

Return rates in studies of life history evolution: are biases large?

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SUMMARY *Studies of life history evolution in passerine birds often depend on examination of annual survival probability of adult birds. Most studies rely on return rates (proportion of marked individuals released in one year that are recaptured in the next year) to estimate annual survival probability. Yet, return rate includes both the probability of survival and the probability of recapturing or resighting the bird in the next time interval. We use numerical estimation to illustrate the increasing bias in return rate as an estimator of annual survival probability as recapture/resighting probability decreases. Recapture/resighting probability is normally assumed to be high and relatively invariant for recapture/resighting studies of color-banded territorial birds. We tested this assumption through examination of 11 color-banding studies of passerines. These studies showed that recapture/resighting probabilities vary strongly and cannot be generalized as high. In short, return rates generally are poor estimators of annual survival probabilities and use of return rates may strongly bias relationships explored in comparative studies or bias results of experiments to test survival costs of reproduction. Recapture/resighting probabilities should be estimated in all studies that attempt to estimate annual survival probabilities.*

1 Introduction

Life history theory assumes that variation in age-specific mortality drives evolution of life history variation (Cole, 1954; Murphy, 1968; Schaffer, 1974a,b; Hirshfield & Tinkle, 1975; Law, 1979; Charlesworth, 1980) and a variety of mostly aquatic studies support this assumption (Lynch, 1980; Reznick & Bryga, 1987; Crowl & Covich, 1990; Reznick *et al.*, 1990; Spitze, 1991; Hutchings, 1993). In birds, food

is thought to affect evolution of fecundity which then influences adult mortality through the cost of reproduction, although empirical tests of a trade-off between fecundity and adult survival are controversial (Lack, 1948, 1968; Williams, 1966a,b; Charnov & Krebs, 1974; Reznick, 1985; Linden & Møller, 1989; Nur, 1990; Roff, 1992; Stearns, 1992). Comparative analyses provide an alternative to experimentation for examining life history trade-offs and they show an inverse relationship between fecundity and annual survival, even when phylogeny is controlled (Sether, 1988; Martin, 1995). Yet, such relationships may be inaccurate when return rate is used to estimate annual survival probability because return rate can be biased (Nichols & Pollock, 1983; Nichols, 1986; Lebreton *et al.*, 1992). Such biases could occlude relationships between annual survival probability and other life history traits if return rates are widely used and bias varies among species or studies. Return rates are widely used; for example, 65 of 82 studies of North American passerines used return rates (see Fig. 9 of Martin (1993) and Martin and Li (1992)), so the important question is: How variable is bias among studies and what are the potential consequences of such biases for estimating life history relationships?

Return rate is often computed as a weighted average over n years as

$$\sum_i^n (m_{i+1}/R_i)/n \quad (1)$$

where R_i is number of newly marked birds that were released plus number of re-releases of previously banded birds that were recaptured or resighted in year i and m_{i+1} is the members of R_i that were recaptured in year $i+1$. The bias in return rate as an estimator of annual survival probability (ϕ) arises because return rate includes both probability of surviving from time i to $i+1$ (ϕ_i) and probability of being recaptured or resighted (p_{i+1}) (Nichols & Pollock, 1983; Nichols, 1986; Pollock *et al.*, 1990; Lebreton *et al.*, 1992). In short, the expectation of the average annual return rate is

$$\frac{\sum_i^n (m_{i+1}/R_i)}{n} = \frac{\sum_i^n (R_i \phi_i p_{i+1}/R_i)}{n} = \frac{\sum_i^n (\phi_i p_{i+1})}{n} \quad (2)$$

Return rate = ϕ when $p = 1$ for all years and ecological (e.g. age, sex) groups, but otherwise return rate $< \phi$ and is increasingly biased as p decreases because bias = $1 - p$. If p is low or variable, return rate may not accurately reflect relationships between annual survival probability and other life history traits.

Return rate has been assumed to provide a reasonable estimate of annual survival probability in field studies of color-marked, territorial birds. This assumption is based on the untested assumption that recapture/resighting probabilities are high and relatively invariant (i.e. p_i approaches 1 for all years and ecological groups under study) in color-banding studies of territorial birds. Sampling rates often vary across years in band-recovery studies (Burnham & Anderson, 1979; Anderson *et al.*, 1981), but year dependence in recapture/resighting rates in color-banding studies is relatively unexplored and may not be strong (see Clobert *et al.*, 1987; Lebreton *et al.*, 1992).

We use numerical methods to illustrate the variable bias in return rates as estimates of annual survival probabilities when recapture/resighting probabilities vary. We then examine empirical data to test specifically the assumption that recapture/resighting probabilities are high and relatively invariant for color-band-

ing studies and further explore the extent of variation in recapture/resighting probabilities and, hence, bias in return rates as estimates of annual survival probabilities among these studies. In addition, we examine the potential consequences of these biases for estimation of relationships between survival and other life history traits such as fecundity.

2 Methods

We used the EXPECT option in program RELEASE (Burnham *et al.*, 1987) to explore numerically effects of recapture/resighting probability (p) on return rate as an estimator of annual survival probability ($\hat{\phi}$). We set the true annual survival probability at 0.65 (i.e. $\phi_i = 0.65$, for all i) and set p as constant across years but varied it from 0.2 to 1.0 among tests. We arbitrarily chose 7 years and 100 new releases each year for our numerical studies.

We obtained 11 data sets from color-banding studies of passerine birds to estimate annual survival probabilities, recapture/resighting probabilities and return rates. All studies, except the studies on cliff swallows and Lazuli buntings, focused on territorial birds and used intensive searching of territories in each year to either resight or recapture previously banded birds. Studies on cliff swallows were based on netting and some sighting of birds at colonies, because they are colonial rather than territorial. Studies on Lazuli buntings were based on mist-netting and some resighting during winter. Except for these two studies, these analyses were focused on territorial birds marked as adults because this is the situation for which return rates are thought to provide the best estimates of ϕ . We present results from all data sets that we could obtain, without making any particular claim that this set is a random sample or completely representative of all such data sets.

We first analyzed these data sets using RELEASE to test for goodness-of-fit (GOF) to the Cormack–Jolly–Seber (CJS) model using results of Test 2 + Test 3 (Burnham *et al.*, 1987) and as a basis for summarizing the data for hand calculation of return rates. We computed return rate as in equation (1) because it is a common means of calculating return rates (see references in Martin and Li (1992) and Martin (1995)).

We used program SURGE (Lebreton *et al.*, 1992) to select the best model for each data set and to compute maximum likelihood estimates of parameters ($\hat{\phi}$ and \hat{p}) and the covariance matrix. Model selection was important because various data sets included gender, habitat and year as possible varying factors. We also examined an artificial dummy age variable, where age was modeled as two-age classes: (1) the first year following banding and (2) all subsequent years. We chose the best model based on Akaike's Information Criterion (AIC: Akaike, 1973) and standard likelihood ratio tests (LRTs) following methods of Lebreton *et al.* (1992). In cases where we directly compared $\hat{\phi}$ and \hat{p} , we used methods described by Sauer and Williams (1989) and based on software developed by Hines and Sauer (1989).

3 Results

3.1 Numerical methods

Numerical methods provided a means to illustrate the known bias in return rate as an estimator of annual survival probability (ϕ) as a function of recapture-resighting

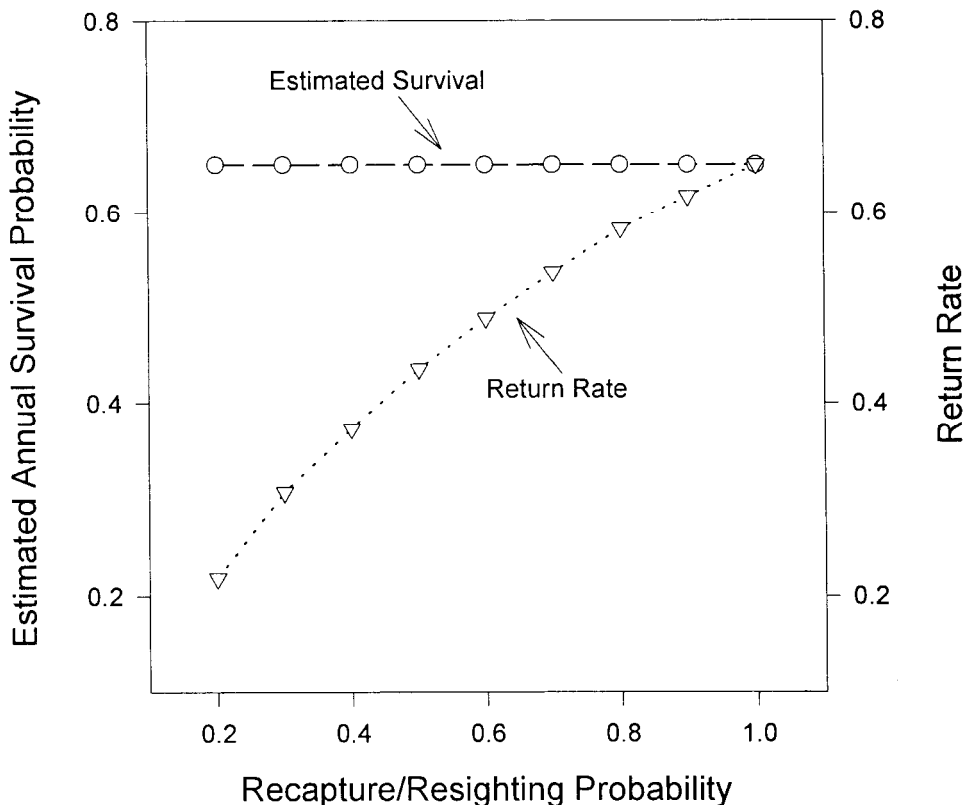


FIG. 1. Estimated annual survival probability ($\hat{\phi}$) and return rate as a function of changing recapture/resighting probabilities (p) under numerical methods where true annual survival probability = 0.65. Recapture/resighting probability is held constant within each of the nine cases.

probability (p); return rate decreases and the disparity (i.e. bias) between it and $\hat{\phi}$ increases as p decreases (Fig. 1). However, CJS estimates of ϕ were unbiased (i.e. $\hat{\phi}$ was 0.65, the true annual survival probability) (Fig. 1). The changing bias in return rate with changing $\hat{\phi}$ indicates that return rate may not accurately reflect relationships between ϕ and other life history traits (e.g. fecundity) when p varies across species or studies. However, accurate relationships may be approximated if recapture/resighting probabilities are high or relatively invariant, which we examine next for color-banding studies.

3.2 Empirical studies

The 11 color-banding studies for which data could be obtained were fairly variable in numbers of birds released and numbers of years of study (Table 1). We found that eight of the 10 studies (one species had insufficient data for analysis) fit the CJS model reasonably well (Table 2). Two species (American redstart in summer, black-throated blue warbler in summer) showed some lack of fit to the CJS model based on Test 3 of RELEASE (Burnham *et al.*, 1987), but sample sizes were small and only one or two cells were the cause of the lack of fit (see Table 2). Test 2 could not be interpreted in any of the 11 cases because of small sample sizes and

TABLE 1. Total numbers of birds released (n), numbers of years of capture/recapture, location and source of data

Species	n^a	Years	Location	Source of data
Dickcissel	207	5	Kansas	J. Zimmerman, unpubl.
Black-throated blue warbler (winter)	184	8	Jamaica	R. T. Holmes & T. W. Sherry, unpubl.
Black-throated blue warbler (summer)	458	8	New Hampshire	R. T. Holmes & T. W. Sherry, unpubl.
European dipper	462	7	France	Marzolin (1988), Lebreton <i>et al.</i> (1992)
Eastern kingbird	275	6	New York	M. T. Murphy, unpubl.
American redstart (winter)	440	8	Jamaica	R. T. Holmes & T. W. Sherry, unpubl.
American redstart (summer)	382	13	New Hampshire	R. T. Holmes & T. W. Sherry, unpubl.
Eastern phoebe	602	8	Indiana	H. P. Weeks, Jr, unpubl.
Hooded warbler	191	3	Maryland	B. J. Stutchbury, unpubl.
Lazuli bunting	1867	7	Utah	A. W. Stokes in Burnham <i>et al.</i> (1987)
Cliff swallow	2701	17	Indiana	H. P. Weeks, Jr, unpubl.

^a n = total number of new (unmarked) birds released plus the number of previously marked birds that were re-released.

TABLE 2. Tests of GOF of the data sets to the general CJS model based on Test 3 of RELEASE (Burnham *et al.*, 1987)

Species	χ^2	df	P
Dickcissel	3.61	3	0.31
Black-throated blue warbler (winter)	1.90	2	0.38
Black-throated blue warbler (summer)	27.80	9	0.001 ^a
European dipper	14.91	18	0.67
Eastern kingbird	4.61	4	0.33
American redstart (winter)	20.05	7	0.05
American redstart (summer)	24.66	10	0.006 ^b
Eastern phoebe	12.56	12	0.40
Hooded warbler	—	—	— ^c
Lazulie bunting	22.10	18	0.23
Cliff swallow	73.67	71	0.39

^a19 of the 27.8 came from only two cells, leaving 8.8 for 7 df, $P = 0.27$.

^b10.45 of the 24.66 came from one cell, leaving 14.21 for 9 df, $P = 0.12$.

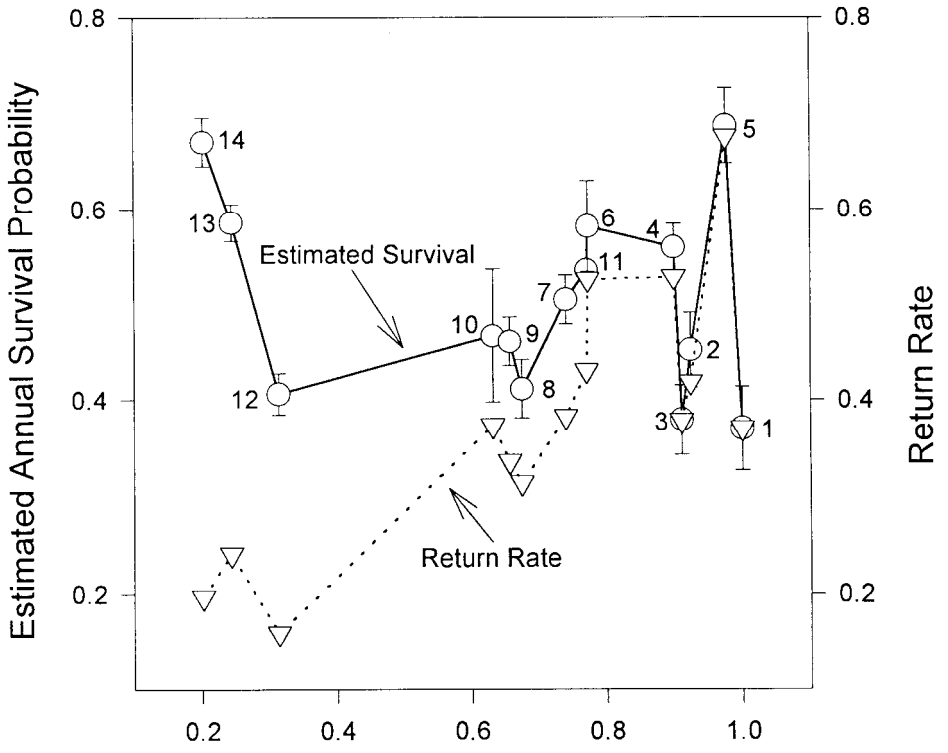
^c $n = 3$, no test exists.

because recapture/resighting probabilities were relatively high. Overall, these studies allowed reasonable parameter estimates.

We summarize the data with mean $\hat{\phi}$ and \hat{p} , which are averaged across years and ecological groups, but return rates are based on pooled data, so that return rate does not necessarily equal the product of mean $\hat{\phi}$ and \hat{p} (Table 3). Recapture/resighting probabilities did not show significant variation with respect to sex, year or habitat within species for most studies (Table 3), but sample sizes were small and sampling rates were low in many cases, particularly for the studies with largest sample sizes (Table 1). Note that the two species with largest sample sizes and

TABLE 3. Summary of analyses of data described in Table 1 to estimate recapture/resighting probability (\hat{p}), return rate and survival ($\hat{\phi}$). Estimates are means averaged over all years, sexes, habitats and ages. Significant variations in parameters were identified by selection of a best model based on AIC and LRTs (see text). Variation in both \hat{p} and $\hat{\phi}$ with respect to sex, dummy age (defined in methods), year and habitat is indicated as statistically significant (+), not significant (0) or blank if an effect was not available to test

Species (reference number)	\hat{p}	Sex	Year	Habitat	Return	$\hat{\phi}$	Sex	Age	Year	Habitat
Dickcissel (1)	1.00	0	0		0.370	0.370	+	0	0	
Black-throated blue warbler (winter) (2)	0.924	0	0		0.418	0.452	0	0	0	
Black-throated blue warbler (summer) (3)	0.911	0	0	0	0.378	0.379	+	+	0	+
European dipper (4)	0.900	0		0	0.529	0.560	0		+	
Eastern kingbird (5, 6)	0.874	+	0		0.526	0.649	+	+	0	
American redstart (winter) (7)	0.740	0	+		0.382	0.505	+	+	0	
American redstart (summer) (8)	0.675	0	0		0.314	0.411	+	+	+	
Eastern phoebe (9)	0.657	0	0	0	0.336	0.461	0	+	+	+
Hooded warbler (10)	0.632	0	0		0.373	0.467	+	0	0	
Lazuli bunting (11, 12)	0.543	0	+		0.200	0.421	0		+	
Cliff swallow (13, 14)	0.249	+	+	+	0.212	0.647	0	+	0	+



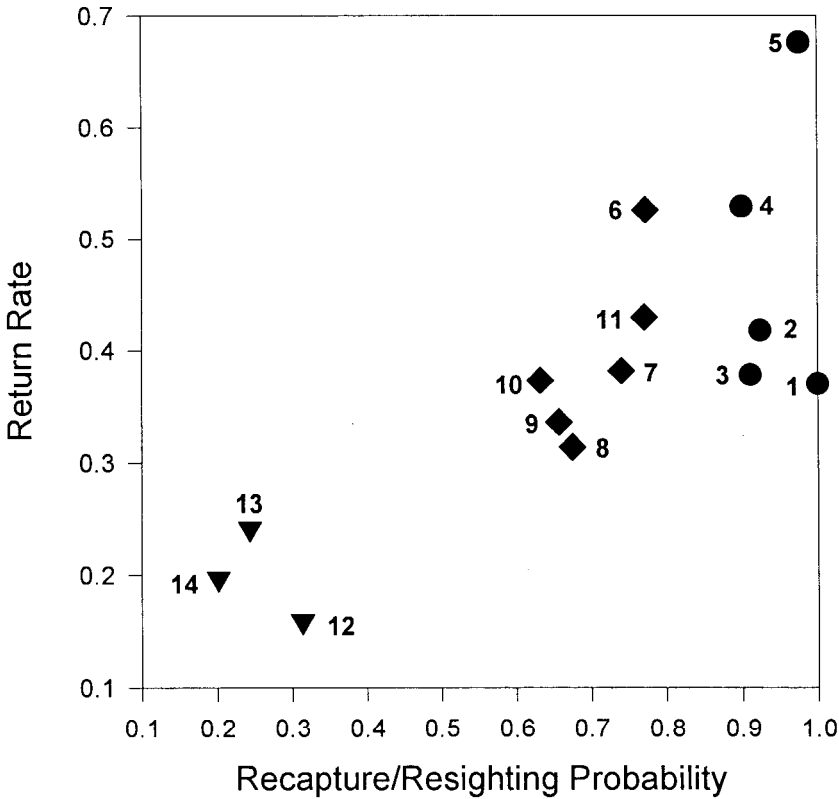


FIG. 3. Relationship between return rate and estimated recapture/resighting probability (\hat{p}) for empirical studies described in Tables 1 and 3. Inverted triangles represent the three studies with lowest recapture/resighting probabilities ($\hat{p} < 0.45$). Diamonds represent studies with $0.63 < \hat{p} < 0.78$. Circles represent studies with $\hat{p} > 0.90$. Numbers are reference numbers listed in Table 3.

recapture/resighting probability (Fig. 3). Of course, there is a built-in positive covariance between return rates and \hat{p} (see equation (2)).

This variability in bias is the greatest problem in examining relationships between annual survival probability and life history traits. Imagine, for example, that some general life history trait is perfectly estimated by $\hat{\phi}$ (correlation (r) = 1.0, slope (b) = 1.0, intercept (a) = 0). If $\hat{p} = 1$, return rate will show this 'true' relationship, i.e. the same correlation, slope and intercept (reflected by the solid line in Fig. 4). Return rate can also roughly reflect the true relationship when \hat{p} is high and relatively invariant; e.g. when $\hat{p} \geq 0.90$ ($n = 5$), then $r = 0.99$, $b = 1.03$, $a = 0.002$ (see dashed-and-dotted line in Fig. 4). However, \hat{p} does not have to be high, it only needs to be relatively invariant for return rate to reflect the relationship between annual survival probability and life history traits. Note that with reduced \hat{p} , the intercept must differ, but slope can be accurately estimated if \hat{p} is constant. If analyses are restricted to studies with $0.63 < \hat{p} < 0.78$ ($n = 6$), then $r = 0.96$, $b = 0.92$, $a = 0.194$; the intercepts clearly differ, but even with this reduced variation in \hat{p} , variation is still sufficient to cause the slopes to differ slightly (compare dashed and solid lines of Fig. 4). Once the full range of bias across all studies ($n = 14$) is included, return rate does not reflect the true relationship at all ($r = 0.35$, $b = 0.26$, $a = 0.406$); the correlation is not significant

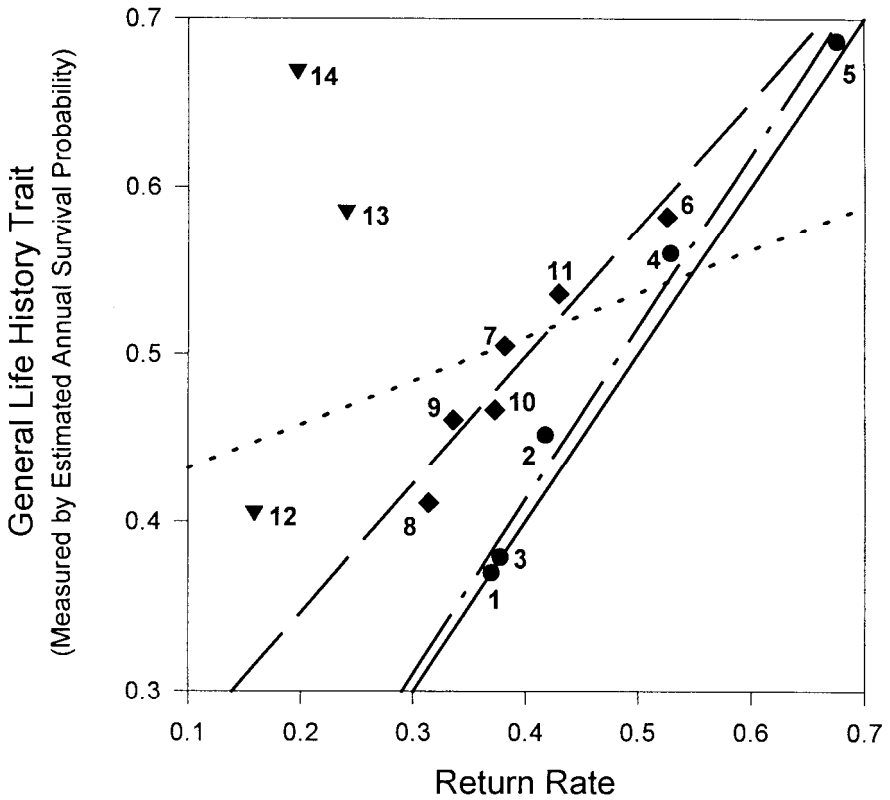


FIG. 4. Relationship between return rate and some general life history trait that theoretically is perfectly estimated by annual survival probability (ϕ) for studies described in Tables 1 and 3. When $\phi = 1$, return rate is perfectly related to the general life history trait with slope = 1.0 and intercept = 0, as illustrated by the solid line. Studies with $\phi \geq 0.90$ are represented by circles and the dotted-and-dashed regression line. Studies with $0.63 < \phi < 0.78$ are represented by diamonds and the dashed regression line. Inverted triangles represent the three studies with $\phi < 0.45$. The dotted line is the regression line for all studies ($n = 14$).

($P = 0.26$) and both the slope and intercept differ from the true relationship (compare dotted and solid lines of Fig. 4). In short, the perfect correlation between annual survival probability and the life history trait is not even reflected as a significant correlation when based on return rates that include strong variation in p . These results are based on a small sample of studies and must be viewed with some caution, but the relationships serve to demonstrate the kinds of results that can arise from life history correlations that are based on return rates with variable or low p across studies or species.

4 Discussion

Survival can play a strong role in evolution of life history tactics (Roff, 1992; Stearns, 1992). As a result, estimation of relationships between annual survival probability and other life history traits is important to the understanding of life history evolution. Accordingly, proper estimation of annual survival probability is necessary. The widespread use of return rate to estimate annual survival probabili-

ity potentially is problematic because of the bias present in return rate. The importance of bias in return rate lies in its potential influence on estimating relationships between annual survival probability (as estimated by return rate) and other life history traits.

When sampling completeness is high and relatively invariant ($p > 0.9$), return rate can roughly estimate the relationship between annual survival probability and a general life history trait (compare the dotted-and-dashed line to the solid line in Fig. 4). Yet, bias ($1 - p$) is still 10% when $p = 0.9$, which can influence inferences about evolutionary responses. On the other hand, estimation of the form of relationships (i.e. correlation, slope) between annual survival probability and life history traits may be more important in many cases than exact estimation of annual survival probability. When sampling completeness is lower, bias is greater (Figs 1 and 2), but greater bias does not necessarily eliminate relationships; if p is low but constant, return rate will estimate the incorrect intercept (and incorrect ϕ 's), but it will estimate the correct correlation and slope. However, as p becomes slightly variable (e.g. $0.63 < p < 0.78$), both the slope and correlation become less accurate (e.g. compare dashed and solid lines in Fig. 4). As p becomes more variable, then return rate may completely occlude significant relationships where they actually exist (e.g. compare dotted and solid lines in Fig. 4).

An important issue, then, centers on whether recapture/resighting probabilities are high or invariant for color-banding studies of territorial birds, as commonly assumed. Our analysis is based on a limited sample of studies, but even with this limited sample it is clear that recapture/resighting probability cannot be generalized for color-banding studies and particularly cannot be generalized as high or invariant. Some studies ($n = 5$) show high (> 0.9) recapture/resighting probabilities, but some ($n = 3$) have low (< 0.45) recapture/resighting probabilities (Fig. 3, Table 3). It is noteworthy that these three lowest values came from the studies that were not based on territorial birds. However, the remaining studies still show substantial variation in \hat{p} and bias (Table 3, Fig. 2). Of course, we do not know if this limited sample of studies is fully representative of the variation in \hat{p} for recapture/resighting studies of territorial birds. Nonetheless, these results certainly demonstrate that we cannot assume that p is high or invariant in such studies.

Recapture/resighting probabilities were similar within each of two species (black-throated blue warbler, American redstart) that were studied separately on both their summer and winter grounds by the same investigators using the same methodology (Tables 1 and 3). Yet, recapture/resighting probabilities did differ strongly between these two species (Table 3). Such results indicate that recapture/resighting probabilities can be species- and locality-specific. Of course, recapture/resighting probabilities are also influenced by recapture methodology or sampling effort, which can mask species affinities. Thus, given the ease with which recapture/resighting probabilities can vary even when controlling for investigators and methodology, and given the importance of variation in recapture/resighting probabilities in estimating life history relationships correctly, it is clearly imperative that recapture/resighting probabilities are included in estimation models for all studies.

This analysis has focused on recapture/resighting studies of color-banded and territorial passerine birds, but another common method for estimating survival in passerines is live recapture of marked individuals using mist-nets. Mist-nets are used to capture birds in both approaches, but these two methods differ in that the former approach uses resighting of color-banded birds for the vast majority of recapture/resighting events, whereas the latter approach relies mostly on recaptur-

ing marked birds in nets. Marked birds may have a lower likelihood of being recaptured than resighted, especially for species that forage and nest above mist-net level. In addition, use of mist-nets can lead to strong trap dependence, where individuals learn to avoid nets (Karr, 1979). As a result, recapture probabilities may be expected to be lower for capture/recapture than for capture/recapture/resighting studies. Nichols *et al.* (1981) summarized studies of 11 species that were sampled largely by mist-nets and recapture probabilities were generally lower (\hat{p} varied from 0.23 to 0.73) than for the recapture/resighting studies examined here (Table 3). Thus, bias in return rates may be greater for mist-netting studies compared to recapture/resighting studies of color-marked territorial birds.

Transients may be over-represented in mist-net samples (Remsen & Parker, 1983), but effects of transients potentially can be incorporated into models (Peach *et al.*, 1990; Peach, 1993). Effects of low sampling completeness and high transients emphasize the importance of proper estimation methods. Intensive color-banding studies of territorial individuals use playbacks to increase captures and intensive visual searches to increase sampling completeness (greater p). Yet, even these studies need to be coupled with appropriate parameter estimation methods such as CJS models (i.e. Lebreton *et al.*, 1992) to adjust for variability in p and gives more reliable estimation and more opportunity to test for violation of model assumptions.

Finally, this paper has focused on problems with estimation of annual survival probability. Annual survival probability is also important to life history evolution through its relationship with fecundity measures. Survival is inversely related to clutch size (Sæther, 1988) and annual fecundity, the latter of which may be most relevant to annual survival probability (Bennett & Harvey, 1988; Martin, 1995). However, estimation of annual fecundity depends on measuring clutch size, which can be measured relatively accurately, and numbers of clutches, which is more difficult to measure and for which few population estimates are available (Martin, 1995). Much greater work on numbers of nesting attempts is needed. Yet, fecundity is generally considered to be more accurately measured than survival (Lebreton *et al.*, 1987).

In sum, demographic parameters used for comparative studies generally are extracted from the literature with little description of experimental design, sampling effort or analytical methods used for estimation. Such details are important because if biases exist but differ in extent among studies, then perceived differences in demographic parameters among species or ecological groups may not be real and instead arise from the methods, the effort used for sampling individuals, or the statistical methods used to derive estimators. Knowledge or proper modeling of sampling completeness (i.e. p) is particularly important in estimating annual survival probability because: (1) most survival estimations rely on incomplete sampling, (2) the extent of sampling can vary with habitat, species and sampling method, and (3) bias in return rate as an estimator of annual survival probability increases as p declines (Figs 1 and 2). Most field studies of North America passerines have used return rate to estimate annual survival probability. This approach is poor practice because of the demonstrated variability in p . Studies of the possible survival costs of reproduction can have low power and potentially invalid inference because of variation in p among treatments (see Nichols *et al.*, 1994). Variability in p can also invalidate results of comparative studies that rely on return rates as estimates of annual survival probability (e.g. Sæther, 1988; Martin, 1995). Valid estimates of survival of adult passerines must rest on valid

sampling design, field procedures and analytic methods. The estimates provided by such approaches are needed to test evolutionary relationships rigorously.

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REFERENCES

- AKAIKE, H. (1973) Information theory and an extension of the maximum likelihood principle. *In:* B. N. PETRAN & F. CSAKI (Eds), *International Symposium on Information Theory*, pp. 267–281 (Budapest, Hungary, Akademiai Kiado).
- ANDERSON, D. R., WYWIALOWSKI, A. P. & BURNHAM, K. P. (1981) Tests of the assumptions underlying life table methods for estimating parameters from cohort data, *Ecology*, 62, pp. 1121–1124.
- BENNETT, P. M. & HARVEY, P. H. (1988) How fecundity balances mortality in birds, *Nature*, 333, p. 216.
- BURNHAM, K. P. & ANDERSON, D. R. (1979) The composite dynamic method as evidence for age-specific waterfowl mortality, *Journal of Wildlife Management*, 43, pp. 356–366.
- BURNHAM, K. P., ANDERSON, D. R., WHITE, G. C., BROWNIE, C. & POLLOCK, K. H. (1987) *Design and Analysis Methods for Fish Survival Experiments Based on Release–Recapture* (American Fisheries Society Monograph 5).
- CHARLESWORTH, B. (1980) *Evolution in Age-structured Populations* (Cambridge, Cambridge University Press).
- CHARNOV, E. L. & KREBS, J. R. (1974) On clutch size and fitness, *Ibis*, 116, pp. 217–219.
- CLOBERT, J., LEBRETON, J.-D. & ALLAINE, D. (1987) A general approach to survival rate estimation by recaptures or resightings of marked birds, *Ardea*, 75, pp. 133–142.
- COLE, L. C. (1954) The population consequences of life history phenomena, *Quarterly Review of Biology*, 29, pp. 103–137.
- CROWL, T. A. & COVICH, A. P. (1990) Predator-induced life-history shifts in a freshwater snail, *Science*, 247, pp. 949–951.
- HINES, J. E. & SAUER, J. R. (1989) Program Contrast—a general program for the analysis of several survival or recovery rate estimates, US Fish and Wildlife Service, *Fish and Wildlife Technical Report*, 24, pp. 1–7.
- HIRSHFIELD, M. F. & TINKLE, D. W. (1975) Natural selection and the evolution of reproductive effort, *Proceedings of the National Academy of Science, USA*, 72, pp. 2227–2231.
- HUTCHINGS, J. A. (1993) Adaptive life histories effected by age-specific survival and growth rate, *Ecology*, 74, pp. 673–684.
- KARR, J. R. (1979) On the use of mist nets in the study of bird communities, *Inland Bird Banding*, 57, pp. 1–10.
- LACK, D. (1948) The significance of clutch size. Part 3. Some interspecific comparisons, *Ibis*, 90, pp. 25–45.
- LACK, D. (1968) *Ecological Adaptations for Breeding in Birds* (London, Methuen).
- LAW, R. (1979) Optimal life histories under age-specific predation, *American Naturalist*, 114, pp. 399–417.
- LEBRETON, J.-D., ALLAINO, D., CLOBERT, J., GAILLARD, J. M., PONTIER, D. & TROUVILLIEZ, J. (1987) Comparative bird demography: methods, data and preliminary results, *Acta Ornithologica*, 23, pp. 77–79.
- LEBRETON, J.-D., BURNHAM, K. P., CLOBERT, J. & ANDERSON, D. R. (1992) Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies, *Ecological Monographs*, 62, pp. 67–118.

- LINDEN, M. & MÖLLER, A. P. (1989) Cost of reproduction and covariation of life history traits in birds, *Trends in Ecology and Evolution*, 4, pp. 367–371.
- LYNCH, M. (1980) The evolution of cladoceran life histories, *Quarterly Review of Biology*, 55, pp. 23–42.
- MARTIN, T. E. (1993) Nest predation and nest sites: new perspectives on old patterns, *BioScience*, 43, pp. 523–532.
- MARTIN, T. E. (1995) Avian life history evolution in relation to nest sites, nest predation, and food, *Ecological Monographs*, 65, pp. 101–127.
- MARTIN, T. E. & LI, P. (1992) Life history traits of open- vs. cavity-nesting birds, *Ecology*, 73, pp. 579–592.
- MARZOLIN, G. (1988) Polygynie du Cincle plongeur (*Cinclus cinclus*) dans les cotes de Lorraine, *L'Oiseau et la Revue Française d'Ornithologie*, 58, pp. 277–286.
- MURPHY, G. I. (1968) Pattern in life history and the environment, *American Naturalist*, 102, pp. 391–403.
- NICHOLS, J. D. (1986) On the use of enumeration estimators for interspecific comparisons, with comments on a 'trappability' estimator, *Journal of Mammalogy*, 67, pp. 590–593.
- NICHOLS, J. D. & POLLOCK, K. H. (1983) Estimation methodology in contemporary small mammal capture–recapture studies, *Journal of Mammalogy*, 64, pp. 253–260.
- NICHOLS, J. D., NOON, B. R., LYNNE STOKES, S. & HINES, J. E. (1981) Remarks on the use of mark–recapture methodology in estimating avian population size, *Studies in Avian Biology*, 6, pp. 121–136.
- NICHOLS, J. D., HINES, J. E., POLLOCK, K. H., HINZ, R. L. & LINK, W. A. (1994) Estimating breeding proportions and testing hypotheses about costs of reproduction with capture–recapture data, *Ecology*, 75, pp. 2052–2065.
- NUR, N. (1990) The cost of reproduction in birds: evaluating the evidence from manipulative and non-manipulative studies. In: J. BLONDEL (Ed.), *Population Biology of Passerine Birds*, pp. 281–296 (Berlin, Heidelberg, Springer-Verlag).
- PEACH, W. J. (1993) Combining mark–recapture data sets for small passerines. In: J.-D. LEBRETON & P. M. NORTH (Eds), *Marked Individuals in the Study of Bird Populations*, pp. 107–122 (Basel, Switzerland, Birkhäuser Verlag).
- PEACH, W. J., BUCKLAND, S. T. & BAILLIE, S. R. (1990) Estimating survival rates using mark–recapture data from multiple ringing sites, *The Ring*, 13, pp. 87–102.
- POLLOCK, K. H., NICHOLS, J. D., BROWNIE, C. & HINES, J. E. (1990) Statistical inference for capture–recapture experiments, *Wildlife Monographs*, 107, pp. 1–97.
- REMSEN, J. V., JR & PARKER, T. A. (1983) Contribution of river-created habitats to bird species richness in Amazonia, *Biotropica*, 15, pp. 223–231.
- REZNICK, D. A. (1985) Costs of reproduction: an evaluation of the empirical evidence, *Oikos*, 44, pp. 257–267.
- REZNICK, D. A. & BRYGA, H. (1987) Life-history evolution in guppies (*Poecilia reticulata*): 1. Phenotypic and genetic changes in an introduction experiment, *Evolution*, 41, pp. 1370–1385.
- REZNICK, D. A., BRYGA, H. & ENDLER, J. A. (1990) Experimentally induced life-history evolution in a natural population, *Nature*, 346, pp. 357–359.
- ROFF, D. A. (1992) *Evolution of Life Histories* (Englewood Cliffs, NJ, Prentice-Hall).
- SÆTHER, B.-E. (1988) Pattern of covariation between life-history traits of European birds, *Nature*, 331, pp. 616–617.
- SAUER, J. R. & WILLIAMS, B. K. (1989) Generalized procedures for testing hypotheses about survival or recovery rates, *Journal of Wildlife Management*, 53, pp. 137–142.
- SCHAFFER, W. M. (1974a) Selection for optimal life histories: the effects of age structure, *Ecology*, 5, pp. 291–303.
- SCHAFFER, W. M. (1974b) Optimal reproductive effort in fluctuating environments, *American Naturalist*, 108, pp. 783–790.
- SPITZE, K. (1991) *Chaoborus* predation and life-history evolution in *Daphnia pulex*: temporal pattern of population diversity, fitness, and mean life history, *Evolution*, 45, pp. 82–92.
- STEARNS, S. C. (1992) *The Evolution of Life Histories* (Oxford, Oxford University Press).
- WILLIAMS, G. C. (1966a) Natural selection, the cost of reproduction, and a refinement of Lack's principle, *American Naturalist*, 100, pp. 687–690.
- WILLIAMS, G. C. (1966b) *Adaptation and Natural Selection* (Princeton, NJ, Princeton University Press).

