly selected bird from all those sighted at time  $j$  is a marked bird. Stated differently,  $\hat{\eta}_j$  estimates the proportion of marked birds among the entire sample of sighted birds. Using resighting data, the usual estimator of  $\lambda_j$  based on equation (5) estimates nothing of interest, whereas the following estimator, denoted as  $\lambda'_j$  and developed to deal with losses on capture (Pradel, 1996), estimates the growth rate for the population:

$$\lambda'_j = \frac{\phi_j(1 - p_j[1 - \eta_j])}{\gamma_{j+1}} \quad (6)$$

Equation (6) is similar to equation (5) but contains an extra term  $(1 - p_j[1 - \eta_j])$  in the numerator. This term represents the probability that a bird present in year  $j$  is not sighted as an unmarked bird (Nichols & Hines, this issue). Such birds do not have the opportunity of being identified subsequently as an 'old' bird, and the extra term in the numerator of equation (6) accounts for this fact. Because the  $\eta_j$  are likely to be relatively small in resighting studies such as this one (see Section 3), we recommend the use of software that explicitly incorporates losses on capture in the implementation of the Pradel (1996) models.

We used the same data set for this analysis as in the robust design approach, except that the capture histories of previously marked individuals and the number of unmarked individuals were generated on a yearly basis. For the annual capture histories, if a marked individual was seen on  $\geq 1$  of the six sampling occasions in a given year, a '1' was generated in the capture history for that year. Because it was unknown if an unmarked individual was seen on more than one sampling occasion within each year, the number of unmarked individuals sighted each year ( $u_j$ ) was estimated as:

$$\hat{u}_j = m_j \left( \frac{\sum_{i=1}^6 u_{ij}}{\sum_{i=1}^6 m_{ij}} \right) \quad (7)$$

where  $m_j$  is the number of marked individuals seen in year  $j$ ,  $u_{ij}$  is the number of unmarked individuals counted at sampling occasion  $i$  of year  $j$  (Table 2), and  $m_{ij}$  is the number of marked individuals seen at sampling occasion  $i$  of year  $j$  (Table 2).

TABLE 2. The number of unmarked,  $\mu_i$ , and marked,  $m_i$ , snail kites sighted during six separate 2- to 3-week sampling occasions during the 1997-2000 breeding season

Sampling occasion		$\mu_i$	$m_i$
1997	1	482	54
	2	325	49
	3	266	37
	4	250	55
	5	394	68
	6	237	12
1998	1	207	34
	2	232	67
	3	279	72
	4	352	73
	5	456	75
	6	220	48
1999	1	264	60
	2	319	88
	3	509	107
	4	453	86
	5	429	80
	6	430	78
2000	1	394	84
	2	387	84
	3	387	70
	4	301	75
	5	257	51
	6	224	35



The need to estimate the number of unmarked birds detected each year is unfortunate and constitutes an additional source of uncertainty in our TSM approach to estimating population growth. However, note that this source of variation is included in our bootstrap estimates of precision.

Using the capture history data for marked birds, together with the estimated number of unmarked birds seen each year, we were able to compute a maximum likelihood estimate of  $\lambda'_2$  using a GAUSS program written by Hines (see Pradel, 1996). The population growth rates for years 1 and 3 are not identifiable under this estimation procedure. We used a parametric bootstrap to estimate standard error and 95% confidence interval for  $\hat{\lambda}'_2$ , using the same general approach as for the robust design.

### 3 Results

#### 3.1 Robust design approach

The total numbers of snail kites detected and classified as unmarked or marked during the six sampling occasions for each year are shown in Table 2. Table 3 presents the  $m_{ij}$ -arrays used in the CJS models to estimate  $\phi_{ij}$  and  $p_{ij}$  showing the number of marked snail kites sighted on each sampling occasion for each year. Since juveniles were considered to be adults in the breeding season following fledging, all sightings were of adult individuals.

The results from the CJS modelling suggest more than one plausible model, given the data (Table 4). A variance inflation factor  $\hat{c}$  of 2.207 was used to adjust for the lack of fit of the most general model. The models with the lowest QAIC<sub>c</sub> had  $\phi$  remaining constant over all years; however,  $p$  was either constant for all years, constant for all years except 1999, or varied by year (Table 4). We model-averaged the estimates of  $\phi_j$  and  $p_{ij}$  due to the outcome of the model selection. Model averaging was conducted in program MARK which uses the QAIC<sub>c</sub> weights of the models to obtain the estimates. Resighting probability was highest during

TABLE 3. Resighting summary ( $m_{ij}$ -array format) of marked adult snail kites during six separate sampling occasions in 1997, 1998, 1999, and 2000

	Sampling occasion of each year											
	1997						1998					
	1	2	3	4	5	6	1	2	3	4	5	6
1	—	13	4	5	6	0	—	6	3	1	2	2
2	—	—	11	5	4	0	—	—	16	5	9	2
3	—	—	—	15	4	0	—	—	—	19	4	3
4	—	—	—	—	12	1	—	—	—	—	11	3
5	—	—	—	—	—	6	—	—	—	—	—	7
	1999						2000					
	1	2	3	4	5	6	1	2	3	4	5	6
1	—	7	5	3	3	3	—	14	2	7	2	0
2	—	—	20	5	2	4	—	—	13	6	3	1
3	—	—	—	22	11	5	—	—	—	16	2	1
4	—	—	—	—	28	4	—	—	—	—	14	3
5	—	—	—	—	—	23	—	—	—	—	—	6

TABLE 4. Cormack-Jolly-Seber models and their QAIC<sub>c</sub> (Akaike’s Information Criteria adjusted for sample size and extra-binomial variation). Model structure indicates whether survival probability ( $\phi$ ) was dependent on year ( $j$ ) and whether resighting probability ( $p$ ) was dependent on year ( $j$ ) and/or sampling occasion ( $i$ ). Note that these models did not contain between-year survival parameters but focused on within-season modelling for each of four seasons

Model	Number parameters	QAIC <sub>c</sub>	$\Delta$ QAIC <sub>c</sub>	QAIC <sub>c</sub> Weight
$\phi p$	2	1028.669	0.00	0.4273
$\phi p_{1999}$	3	1028.762	0.09	0.4078
$\phi p_j$	5	1032.475	3.81	0.0637
$\phi p_i$	5	1033.451	4.78	0.0391
$\phi_j p$	5	1033.784	5.12	0.0331
$\phi_j p_{1999}$	6	1034.685	6.02	0.0211
$\phi_j p_j$	8	1037.600	8.93	0.0049
$\phi_j p_i$	8	1038.659	9.99	0.0029
$\phi p_{j^*i}$	17	1046.411	17.74	0.0001
$\phi_j p_{j^*i}$	20	1050.640	21.97	0.0000
$\phi_{j^*i} p_{j^*i}$	38	1073.902	45.23	0.0000

the 1999 sampling occasions when breeding activity was reported to be relatively low (Table 5). The average number of individuals entering the sampled population between successive sampling occasions during a given year was highest in 1999, consistent with increased movement associated with low breeding activity, and lowest in 2000. Estimates of total population size,  $\hat{N}^*$ , for the years of study were  $\hat{N}_{97} = 3145$ ,  $\widehat{SE}(N_{97}^*) = 183$ ;  $\hat{N}_{98}^* = 3136$ ,  $\widehat{SE}(N_{98}^*) = 266$ ;  $\hat{N}_{99}^* = 3577$ ,  $\widehat{SE}(N_{99}^*) = 275$ ; and  $\hat{N}_{00}^* = 2772$ ,  $\widehat{SE}(N_{00}^*) = 296$ . The three estimated rates of annual population change ( $\hat{\lambda}_j$ ) were  $\hat{\lambda}_{98/97} = 1.00$ ,  $\widehat{SE}(\hat{\lambda}_{98/97}) = 0.10$ ,  $\widehat{CI}(\hat{\lambda}_{98/97}) = [0.79, 1.18]$ ;  $\hat{\lambda}_{99/98} = 1.14$ ,  $\widehat{SE}(\hat{\lambda}_{99/98}) = 0.13$ ,  $\widehat{CI}(\hat{\lambda}_{99/98}) = [0.94, 1.45]$ ; and  $\hat{\lambda}_{00/99} = 0.78$ ,  $\widehat{SE}(\hat{\lambda}_{00/99}) = 0.10$ ,  $\widehat{CI}(\hat{\lambda}_{00/99}) = [0.62, 1.02]$ .

### 3.2 Pradel’s temporal symmetry approach

The total number of marked snail kites observed from 1997 to 2000 was 327 (Table 6). The number of marked individuals,  $m_j$ , and the unmarked individuals for each year,  $u_j$ , are shown in Table 7. The estimates of  $\phi_j$ ,  $p_j$ , and  $\eta_j$  are shown in Table 8. The estimated detection probabilities suggest that the intensive sampling yielded a fairly high probability of sighting a bird at least once during each year’s sampling. As noted above, the TSM approach permitted estimation of only a single population growth rate,  $\hat{\lambda}'_{99/98}$ . The estimated value was  $\hat{\lambda}'_{99/98} = 0.92$  with  $\widehat{SE}(\hat{\lambda}'_{99/98}) = 0.12$  and  $\widehat{CI}(\hat{\lambda}'_{99/98}) = [0.73, 1.18]$ .

## 4 Discussion

Because we were only able to obtain one estimate from the TSM approach, we will focus on the three estimates of  $\lambda_j$  based on the robust design. The 95% confidence intervals associated with these estimates are fairly large, and all three cover  $\lambda_j = 1$ . Naive estimates from previous survey or count data have indicated substantially more dramatic fluctuations than those suggested by the point estimates, and these fluctuations have often been interpreted as reflecting a natural

TABLE 5. Within-season estimates of resighting probability,  $\hat{p}_{ij}$ , abundance,  $\hat{N}_{ij}$ , survival probability,  $\hat{\phi}_j$ , the number of new individuals in the sampled population,  $\hat{B}_{ij}$ , and the superpopulation size,  $\hat{N}_j^*$ , for snail kites from 1997 to 2000. Estimates of  $p_{ij}$  and  $\phi_j$  were obtained using model-averaging

Sampling occasion		$\hat{p}_{ij}$	$\hat{SE}(\hat{p}_{ij})$	$\hat{N}_{ij}$	$\hat{\phi}_j$	$\hat{SE}(\hat{\phi}_j)$	$\hat{B}_{ij}$	$\hat{N}_j^*$
1997	1	0.2799	0.0336	1918.76	0.7411	0.0386		
	2	0.2799	0.0336	1336.34	0.7411	0.0386	0.000	
	3	0.2802	0.0331	1081.55	0.7411	0.0386	91.123	
	4	0.2810	0.0329	1085.50	0.7411	0.0386	283.921	
	5	0.2791	0.0329	1655.55	0.7411	0.0386	851.034	
	6	0.2791	0.0329	892.28	0.7411	0.0386	0.000	3145
1998	1	0.2785	0.0333	865.40	0.7407	0.0385		
	2	0.2785	0.0352	1073.67	0.7407	0.0385	432.627	
	3	0.2788	0.0347	1259.08	0.7407	0.0385	463.763	
	4	0.2796	0.0351	1520.10	0.7407	0.0385	587.439	
	5	0.2777	0.0346	1912.27	0.7407	0.0385	786.262	
	6	0.2777	0.0346	965.14	0.7407	0.0385	0.000	3136
1999	1	0.3160	0.0481	1025.23	0.7406	0.0388		
	2	0.3160	0.0481	1287.86	0.7406	0.0388	528.622	
	3	0.3163	0.0476	1947.36	0.7406	0.0388	993.625	
	4	0.3171	0.0474	1699.59	0.7406	0.0388	257.450	
	5	0.3152	0.0481	1614.65	0.7406	0.0388	356.009	
	6	0.3152	0.0481	1611.48	0.7406	0.0388	415.736	3577
2000	1	0.2806	0.0351	1703.38	0.7396	0.0385		
	2	0.2806	0.0351	1678.43	0.7396	0.0385	418.642	
	3	0.2809	0.0347	1270.89	0.7396	0.0385	29.552	
	4	0.2817	0.0351	1334.66	0.7396	0.0385	39.473	
	5	0.2798	0.0346	1100.76	0.7396	0.0385	113.665	
	6	0.2798	0.0346	925.64	0.7396	0.0385	111.534	2772

TABLE 6. Resighting summary of marked snail kites sighted annually in Florida from 1997-2000

Year of capture or resighting	1997	1998	1999	2000	Never resighted
1997	—	75	40	8	123
1998	—	—	80	21	101
1999	—	—	—	103	103
Total resighted		75	120	132	

TABLE 7. The number of marked individuals,  $m_j$ , and the estimated number of unmarked individuals,  $\hat{u}_j$  observed each year from 1997-2000

Year	$m_j$	$\hat{u}_j$
1997	189	1343.6181
1998	234	1230.6145
1999	287	1382.6613
2000	190	880.9524

TABLE 8. Annual estimates of survival ( $\hat{\phi}_j$ ), resighting probability ( $\hat{p}_j$ ), and probability an individual sighted is marked ( $\hat{\eta}_j$ ) using the temporal symmetry approach to estimate the rate of population growth from 1997 through 2000. Standard errors were obtained using a parametric bootstrap approach

Year	Parameter					
	$\hat{\phi}_j$	$\hat{SE}(\hat{\phi}_j)$	$\hat{p}_j$	$\hat{SE}(\hat{p}_j)$	$\hat{\eta}_j$	$\hat{SE}(\hat{\eta}_j)$
1997	0.8145	0.0599	— <sup>a</sup>	— <sup>a</sup>	0.1284	0.0063
1998	0.7447	0.0619	0.4656	0.0468	0.1294	0.0073
1999	0.3622 <sup>b</sup>	0.0278	0.5976	0.0519	0.1704	0.0066
2000	— <sup>c</sup>	— <sup>c</sup>	1.0000 <sup>b</sup>	NA <sup>d</sup>	— <sup>c</sup>	— <sup>c</sup>

<sup>a</sup>Parameter is not identifiable for year.

<sup>b</sup>Because  $\phi_j$  and  $p_j$  were variable over time, we were only able to estimate a product of the two parameters.

<sup>c</sup>Parameter is not defined for occasion.

<sup>d</sup>NA, not available.

response to environmental fluctuations (Beissinger, 1995; Sykes *et al.*, 1995; Bennetts *et al.*, 1999b). From a biological perspective, it is not likely that a population of a long-lived species, such as the snail kite, truly exhibits dramatic fluctuations from year to year, especially in the absence of any apparent environmental pulse. Bennetts *et al.* (1999b) also showed that the count data could have been strongly influenced by several sources of error.

Reliable inferences about annual variation in  $\lambda_j$  clearly require estimates over a larger series of years to enable better partitioning of the variation associated with the demographic process and sampling error. Continued sampling should lead to a better understanding of variation in the population dynamics of the snail kite, especially if key variables reflecting environmental variation can be incorporated into the sampling to enable explicit testing of hypotheses regarding factors that influence annual variation in  $\lambda$ . In this section, we will discuss the relevance of the robust design and TSM approaches to the biology of the snail kite population.

#### 4.1 Robust design approach

Although all evidence suggests that this population is geographically closed at the scale of central and south Florida (Sykes, 1979; Sykes *et al.*, 1995), there are numerous small wetlands scattered throughout this region that are not surveyed, but that are regularly used by snail kites (Valentine-Darby *et al.*, 1998). Consequently, it is not surprising that our closure tests provided strong evidence of an open population and that our estimates indicate a substantial difference between  $\hat{N}_{ij}$  and  $\hat{N}_j^*$ . In fact, our estimates indicate that the superpopulation tends to be more than twice the estimated number of birds in the sampled area at any given sampling occasion ( $\bar{x}$  ratio between  $\hat{N}_{ij}$  and  $\hat{N}_j^* = 2.3$ ). This is almost certainly an effect of temporary emigration, as kites regularly shift among wetlands within a day for foraging, or for longer periods in some cases (Bennetts & Kitchens, 1997a; Valentine-Darby *et al.*, 1998). Thus, they can easily escape detection by foraging in wetlands not surveyed.

Further, our estimates of the superpopulation ( $\hat{N}_j^*$ ) between years is more stable than the abundance estimates among the 2–3 week sampling occasions. From a biological perspective, this is likely a result of temporary emigration. The individual wetlands comprising the ecosystem network in which snail kites reside experience

substantial fluctuations within and between years as a result of rainfall and manipulated hydrological regimes. Although kites can temporarily escape detection when in wetlands that are not surveyed, they will, in all likelihood, return to the major wetlands included in our survey. The probability of detecting a bird during any given sampling occasion is, of course, lower than the probability of detecting it at least once over the six sampling occasions. This emphasizes that sampling designs for birds that exhibit frequent and substantial movements should take into account whether the parameter of interest is the number of birds using a local site at any given point in time, or the larger superpopulation that uses the sampling area over longer time scales.

#### 4.2 Temporal symmetry modelling

We explored the use of the open population TSM approach because it provides a convenient means of modelling and estimating  $\lambda_j$ . Because of the short duration of the study, only a single estimate could be obtained and additional modelling was not possible. A longer time series of data is needed to evaluate the TSM approach properly. The TSM and robust design estimates of  $\lambda_{99/98}$  differed (0.92, 1.14, respectively), but the 95% confidence intervals overlapped substantially (Fig. 2). It is useful to know that the TSM approach can be used to estimate the population growth rate from resighting data by treating unmarked birds as ‘losses on capture’ and using the appropriate estimator ( $\hat{\lambda}'_j$  of equation (6)). Naive use of the standard estimator of equation (5) yields a substantial overestimate of  $\hat{\lambda}_{99/98} = 1.54$  as the number and proportion of ‘new’ birds in 1999 is overestimated. Unmarked birds that are resighted cannot be identified as ‘old’ birds, leading to negative bias in  $\hat{\gamma}_{99}$  and thus to positive bias in  $\hat{\lambda}_{99/98}$ .

#### 4.3 Summary

In summary, the recent improvements toward flexible modelling of resighting data now permit assessment of the population dynamics of a species. Both methods presented in this study differ from conditional resighting models (e.g. CJS), by requiring counts of the number of unmarked individuals also sighted in the

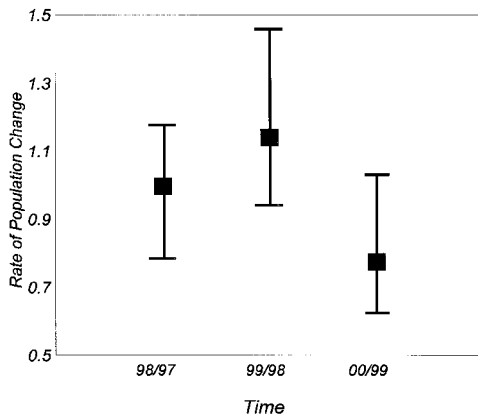


FIG. 2. The annual rate of population change of the snail kite in Florida with 95% confidence intervals for 1997 to 2000.

population. The robust design approach required this information to estimate abundance, and then to estimate  $\lambda$ , whereas TSM used it to estimate  $\lambda$  directly. We believe that with the continued collection of field data on the snail kite, these methods will provide reliable and reasonable estimates of  $\lambda$ . A common problem with parameter estimation is non-identifiability of model parameters because of sparse data rather than because of the model structure itself. Increasing the quantity and quality of data should be a priority, not only to understand the population dynamics of the snail kite, but also of other species.

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