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Measures of productivity and survival derived from standardized mist-netting are consistent with observed population changes

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To investigate potential biases in productivity indices and survival-rate estimates from four years (1992–95) of data from the Monitoring Avian Productivity and Survivorship (MAPS) Programme, we examined correlations and regressions of trends in adult captures on population changes modelled from productivity indices and survival-rate estimates for target species at both local and regional scales. We estimated trends in adult captures from regressions of chain indices on year. We calculated mean numbers of young per adult, and estimated time-constant, annual adult survival rates from mark–recapture data using both non-transient and transient models. We used these productivity indices and survival-rate estimates in a simple demographic model to calculate predicted rates of population change. We modelled survival of young birds (ϕ_j ; from initial capture, generally during juvenile dispersal, to recruitment into the following year's breeding population) relative to adults (ϕ_a) as $\phi_j = 0.75 \times \phi_a$. At the local scale, correlation coefficients between trends in adult captures and modelled population changes tended to be positive, but the strengths of the correlations were often weak. As expected, trends in adult captures generally were better correlated with modelled population changes than with either productivity or survival. Stronger correlations between trends in adult captures and modelled population changes tended to be found using survival estimates from the non-transient model, but modelled population changes using the transient model gave values for mean population changes closest to those derived from trends in adult captures. Modelled population changes sometimes were less well correlated with trends in adult captures at the regional than at the local scale, presumably because of spatial heterogeneity in the factors affecting population dynamics of target species. These results suggest that absolute measures of productivity derived from MAPS are likely to be biased, but do not show unequivocally the extent to which such biases might differ between species. Nevertheless, given the relatively low precision of analyses based on only a few years of data, these results suggest that relative measures of productivity and survival derived from MAPS do reflect observed population changes. Longer runs of data should allow the demographic mechanisms causing population changes to be investigated.

The integrated monitoring of both primary demographic parameters (e.g. productivity, survival) and secondary population trends of

birds is critical for determining the demographic causes of population changes, for identifying management actions and conservation strategies to reverse population declines and, perhaps most importantly, for evaluating the effectiveness of conservation actions.^{1,2}

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Monitoring primary demographic parameters is important because environmental stressors and management actions affect primary demographic parameters directly and without time lags caused by density-dependence, buffering effects of floater individuals and local variation in recruitment.³ Moreover, monitoring only population trends provides little or no information as to the stage(s) of the life cycle at which population change is being affected.⁴

Integrated monitoring programmes will be most useful if they can provide reasonable hypotheses regarding proximal demographic causes of population change that can be tested by subsequent research efforts.⁵ Stronger hypotheses can be formulated and tested if spatial and temporal patterns in primary and secondary parameters can be described and examined at multiple spatial scales.⁵

The Monitoring Avian Productivity and Survivorship (MAPS) Programme was established in 1989 to provide both local and regional information on productivity and survival of North American landbirds.⁶ MAPS has grown from 16 stations in 1989 to nearly 450 stations operated across continental USA and Canada in 1997. Like the Constant Effort Sites (CES) Programme operated by the British Trust for Ornithology since 1981,⁷ MAPS utilizes constant-effort mist-netting during the breeding season at a network of sites to: (1) estimate survival rates of adult landbirds using modified Cormack–Jolly–Seber (CJS) mark–recapture analyses; and (2) index productivity by using the proportion of young in the catch.

Any bias in estimates of apparent survival (i.e. that include an unknown component of emigration) will be minimized when a modified CJS model is used to account for the effects of transient individuals, because both the recapture probability and the proportion of transients among the sample of newly-marked birds are estimated.^{8,9} Biases in survival-rate estimates may still exist if the sample of sites from which mark–recapture data are obtained are not 'representative'.¹⁰

In marked contrast to survival-rate estimates, productivity indices from MAPS are likely to be biased because differences in dispersal and other behaviours between young and adult birds are likely to cause age-specific differences in capture probabilities.^{2,6} Young birds are mostly transient individuals present in the

netting area for only one or a few days, while adults are largely resident individuals present in the netting area for most of the summer.^{6,11} Moreover, young birds often concentrate in favourable areas during their juvenile dispersal and post-juvenile moult,^{11,12} while adults tend to remain on a territory, sometimes even after they have finished breeding.¹¹ Foraging and nesting behaviour might also cause differences in capture probabilities between young and adults. Adults of canopy-foraging species that nest in shrubs or on the ground, for example, might be captured more frequently during trips to or from the nest, than young that move into the canopy immediately upon fledging.

Even if capture probabilities of young and adults do differ so that MAPS productivity indices provide biased estimators of actual productivity, temporal, spatial and between-species comparisons of productivity indices will not be biased, provided that the ratios of capture probabilities and rates of local immigration and emigration of young to adults remain constant over time (between years) and space (between habitats or geographical areas) and among species, respectively.^{2,6} Unfortunately, because the young birds captured in the MAPS Programme are primarily transient individuals, capture probabilities of young are difficult to estimate by mark–recapture methods.² Thus, it is difficult to determine rigorously the biases in such comparisons of productivity indices.

We report on cross-species correlation analyses between short-term (four-year) trends in adult captures and modelled population changes calculated from productivity indices and survival-rate estimates derived from MAPS data. We conducted these analyses at two spatial scales: ten small-scale 'locations' (clusters of about six stations within a national park, national forest or military installation); and two large-scale 'regions' (Northwest, 60 stations and Northeast, 25 stations).

METHODS

MAPS stations were established in 20-ha study areas in forest, woodland, riparian or scrub habitats. About ten 12-m mist-nets were located opportunistically, but rather uniformly, within the central 8 ha of the study areas at fixed locations where substantial numbers of birds were

likely to be captured. Stations were operated in a standardized manner for six hours per day (beginning at local sunrise), for one day per ten-day period, and for eight to 12 consecutive ten-day periods from May or early June (depending on latitude) through August. All birds captured (including recaptures) were identified to species, age and sex, and all unringed birds were ringed. The field procedures and analytical methods used by MAPS are described in detail elsewhere.^{11,13,14}

Following procedures used in the CES Scheme,⁷ we computed the numbers of individual adult and young birds of each species captured during each of the four years, 1992–95 (1993–96 at Shenandoah National Park). Data were pooled over all stations within the geographic area of interest that lay within the breeding range of the species concerned. We used the pooled numbers of individual young birds captured each year divided by the pooled numbers of individual adult birds captured each year (young per adult) as our measure of reproductive rate for each species. Year-to-year changes in numbers of adults captured were calculated in a rigorous, constant-effort manner using net-opening and net-closing times and net-check times on a net-by-net and period-by-period basis, to exclude captures that occurred in a given net in a given period in one year at a time when that net was not operated in that period in the other year.¹¹

We estimated constant adult survival rates (using the computer program SURVIV¹⁵) from four years of MAPS mark–recapture data (1992–95; 1993–96 at Shenandoah National Park), pooled over all stations within the geographic area of interest at which the species was a breeder or summer resident during at least three of the four years. We estimated constant survival rates using both the non-transient model (ϕ , P)⁸ and a transient model (ϕ , P , γ).⁹ These models are time-constant extensions of the CJS model (ϕ , P) in which the parameters are year-specific. The model parameters are the apparent survival rate of resident adults (ϕ), the recapture probability (P) and the proportion of residents among newly-captured birds (γ).⁹ Species were included in the analyses if survival could be modelled and meaningful parameter estimates obtained ($0.1 < \phi < 0.9$).

Data from a station were included in the analyses only if the station was operated for at

least five periods, at least three of which occurred during the first portion of the season (when adult birds predominate in the catch) and at least two of which occurred during the second portion of the season (when young birds predominate in the catch), during each of the four years.

We estimated short-term (four-year: 1992–95; 1993–96 at Shenandoah National Park) trends in adult captures (TAC) using a 'chain-index' method as follows:

1 setting the adult population size index (PSI) to 1.0 for year $t = 1$;

2 calculating PSI for subsequent years as:

$$PSI_{t+1} = PSI_t * (a_{t+1} / a_t)$$

where a_t and a_{t+1} are the numbers of adult birds captured in years t and $t + 1$, respectively, in a constant-effort comparison of the two years;

3 calculating the slope of the regression of PSI (measured on an arithmetic scale) on year;

4 using that slope (additive change per year) as the estimated trend in adult captures (TAC).

We modelled adult population change (MPC; again defined as additive change per year) using a simple demographic model as:

$$MPC = (\phi_a + R * \phi_y) - 1.0$$

where R is the mean (four-year) reproductive index (young per adult), ϕ_a is the annual survival rate of adults and ϕ_y is the survival rate of young (from the time when juveniles are ringed, generally during their juvenile dispersal, to recruitment into the next year's breeding population), modelled as: $\phi_y = 0.75 * \phi_a$.

Our choice of 0.75 for ϕ_y / ϕ_a may seem high, because first-year survival rates in the neighbourhood of 0.3 are often estimated from theoretical considerations,¹⁶ and some European tits have a first-year survival rate of about 0.1.¹⁷ Such values for first-year survival suggest that ϕ_y / ϕ_a might range from about 0.25 to 0.50. These first-year survival estimates, however, incorporate all mortality from fledging until recruitment into the next year's breeding population. Recent work indicates that substantial mortality occurs in passerines after fledging but before dispersal begins.¹⁸ Studies of radiotagged Wood Thrushes *Hylocichla mustelina*¹⁸ and colour-banded Yellow-eyed

*Juncos Junco phaeonotus*¹⁹ indicate that two pronounced peaks in mortality occur, one immediately after fledging and another upon attaining independence from parents but before dispersal. Passerine survival estimates during the first three to ten weeks after fledging for various passerines range from about 0.25 to 0.43 with most mortality occurring during the first three weeks.^{17–21} Because the vast majority of young birds captured in the MAPS Programme are dispersing young that have already survived this period of high mortality, the ratio of ϕ_y (from the date of ringing as juveniles to recruitment into the next year's breeding population) to ϕ_a is likely to be about 0.75 or higher. Indeed, such estimates of ϕ_y/ϕ_a can be calculated as 0.70 for Kirtland's Warbler *Dendroica kirtlandii*,²² 0.91 for Wood Thrush¹⁸ and 0.84 for Song Thrush *Turdus philomelos* prior to its recent decline in Britain (0.71 during its recent decline).²³ Moreover, the mean ϕ_y/ϕ_a (calculated this way) for 15 British species was found to be 0.74.²⁴

Finally, for each location or region, we ran regression analyses of the trends in adult captures (*TAC*) of the various target species on their modelled population changes (*MPC*; calculated using both non-transient (ϕ, P) and transient (ϕ, P, γ) survival models) and examined the correlation between *TAC* and *MPC*. We also ran regression analyses of the trends in adult captures (*TAC*) for each species on their mean reproductive indices (*R*) and on their annual adult survival-rate estimates (ϕ_a ; again from both non-transient and transient models) and examined the correlations between *TAC* and *R* and between *TAC* and each estimate of ϕ_a . Because the precision (se) of the trends in adult captures differed substantially among the various species at each location (Table 1), we weighted the *TAC*s in these regressions and correlations by 1/se.

We tested the null hypothesis that the correlation coefficient (*r*) between *TAC*s and *MPC*s was not greater than zero and used a one-tailed alpha level of 0.05 for statistical significance. All statistical analyses reported here were completed using the computer program STATA.²⁵

RESULTS

Four-year (1992–95) trends in adult captures for eight target species on the Wenatchee National

Forest (Fig. 1) were typical of most locations. Three species (Dusky Flycatcher *Empidonax oberholseri*, Warbling Vireo *Vireo gilvus*, Western Tanager *Piranga ludoviciana*) showed decreasing trends, three (Chipping Sparrow *Spizella passerina*, Song Sparrow *Melospiza melodia*, Dark-eyed Junco *Junco hyemalis*) showed increasing trends and two (MacGillivray's Warbler *Oporornis tolmiei*, Lincoln's Sparrow *Melospiza lincolnii*) showed relatively stable trends.

An indication of the average values and standard errors (precision) of the trends in adult captures, four-year mean reproductive indices, annual adult survival rates (from both the non-transient (ϕ, P) and transient (ϕ, P, γ) models) and modelled population changes (again from both the non-transient and transient models) are presented in Table 1 for up to 94 location–species and 51 region–species combinations. Average reproductive indices (0.771 for location–species and 0.943 for region–species combinations) suggest reasonable reproductive rates of about 1.5 to 1.9 young per pair reaching independence and beginning juvenile dispersal. Average annual adult survival rates using the transient model (0.554 for location–species and 0.516 for region–species combinations) were higher and probably more accurate than those using the non-transient model (0.452 for location–species and 0.409 for region–species combinations). Average modelled population changes were strongly negative and substantially lower than average trends in adult captures, which tended to be near zero; those obtained using the transient model, however, were less negative and closer to, although still lower than, trends in adult captures.

The mean precision of the trends in adult captures, reproductive indices and survival-rate estimates was low, especially for location–species combinations (mean se values ranged from 0.121 to 0.238), presumably because of the minimal four years of data and relatively small local sample sizes. The precision of these indices and estimates for region–species combinations was substantially higher (mean se values ranged from 0.065 to 0.158), presumably because of the larger sample sizes involved.

The results of correlation analyses between trends in adult captures (*TAC*) and modelled population change (*MPC*), reproductive indices

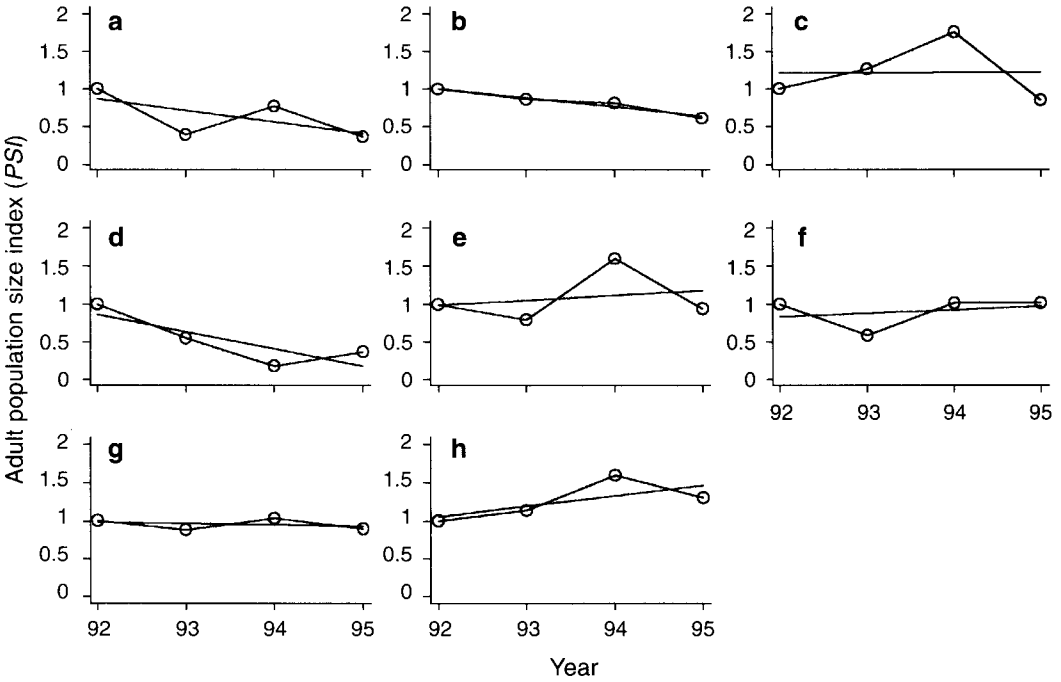


Figure 1. Short-term trends in adult captures (*TAC*) for eight target species on the Wenatchee National Forest from 1992 to 1995. For each species, the adult population size index was set at 1.0 in 1992. Indices for subsequent years were determined from constant-effort between-year changes in the pooled numbers of adult birds captured at six MAPS stations. The slope of the regression line was used as the trend in adult captures (*TAC*). (a) Dusky Flycatcher, *TAC* -0.152 ± 0.131 se; (b) Warbling Vireo, *TAC* -0.124 ± 0.105 se; (c) MacGillivray's Warbler, *TAC* $+0.003 \pm 0.218$ se; (d) Western Tanager, *TAC* -0.226 ± 0.105 se; (e) Chipping Sparrow, *TAC* $+0.062 \pm 0.188$ se; (f) Song Sparrow, *TAC* $+0.048 \pm 0.111$ se; (g) Lincoln's Sparrow, *TAC* -0.017 ± 0.040 se; (h) Dark-eyed Junco, *TAC* $+0.138 \pm 0.103$ se.

Table 1. Average values and standard errors of trends in adult captures, vital rates and modelled population changes by location–species and region–species combinations.

Parameter	Location–species combinations			Region–species combinations		
	n ^a	Mean value (sd)	se (sd)	n ^a	Mean value (sd)	se (sd)
<i>TAC</i> ^b	94	0.045 (0.254)	0.121 (0.110)	51	-0.021 (0.068)	0.065 (0.057)
<i>R</i> ^c	94	0.771 (0.707)	0.221 (0.229)	51	0.943 (0.570)	0.158 (0.147)
$\phi_a(\phi, P)$ ^d	94	0.452 (0.154)	0.194 (0.153)	51	0.409 (0.130)	0.102 (0.067)
$\phi_a(\phi, P, \gamma)$ ^e	91	0.554 (0.181)	0.238 (0.154)	51	0.516 (0.145)	0.132 (0.070)
<i>MPC</i> (ϕ, P) ^f	94	-0.308 (0.279)		51	-0.316 (0.248)	
<i>MPC</i> (ϕ, P, γ) ^g	91	-0.155 (0.363)		51	-0.133 (0.305)	

^aNumber of location–species or region–species combinations.

^bTrend in adult captures (additive change per year).

^cMean annual reproductive index (young per adult).

^dAdult survival rate (probability of survival to the following year) from the non-transient model.

^eAdult survival rate (probability of survival to the following year) using survival estimates from the transient model.

^fModelled population change (additive change per year) using survival estimates from the non-transient model.

^gModelled population change (additive change per year) using survival estimates from the transient model.

Table 2. Correlation coefficients (r) for the correlations between trend in adult captures^a (TAC) and modelled population change^b (MPC), mean annual reproductive index (R) and adult survival-rate estimate^b (ϕ_a); and regression coefficients (slopes) and regression constants (y -intercepts) for the regression of trend in adult captures on modelled population change. Data are presented for each of the ten locations and two regions.

Location ^c	No. of species ^d	Modelled population change						Mean annual reproductive success r	Survival-rate estimate	
		Non-transient (ϕ, P)			Transient (ϕ, P, γ)				(ϕ, P) r	(ϕ, P, γ) r
		r	slope	y -int	r	slope	y -int			
Denali	8	+0.850***	+0.506***	+0.100	+0.669*	+0.271*	+0.005	+0.426	+0.657*	+0.474
Yosemite	9	+0.668***	+1.094***	+0.519*	+0.487	+0.808	+0.243	+0.437	+0.567	+0.055
Shenandoah	11	+0.380	+0.443	+0.398*	+0.581*	+0.504*	+0.372***	+0.414	+0.185	+0.360
Navy	9	+0.521	+0.397	+0.138	+0.330	+0.134	-0.012	+0.199	+0.515	+0.330
Siuslaw	5	+0.587	+0.248	+0.071	+0.483	+0.144	+0.009	-0.762	+0.675	+0.595
Willamette	11	+0.420	+0.116	-0.002	+0.477	+0.149	-0.010	-0.105	+0.371	+0.334
Wenatchee	8	+0.805***	+0.307***	+0.079	+0.754**	+0.361**	+0.029	+0.889***	+0.614	+0.237
Fremont	12	-0.301	-0.211	-0.189	-0.315	-0.178	-0.160**	+0.313	-0.600	-0.548
Umatilla	13 ^e	+0.534*	+0.327*	+0.048	+0.144	+0.105	-0.074	-0.049	+0.549*	+0.361
Flathead	8 ^e	+0.571	+0.537	+0.179	+0.156	+0.072	-0.067	+0.875***	-0.024	+0.124
Mean		+0.504***	+0.377***	+0.134	+0.377***	+0.237**	+0.034	+0.267	+0.351**	+0.231**
se		0.101	0.105	0.063	0.099	0.085	0.050	0.154	0.127	0.099
Northwest	35	-0.010	-0.002	-0.034	-0.040	-0.009	-0.034**	+0.130	-0.139	-0.182
Northeast	16	+0.546**	+0.269**	+0.104*	+0.547**	+0.206**	+0.048	-0.117	+0.583***	+0.618***
Mean		+0.268	+0.134	+0.035	+0.254	+0.099	+0.007	+0.007	+0.222	+0.218
se		0.278	0.136	0.069	0.294	0.108	0.041	0.124	0.361	0.400

^aTrends in adult captures are weighted by 1/se.

^bCorrelation coefficients are provided for both the non-transient (ϕ, P) and transient (ϕ, P, γ) survival-rate models.

^cDenali: Denali National Park, Alaska; Yosemite: Yosemite National Park, California; Shenandoah: Shenandoah National Park, Virginia; Navy: US Navy Installations, Maryland and Virginia; Siuslaw: Siuslaw National Forest, Oregon; Willamette: Willamette National Forest, Oregon; Wenatchee: Wenatchee National Forest, Washington; Fremont: Fremont National Forest, Oregon; Umatilla: Umatilla National Forest, Oregon; Flathead: Flathead National Forest, Montana; Northwest, northwest MAPS region; Northeast, northeast MAPS region.

^dNumber of target species at each location.

^eFor the transient model, the numbers of species were 12 (Umatilla) and six (Flathead) because survival or recapture probabilities could not be estimated for one and two species, respectively.

* $0.025 < P < 0.05$; ** $0.01 < P < 0.025$; *** $P < 0.01$. One-tailed tests were used to determine if the correlation coefficient (r), the slope of each correlation and the means of these measures were greater than zero. Two-tailed tests were used to determine if the y -intercept for each location and mean y -intercept were different from zero.

(R), and survival-rate estimates (ϕ_a), and regression analyses of TAC on MPC are summarized in Table 2 for each of the ten locations and two regions. Significant positive correlations between trends in adult captures (TAC) and modelled population changes (MPC) were found for four out of the ten locations using the non-transient survival model, and for three out of the ten locations using the transient survival model. The mean correlation coefficient between TAC and MPC for the ten locations, using either the non-transient (mean $r = 0.504 \pm$

0.101 se) or transient (mean $r = 0.377 \pm 0.099$ se) model, was significantly greater than zero (one-tailed t -tests, $P = 0.0005$ and $P = 0.002$, respectively). Correlations between TAC and MPC using the non-transient model tended to be stronger for the ten locations than those using the transient model, but the difference was not significant (matched pairs t -test, $t = 2.12$, $df = 9$, $P = 0.063$).

The mean slope of the regressions of TAC on MPC was significantly greater than zero for both non-transient and transient survival

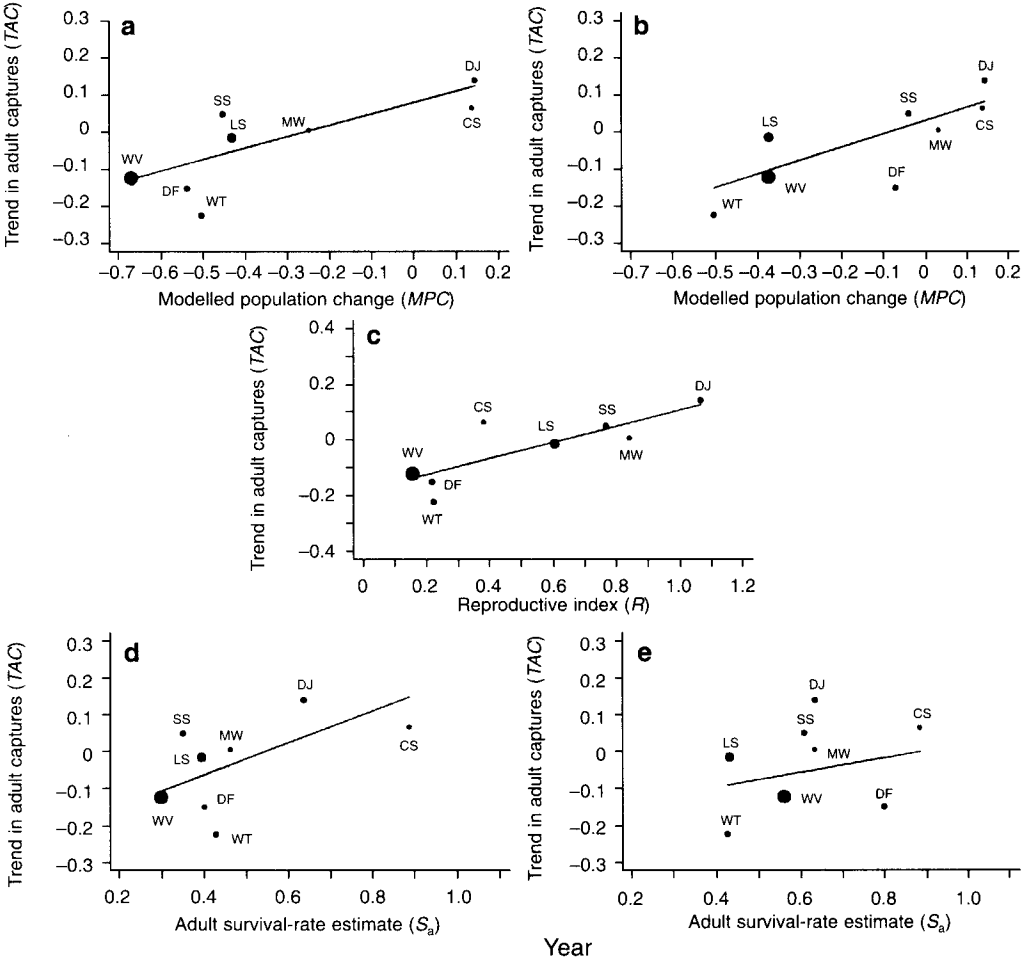


Figure 2. Regressions, for eight target species on the Wenatchee National Forest, of trend in adult captures (*TAC*) on: (a) modelled population change (*MPC*) calculated with the non-transient model (ϕ, P); (b) modelled population change (*MPC*) calculated with the transient model (ϕ, P, γ); (c) four-year mean reproductive index (*R*); (d) time-constant annual adult survival-rate estimate (ϕ_a) calculated with the non-transient model (ϕ, P); and (e) time-constant annual adult survival-rate estimate (ϕ_a) calculated with the transient model (ϕ, P, γ). Trends in adult capture were weighted by $1/se$ and the size of each point reflects the relative weight of each species. DF, Dusky Flycatcher; WV, Warbling Vireo; MW, MacGillivray's Warbler; WT, Western Tanager; CS, Chipping Sparrow; SS, Song Sparrow; LS, Lincoln's Sparrow; DJ, Dark-eyed Junco.

models (mean slope = 0.377, $P = 0.003$ and mean slope = 0.237, $P = 0.011$, respectively, one-tailed test), but was also significantly different (less) than 1.0 for both models ($P = 0.0002$ and $P < 0.0001$, respectively, two-tailed test). This suggests that large between-species differences in *MPC* generally were reflected in considerably smaller differences in *TAC*. The mean *y*-intercept of the regressions of *TAC* on *MPC* was not significantly different from zero (non-transient model, $y_0 = 0.134$, $P = 0.063$; transient

model, $y_0 = 0.034$, $P = 0.518$). The mean *x*-intercept of the regressions of *TAC* on *MPC* was significantly different from zero ($x_0 = -0.382$, $P = 0.003$) using the non-transient model but not significantly different from zero ($x_0 = -0.031$, $P = 0.866$) using the transient model. These results suggest that *MPC*s based on the transient model may be less biased than those based on the non-transient model.

Significant positive correlations between trends in adult captures and reproductive

indices were found for two of the ten locations, but the mean correlation coefficient between *TAC* and *R* (mean $r = 0.267 \pm 0.154$ se) was not significantly greater than zero (one-tailed *t*-test, $P = 0.061$). The correlation coefficients between *TAC* and *R* tended to be less than those between *TAC* and *MPC*, but the differences were not significant (matched-pairs *t*-tests: comparison with non-transient model, $P = 0.198$; comparison with transient model, $P = 0.537$). Significant positive correlations between *TAC* and ϕ_a were found for two locations using the non-transient model but not using the transient model. The mean correlation coefficient was significantly greater than zero using either model (one-tailed tests, non-transient model, mean $r = 0.351$, $P = 0.011$; transient model, mean $r = 0.231$, $P = 0.023$). Again, the correlation coefficients between *TAC* and ϕ_a tended to be less than those between *TAC* and *MPC*; here, the difference was significant ($P = 0.035$) for the comparison with the non-transient model, but not ($P = 0.075$) for comparison with the transient model (matched-pairs *t*-tests). As with modelled population change (*MPC*), stronger correlations between *TAC* and ϕ_a were obtained using the non-transient than the transient model, but the difference was not significant (matched-pairs *t*-test, $P = 0.120$).

Graphical representations of these correlations are presented for the eight species studied at Wenatchee National Forest (Fig. 2), a location at which *TAC*s were generally well-correlated with *MPC*, *R* and ϕ_a values. Analogous correlations at most locations were weaker than those at Wenatchee.

A significant positive correlation between *TAC* and *MPC* was obtained for the northeast region ($P = 0.014$, one-tailed test, using either the non-transient or transient survival model), but not for the northwest region. Significant positive correlations were also obtained for the northeast region between *TAC* and ϕ_a ($P = 0.009$ for the non-transient and $P = 0.005$ for the transient model, one-tailed tests), but not between *TAC* and *R*. No significant correlations between *TAC* and any of the variables were found for the northwest region.

DISCUSSION

At the local scale, trends in adult captures tended to be positively correlated with mod-

elled population changes, but the strengths of the correlations were generally weak. As expected, trends in adult captures were generally better correlated with modelled population changes than with either reproductive indices or survival rates alone. Modelled population changes were generally lower when survival rates were estimated using the non-transient model than with the transient model. The difference between *TAC* and *MPC* was substantially reduced, but not eliminated, when survival rates were estimated using the transient model, suggesting that the application of the transient model produced more reliable survival-rate estimates and that reproductive indices were probably too low.

Because survival (ϕ_a) appears in both elements of the modelled population change (*MPC*), while productivity (*R*) appears in only one element, we might expect that, in general, *TAC* would tend to be correlated better with ϕ_a than with *R*. This was the case at six of the ten locations; but at four locations, however, *TAC* tended to correlate better with *R* than with ϕ_a , suggesting that productivity, rather than survivorship, may have a greater influence on the overall population dynamics of the target species at these four locations.

Correlations between *TAC* and *MPC* or between *TAC* and ϕ_a tended to be stronger using the non-transient, rather than the transient, survival model, despite the fact that use of the transient model tended to produce higher survival estimates and to reduce the difference between mean *TAC* and mean *MPC*. These effects were achieved, however, only for those species for which the data were sufficient to estimate γ , the proportion of residents among newly captured adults, as substantially less than 1.0. In fact, estimation by the transient model of such a γ only occurred for about 67% of the species at any location or region. Thus, if the true values of γ were rather similar among most target species (perhaps about 0.4–0.5), use of the transient model would reduce the average bias in survivorship estimates, but would increase the between-species differences in that bias. This is what probably happened.

The generally weak correlations between *TAC* and *MPC*, even for the non-transient model, suggest that between-species differences in bias in the reproductive indices might exist. Several other factors, however, could also

contribute to the weak correlations. First, the chain index method used to estimate population trends is known to be statistically inefficient and can lead to problems of random drift in the index values. Peach *et al.*²⁶ have recently assessed changes in abundance of young and adult birds sampled by the British CES Programme through application of log-linear Poisson regression models, which may provide a more robust method of analysis. Secondly, the low precision of the trends in adult captures and primary demographic parameters would tend to weaken the resulting correlations. Thirdly, because vital rates were modelled in a time-constant manner, substantial temporal variation in any of the vital rates would also tend to weaken the correlations. Fourthly, because recruitment into the adult population was modeled only through the ratio of ϕ_y/ϕ_w , which was held constant at 0.75, between-species differences in this ratio and in recruitment *per se* would also tend to weaken the correlations. Given these other potential causes for weak correlations between TAC and MPC, it is not possible to assess the extent of between-species differences in the bias in reproductive indices, survival estimates and population trends from MAPS. What we can conclude is that even the very limited data set analysed here showed considerable agreement between TACs and MPCs based on MAPS estimates of vital rates. This suggests that MAPS does produce useful indices of these population variables for most of the study species, even though the absolute values of some of them may be biased.

Regional TACs were not necessarily better correlated with MPCs than were local TACs, despite that fact that precision of the vital rates was generally better at regional than local scales because of larger sample sizes. Presumably, spatial variation in the factors affecting the population dynamics of the target species created greater heterogeneity of both the TACs and vital rates over the larger regions that more than offset the increased precision. This may have been particularly true in the northwest region, a diverse geographical area where stations were located over a wide altitudinal range and where recruitment of young is known to vary substantially with timing of snowmelt and, perhaps, other weather variables.²⁷ Such large amounts of heterogeneity

between sites may have important implications for the validity of indices that combine data across many sites and for the ways in which such indices should be calculated.¹⁰

DeSante^{28,29} examined MAPS productivity indices pooled over species with various nest-location and migration-strategy classes as a function of year, geographic area and habitat. The relative productivity indices for the species groups tended to be consistent over time and geographic area, but varied among habitats, suggesting that temporal and geographic comparisons of productivity indices should be relatively unbiased, provided that the distribution of stations among habitats remained consistent. Martin *et al.*³⁰ showed, for several species, that patterns of temporal variation in MAPS productivity indices and in productivity estimates obtained from direct nest monitoring were similar. Moreover, age ratios of Kirtland's Warblers in mist-net samples, based on population-wide netting, provided a reliable index of productivity,²² suggesting that temporal variation in MAPS-type productivity indices for this species was unbiased. In addition, relative differences among MAPS productivity indices as a function of nest-location class were consistent with analogous differences in productivity estimates obtained from direct nest monitoring,³¹ suggesting that between-species biases in MAPS productivity indices may be small.^{28,29} Clearly, more work is needed to determine the reliability of between-species comparison of MAPS productivity indices.

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