

# SENSITIVITY ANALYSES OF THE LIFE CYCLE OF MIDCONTINENT MALLARDS

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**Abstract:** Relationships between vital rates and population growth rate ( $\lambda$ ) are critical to understanding and managing population dynamics. Considerable study of the midcontinent mallard (*Anas platyrhynchos*) population has been directed to understanding how vital rates respond to environmental fluctuations and management, but inference to the relative importance of specific vital rates to  $\lambda$  remains weak. We used analytic and simulation-based sensitivity analyses of a stage-based matrix model of female midcontinent mallards to compare the relative importance of vital rates to  $\lambda$ . For each vital rate, we estimated mean values and process variation (biological variation across space and time) for females breeding on sites of approximately 70 km<sup>2</sup> in the Prairie Pothole Region (PPR) of the United States (Montana, North Dakota, South Dakota, Minnesota) and Canada (Saskatchewan, Manitoba, Alberta). We conducted perturbation analyses (i.e., analytic sensitivities and elasticities) to predict the relative influence of changes in vital rates on  $\lambda$ . We conducted variance decomposition analyses to assess the proportion of spatial and temporal variation in  $\lambda$  explained by process variation in each vital rate. At mean values of vital rates, analytic sensitivity of  $\lambda$  was highest to nest success and survival of adult females during the breeding season and non-breeding season; hence, equal absolute changes in these vital rates would be predicted to result in the largest  $\Delta\lambda$ , relative to other vital rates. Variation in sensitivities and elasticities across process variation in vital rates was primarily explained by variation in nest success and survival of ducklings. Process variation in breeding parameters was driving variation in  $\lambda$ : vital rates explaining the most variation were nest success (43%), survival of adult females during the breeding season (19%), and survival of ducklings (14%). Survival of adult females outside the breeding season accounted for only 9% of variation in  $\lambda$ . Our analyses suggested that predation processes on the breeding grounds were the primary proximate factors limiting population growth.

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Relationships between birth and mortality processes making up the life cycle (hereafter, vital rates) and the finite rate of population growth,  $\lambda$ , are critical to understanding population dynamics (Williams and Nichols 1990, Saether et al. 1996, Bro et al. 2000). Demographic models link probabilities for vital rates (e.g., number of young, age specific survival) of individuals to  $\lambda$ . Sensitivity analyses of  $\lambda$ , which predict  $\Delta\lambda$  in response to change in vital rates (Horvitz et al. 1997, Wisdom et al. 2000, Caswell 2001; Mills and Lindberg 2002), identify vital rates with high potential to influence  $\lambda$  (Crouse et al. 1987, Wootton and Bell 1992, Doak et al. 1994, Silvertown et al. 1996) and provide insight to how variation in vital rates contributes to vari-

ation in  $\lambda$  (Brault and Caswell 1993, Crooks et al. 1998, Pfister 1998, Cooch et al. 2001).

The midcontinent population of mallards, which breeds primarily in the PPR and winters in the Mississippi Alluvial Valley (Munro and Kimball 1982), has been intensively studied and managed. In response to mandates to protect waterfowl populations and provide compatible harvest opportunities, management efforts have focused on increasing  $\lambda$  by improving vital rates through management of habitat or predator communities and by regulating harvest (Nichols et al. 1995). Considerable effort has been directed to determining how specific vital rates are influenced by environmental fluctuations (e.g., Rotella and Ratti 1992, Greenwood et al. 1995, Sovada et al. 1995) or management actions (e.g., Smith and Reynolds 1992, Kruse and Bowen 1996, McKinnon and Duncan 1999, Garretson and Rohwer 2001). Yet, inference to the relative importance of spe-

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cific vital rates to  $\lambda$ , and hence to population dynamics, remains weak (Williams et al. 1999).

Most studies of midcontinent mallards have related vital rates only to partial measures of  $\lambda$ . Sensitivity analyses have been used to infer relative importance of vital rates in the breeding season to recruitment into the fall population (Johnson et al. 1987, 1992) but have not incorporated adult survival. Other studies have examined influence of harvest on annual survival. This relationship remains equivocal for females (Burnham and Anderson 1984, Trost 1987, Smith and Reynolds 1992), and females limit reproduction and hence  $\lambda$  (Johnson et al. 1987). Ultimately, vital rates should be directly compared through their relative influence on  $\lambda$  (Weller and Batt 1988, Koford et al. 1991). Cowardin and Johnson (1979) compared the relative importance of annual survival of adults versus recruitment to  $\lambda$ . However, inferences were limited because this analysis did not compare the relative contributions of specific vital rates in the breeding season or the relative importance of breeding versus nonbreeding survival, which occur in different regions and hence are subject to different ecological influences. Furthermore, previous analyses have lacked reliable estimates for many vital rates during the breeding season.

Knowledge of variation in vital rates is crucial to interpreting sensitivity analyses (Gaillard et al. 1998, Mills et al. 1999, Wisdom et al. 2000, Caswell 2001). We distinguish between 2 biologically distinct sources of variation in vital rates: management and natural variation. Management seeks to alter vital rates through manipulation of environmental conditions or harvest regulations. Given an array of potential management options, managers must compare predicted  $\Delta\lambda$  resulting from implementing each option. Alternatively, natural variation in vital rates (hereafter, process variation) results from fluctuations in environmental conditions, given existing management and habitat conditions. Midcontinent mallards are characterized by high process variation and hence high variation in  $\lambda$ . Management actions are implemented and evaluated in the context of process variation, which often is beyond the influence of management. Therefore, managers need to understand how (1) process variation alters predictions of  $\Delta\lambda$  resulting from management actions (de Kroon et al. 2000, Wisdom et al. 2000, Alpizar-Jara et al. 2001); and (2) process variation drives population dynamics (Bethke and Nudds 1995, Williams et al. 1999).

We used a stage-based matrix model of the midcontinent population of female mallards to compare the relative importance of vital rates to  $\Delta\lambda$ . In addition to published data, we incorporated unpublished data collected by the Institute for Wetland and Waterfowl Research (IWWR) as part of the Prairie Habitat Joint Venture Assessment Program to estimate key vital rates occurring during the breeding season. We explicitly incorporated process variation in simulations of population dynamics using life-stage simulation analysis (LSA; Wisdom et al. 2000). We then conducted analytic perturbation analyses to predict how potential changes in vital rates effected through management would influence  $\lambda$ , both at mean values and across process variation in vital rates. We conducted variance decomposition analyses to estimate how process variation in each vital rate contributed to variation in  $\lambda$  (Horvitz et al. 1997, Caswell 2000, Wisdom et al. 2000).

## METHODS

We constructed the model as a problem-solving tool to compare the relative importance of different vital rates. Consequently, we restricted the model to a level of complexity appropriate for this purpose (Dixon et al. 1997, Starfield 1997). Our objective was to achieve realism sufficient to effectively address key questions, yet to keep the model as parsimonious and interpretable as possible. Throughout, we preferred simplicity to complexity if resultant differences in model output were small.

Variation in estimates is related to spatial and temporal scale of the sampling unit (McArdle et al. 1990). We therefore restricted our analyses to data collected for individual years and at similar scales to meaningfully compare variation in vital rates. Most reliable estimates of vital rates have been reported for study sites of approximately 60–70 km<sup>2</sup>. Whenever possible, we used this landscape scale as our frame of reference for estimation of vital rates and inference to population dynamics.

Because males substantially outnumber females and hence do not limit reproduction (Johnson and Sargeant 1977, Johnson et al. 1987), our model included only data from female mallards. We created a stage-based matrix model with a yearly projection interval. We defined a birth-pulse population (McDonald and Caswell 1993, Caswell 2001) with a prebreeding census. Each time step began at the start of the breeding season (20 Apr), and most females reproduced shortly thereafter (<60 days). We followed the 2

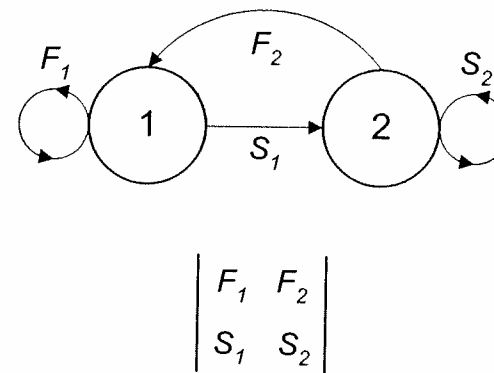


Fig. 1. The life-cycle graph and corresponding stage-classified matrix for a model of the midcontinent population of female mallards. Stage classes 1 and 2 contain second-year (SY) and after-second-year (ASY) females. Vectors represent stage-specific transition probabilities. Fecundity transitions ( $F_i$ ) are the number of female offspring added to the SY stage class at each time step per female in stage class  $i$ . Survival transitions ( $S_i$ ) are the probability of females surviving through stage class  $i$ .

age classes of adults distinguished in field studies: females entered the second-year (SY) and after-second-year (ASY) stage classes at the start of their first and second breeding seasons (Fig. 1). We calculated asymptotic  $\lambda$  as the dominant eigenvalue of the matrix, assuming a stable stage distribution, density independence, invariant vital rates, and no immigration or emigration (Caswell

Table 1. Parameters for a demographic model of female midcontinent mallards. Parameters describe events occurring within each time step (20 Apr in year  $t$  to 20 Apr in year  $t+1$ ). The first 7 parameters describe vital rates occurring during the breeding season (20 Apr to 15 Aug), and the last describes the nonbreeding season (16 Aug to 20 Apr).

Parameter	Definition
Clutch size	Number of female eggs laid per nest initiated.
Egg hatch	Probability of an egg hatching, given that a nest is successful.
Nest success	Probability of a nest hatching at least 1 egg.
Duckling survival	Probability of a duckling surviving from hatching to the end of the breeding season.
Breeding incidence	Probability of an adult female initiating at least 1 nest.
Renesting intensity	Regression coefficient describing the probabilities of an adult female initiating an $x$ th nest ( $2 \leq x \leq 6$ ), given that she is alive and her previous nesting attempt was unsuccessful. The probability of renesting is a declining function of $x$ . (See text for details.)
Breeding survival	Probability of an adult female surviving through the breeding season.
Nonbreeding survival	Probability of a female surviving through the nonbreeding season.

2001). The latter assumption was clearly not tenable because of variable fidelity to breeding sites in midcontinent mallards (Lokemoen et al. 1990). Therefore, our model was not useful for predicting changes in local breeding populations. Rather,  $\lambda$  was used to assess relative annual demographic trends for differing sets of vital rates.

**Model Parameters.**—Although many alternative parameterizations were possible, we attempted to define parameters meaningful in a management context (Table 1). Our goal was to define a minimum number of parameters influenced by different underlying biological processes and hence different potential management actions. Most parameters follow published definitions and were defined as a number or probability, except for renesting intensity (Fig. 2). Female mallards re-nest extensively after nest failure (Cowardin et al. 1985). However, the number of renesting attempts is influenced not only by renesting effort but also by the survival of nests and the female. To directly estimate renesting effort, we calculated the proportion of females initiating a second through sixth nesting attempt if they were alive and their previous nest was unsuccessful. Renesting intensity is a regression slope coefficient that describes the proportion of females renesting as a linear function of nesting attempt.

**Parameter Estimation.**—We used a variety of published and unpublished sources to estimate parameter values (Table 2). We used unpublished

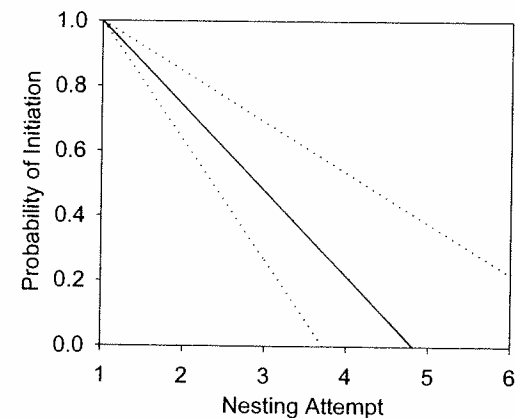


Fig. 2. Probability that a female will initiate a second through sixth nesting attempt at the mean (solid line) and upper and lower standard deviation (dotted lines) across sites for renesting intensity. Renesting intensity is a regression coefficient (see additional details in text) describing the proportion of females initiating a second through sixth nesting attempt on attempt number, with the intercept forced through a probability of 1 for the first nesting attempt. The probability of initiating an  $x$ th nest is  $1 + \text{renesting intensity} \times (x - 1)$ .

Table 2. Estimates of the mean value, empirical SD, SD of process variation and 90% CI of  $\hat{\sigma}$  for parameters of a demographic model of female midcontinent mallards.

Parameter	Parameter estimates				n	Data Source(s)
	Mean	Empirical SD	$\hat{\sigma}$	90% CI of $\hat{\sigma}$		
Clutch size <sup>a</sup>	4.55	Uniform distribution	3.55–5.55			Bellrose 1976
Egg hatch	0.91	N/A	0.050	N/A		Johnson et al. 1992
Nest success <sup>b</sup>	0.13	0.089	0.075 <sup>c</sup>	0.058–0.101	42	Klett et al. 1988; Greenwood et al. 1995; IWWR, unpublished data
Duckling survival	0.39	0.134	0.110 <sup>c</sup>	0.075–0.177	14	Rotella and Ratti 1992; IWWR, unpublished data; Hestbeck et al. 1989
Breeding incidence <sup>d</sup>	0.968	0.040	0.024 <sup>c</sup>	0.009–0.053	11	IWWR, unpublished data
Renesting intensity <sup>e</sup>	-0.26	0.106	0.097 <sup>c</sup>	0.069–0.164	11	IWWR, unpublished data
Breeding survival	0.72	0.071	0.067 <sup>c</sup>	0.051–0.095	19	IWWR, unpublished data
Nonbreeding survival	0.80	N/A	0.051 <sup>f</sup>	0.000–0.088		Derived from breeding and annual survival
Annual survival <sup>g</sup>	0.58	0.192	0.065 <sup>c</sup>	0.044–0.086	313	Chu and Hestbeck 1989

<sup>a</sup> Clutch size differed between stage classes. Mean values for second-year (SY) and after-second-year (ASY) females were 4.30 and 4.80.

<sup>b</sup> Values of nest success used in sensitivity analyses were multiplied by 1.1 so that nest success was independent of breeding survival. See text for additional explanation.

<sup>c</sup> Standard deviation of process variation estimated using weighted estimator (see text for details).

<sup>d</sup> Breeding incidence differed between stage classes. Means for SY and ASY females were 0.945 and 0.984.

<sup>e</sup> Renesting intensity differed between stage classes. Means for SY and ASY females were -0.28 and -0.23.

<sup>f</sup> Standard deviation of process variation estimated using bootstrap estimator (see text for details).

<sup>g</sup> Annual survival was not a model parameter, but was used in conjunction with breeding survival to derive parameter estimates for nonbreeding survival.

data collected by IWWR (Appendix). Empirical variation in a sample of estimates is composed of both process variation (true biological variation) and variation due to sampling error: hence, empirical variation overestimates process variation (Burnham et al. 1987, Link and Nichols 1994, Gould and Nichols 1998). Process variation can encompass both spatial and temporal variation, but we were unable to partition these components of variation because most parameter estimates lacked replication across years at a site. Except when indicated otherwise, we used a weighted procedure to estimate process variation (equations 4.2–4.4; Burnham et al. 1987:263) and associated confidence intervals (equations 4.7–4.8; Burnham et al. 1987:265).

We used averaged clutch size for nests ( $n = 5,170$ ) across many studies in Bellrose (1976) and assumed a sex ratio of 0.5 (Johnson et al. 1987). We adjusted clutch size by +0.25 and -0.25 female eggs for SY and ASY females to account for stage class differences (Cowardin et al. 1985). We used an average estimate of egg hatch reported for studies in Johnson et al. (1992;  $n = 6$ ). Estimates of these parameters rarely have been reported for individual sites and years, so we were unable to estimate their process variation. We attempted to overestimate variation in these parameters so that their influence on variation in  $\lambda$  would not be

underestimated due to uncertainty about their variation. For clutch size, we defined a uniform distribution from the observed extremes of mean clutch sizes at a site in Bellrose (1976). For egg hatch rate, we used the extreme deviations around the average ( $\pm 0.05$ ) from Johnson et al. (1992) as the standard deviation of process variation.

We used Mayfield estimates of daily survival rates of nests from studies that sampled representatively among habitat types (Klett et al. 1988,  $n = 4$ ; Greenwood et al. 1995,  $n = 27$ ; IWWR, unpublished data,  $n = 11$ ; Table 2). We excluded estimates based on <200 exposure days or <75 nests. Where estimates were pooled across years, they were weighted by number of years within the period to estimate the mean, but excluded when estimating process variation. We estimated the mean and process variation from estimates of daily survival rates. We then calculated mean nest success assuming a 35-day nesting period, and we calculated its process variation using the Delta Method (Seber 1982).

We used estimates of duckling survival to 30 days post-hatching (Rotella and Ratti 1992,  $n = 3$ ; IWWR, unpublished data,  $n = 11$ ; Table 2) from females with all transmitter types because transmitter type does not appear to influence estimates (Pietz et al. 1995, Dzus and Clark 1996). Hestbeck et al. (1989), using banding data from

1956 to 1959, estimated survival from approximately 35 days post-hatching to the fall banding period as 0.84. We estimated mean values and process variation for 30-day duckling survival. We then calculated duckling survival as the product of 30-day survival and 0.84, and we calculated its process variation using the Delta Method.

To estimate parameter values for breeding incidence and renesting intensity, we included only studies that used primarily abdominally implanted transmitters (IWWR,  $n = 11$ ; Table 2) because backpack transmitters reduce breeding effort (Pietz et al. 1993, Rotella et al. 1993). When estimating mean values and process variation across sites, we pooled stage classes within sites. We then adjusted parameter values to reflect higher estimates for ASY relative to SY females (Appendix). We found that as breeding incidence decreased, the difference between classes increased. We regressed this difference  $d$  on  $(1 - \text{breeding incidence})$  with the intercept at the origin to predict  $[d = 1.16 \times (1 - \text{breeding incidence})]$ ,  $n = 11$ ,  $r^2 = 0.73$ ] differences between classes based on values of breeding incidence. Renesting intensity was higher ( $\bar{x} \pm \text{SE}$ ;  $0.055 \pm 0.019$ ,  $n = 8$ ) for ASY relative to SY females. We weighted total differences between classes based on the 40:60 SY:ASY stage class ratio in our sample. Therefore, breeding incidence was decreased by  $[0.6 \times 1.16 \times (1 - \text{breeding incidence})]$  for the SY stage class and increased by  $[0.4 \times 1.16 \times (1 - \text{breeding incidence})]$  for the ASY class. Renesting intensity was decreased by  $(0.6 \times 0.055)$  for the SY stage class and increased by  $(0.4 \times 0.055)$  for the ASY stage class. Our methods resulted in perfect correlation between stage classes. We judged this approach reasonable because strong correlations between classes for breeding incidence ( $r = 0.70$ ,  $n = 11$ ) and renesting intensity ( $r = 0.90$ ,  $n = 8$ ) likely reflected similar responses to environmental conditions.

We included estimates of survival of breeding females only from females radiomarked with abdominally implanted transmitters (IWWR, unpublished data,  $n = 19$ ; Table 2) because of detrimental effects of backpack transmitters on behavior and likely survival of breeding females. Analyses did not support differences in breeding survival between SY and ASY females. We derived parameter values for nonbreeding survival from breeding survival and annual survival. We used annual estimates of survival for fall-banded mallards (median date approx. 15 Aug) from banding reference areas within the PPR (Chu and

Hestbeck 1989). Because we did not find trends in survival or process variation in survival over time, we used estimates since 1960 to maximize sample size. Annual survival estimates were based on 2 sets of analyses that sometimes overlapped temporally. Where overlap occurred, we used estimates from the later set. We excluded the last estimate from each set because these had few recoveries and high sampling variance. Average survival estimates for young (hatch year,  $\bar{x} \pm \text{SE}$ ;  $0.576 \pm 0.017$ ,  $n = 154$ ) and adults (SY and ASY females;  $0.581 \pm 0.014$ ,  $n = 154$ ) were similar for the same sites and years. Because survival estimates for each age were independent and nearly identical, we pooled estimates ( $n = 313$ ) to estimate the mean and process variation of annual survival (Table 2). We did not account for sampling covariance (Brownie et al. 1985, Gould and Nichols 1998) because its influence was negligible.

We estimated the mean and process variation for nonbreeding survival assuming that breeding survival and nonbreeding survival were independent. We could not test this assumption, but we felt that strong correlation was unlikely because breeding and wintering areas are largely segregated, and survival likely is influenced by different factors. Furthermore, individuals at a breeding site disperse widely in winter and likely experience differing wintering conditions. Because annual survival  $a$  is the product of breeding survival  $b$  and nonbreeding survival  $w$ , we estimated  $w$  as  $\hat{a} / \hat{b}$  and the standard deviation of process variation of nonbreeding survival  $\hat{\sigma}_w$  by solving

$$\hat{\sigma}_a = \sqrt{\hat{b}^2 \hat{\sigma}_a^2 + \hat{w}^2 \hat{\sigma}_b^2 - \hat{\sigma}_a^2 \hat{\sigma}_b^2}, \quad (1)$$

where  $\hat{\sigma}_a$  and  $\hat{\sigma}_b$  are the estimated standard deviation of process variation for annual survival and breeding survival (Seber 1982). We used a parametric bootstrap to estimate confidence intervals for  $\hat{\sigma}_w$  (Efron and Tibshirani 1993). We input random values from a  $\chi^2$  distribution into equation 4.7 in Burnham et al. (1987) to generate 5,000 pairs of values from the sampling distributions of  $\hat{\sigma}_a$  and  $\hat{\sigma}_b$ , then solved for  $\hat{\sigma}_w$  in each case and used the 5 and 95 percentiles of this distribution as the 90% confidence limits.

Differences in the size of sites used to estimate breeding survival (approx. 70 km<sup>2</sup>) and annual survival (>1,000 km<sup>2</sup>) may have resulted in inaccurate estimates of variation in nonbreeding survival. Because sampling over a large area may average out local variation, variation in annual

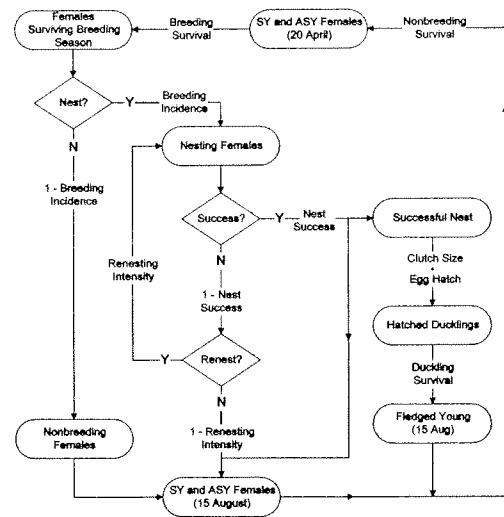


Fig. 3. Flow diagram for a model of the midcontinent population of mallards showing functional relationships between parameters. Vectors and corresponding parameters show possible transitions within each annual time step (20 Apr in year  $t$  to 20 Apr in year  $t + 1$ ). Renesting intensity is a regression coefficient describing the probability of a female initiating a second through sixth nest attempt. Hatch-year young enter the second-year (SY) stage class. Second-year and after-second-year (ASY) females surviving to the end of a time step enter or remain in the ASY stage class. The contribution of SY and ASY females to the ASY stage class differs because of differences in clutch size, breeding incidence, and renesting intensity.

survival may have been underestimated relative to breeding survival, which would have resulted in an underestimate of variation in nonbreeding survival. Alternatively, banding occurs at only a few sites within each reference area, and estimates of annual survival may not capture the full spectrum of variation within the area. Therefore, the direction and magnitude of error in estimates for nonbreeding survival was difficult to assess.

We did not incorporate within-year variation in parameters. In contrast to some previous studies (Orthmeyer and Ball 1990, Rotella and Ratti 1992), we did not find a decrease in duckling survival through the breeding season (IWWR, unpublished data). Although clutch size decreases through the breeding season (Krapu et al. 1983, Cowardin et al. 1985, Lokemoen et al. 1990), we did not incorporate this decrease because the accompanying increase in model complexity was large relative to its influence on population dynamics and because within-year variation had little bearing on our goal of analyzing variation between sites and years.

**Model Structure.**—Model parameters (Table 1) in combination determine matrix transitions  $F_i$  and  $P_i$  (Fig. 1). The flow chart of model structure (Fig. 3) shows functional relationships among parameters within each time step. The  $F_i$  matrix transitions sum probabilities of all routes by which SY females can be added to the breeding population each time step from adults in stage class  $i$ ; the  $S_i$  matrix transitions sum probabilities of adults in stage class  $i$  surviving through each time step. The stage-specific fecundity  $F_i$  is the mean number of female offspring per female in stage class  $i$  that survive to the end of the time step (20 Apr). Given breeding survival  $b$ , clutch size  $c$ , egg hatch  $e$ , nest success  $n$ , duckling survival  $d$ , and nonbreeding survival  $w$ , we defined  $F_i$  as

$$F_i = bcedw \sum_{x=1}^6 n(1-n)^{x-1} \prod_{z=1}^x p_z, \quad (2)$$

where  $x$  is the number of the nesting attempt,  $p_z$  is the probability of initiating a  $z$ th nest,  $p_1$  is described by breeding incidence, and  $p_2$  through  $p_6$  are described by renesting intensity. We limited females to the observed maximum of 6 nests. Second-year and ASY female parameter values for breeding incidence, renesting intensity, and clutch size are used to calculate stage specific  $F_1$  and  $F_2$  values. We calculated  $S_i$  as  $bw$ .

Functional relationships between most of the parameters were straightforward, but relationships between nest success, renesting intensity, and breeding survival were relatively complex. Females that hatch a nest seldom renest. Therefore, successful females bypassed the opportunity to renest. Furthermore, the probability that unsuccessful females will renest likely varies inversely with nest success, because increases in nest success increase the duration of and intervals between nesting attempts (Cowardin and Johnson 1979, Swanson et al. 1986). However, regression of renesting intensity on nest success explained little variation in renesting intensity (IWWR, unpublished data;  $r^2 = 0.11$ ,  $n = 11$ ). Therefore, we felt that the increased complexity of a temporally explicit model of events during the breeding season (e.g., Pease and Grzybowski 1995) was not justified.

Increased breeding effort may decrease breeding survival if behaviors associated with breeding (i.e., incubation or increased foraging) increase vulnerability to predation (Reynolds et al. 1995). However, we failed to find a strong correlation between breeding survival at a site and mean number of nests ( $r = 0.24$ ), median days nesting ( $r = -0.07$ ), or median days breeding (initiation of

Table 3. Pearson correlation coefficients ( $r$ ) among breeding season parameters for a demographic model of female midcontinent mallards. Correlations were estimated for parameters estimated for the same site and year ( $n = 11$  in all cases).

Parameter	Parameter			
	Nest success	Duckling survival	Breeding survival	Breeding incidence
Duckling survival	0.13			
Breeding survival	-0.10	-0.14		
Breeding incidence	0.36	0.62 <sup>a</sup>	0.22	
Renesting intensity	-0.33	0.46	-0.14	0.06

<sup>a</sup> After removal of an outlier,  $r = 0.14$ .

first nest to termination of last nest;  $r = -0.07$ ) per female (IWWR, unpublished data,  $n = 11$ ). Therefore, we did not functionally link breeding survival to breeding incidence and renesting intensity. However, we assumed that a female must survive the breeding season to fledge young. Therefore, we accounted for breeding survival at the start of the breeding season. Because mortality of nesting females was associated with approximately 10% of nest failures (IWWR, unpublished data), we multiplied estimates of nest success by 1.1 for the subset of surviving females.

Parameters may covary if each responds similarly to environmental changes or if trade-offs exist between parameters, and covariation can be important in both analytic perturbation and variance decomposition analyses (van Tienderen 1995, Horvitz et al. 1997). However, correlations generally were weak between parameters estimated at the same sites and years (Table 3). Simulations indicated that true correlations among parameters likely were obscured by sampling error (unpublished analyses). Although we do not dispute the potential importance of covariance structure, we did not include it in our analyses because we found that incorporating estimated covariance structure had negligible effects on our results (e.g., covariance explained <10% of variation in  $\lambda$ ).

**Simulating Variation.**—We used the parametric matrix method to simulate population dynamics (Fieberg and Ellner 2001). We defined a probability distribution for each parameter based on its estimated mean value and process variation. A uniform distribution was used to simulate variation in clutch size. Biologically realistic values for all other parameters were bounded by absolute values of 0 and 1, and we assumed these followed a Beta distribution (Port 1994, Fieberg and Ellner 2001).

**Model Analyses.**—We employed analytic perturbation analyses to predict how changes in mean

values of parameters would affect  $\lambda$ . We calculated analytic sensitivities and elasticities for each parameter from a model of mean parameter values. Sensitivity ( $\Delta\lambda$  resulting from infinitesimal, absolute change in a vital rate) and elasticity (proportional  $\Delta\lambda$  resulting from infinitesimal, proportional change in a vital rate) describe the relative  $\Delta\lambda$  due to standardized changes in vital rates (Mills et al. 1999, Caswell 2001). We presented both sensitivities and elasticities for comparison with other studies, but we focused primarily on sensitivities because assessments of management actions typically have reported effects on vital rates in absolute rather than proportional units.

We used LSA to simulate process variation in model parameters. We generated simulations of 5,000 replicate sets of parameters by independent sampling from the probability distribution defined for each parameter. We evaluated how sensitivities and elasticities varied across process variation in parameters by calculating analytic sensitivities and elasticities for each replicate. We also used LSA to decompose the variance of  $\lambda$  into contributions by variation in each parameter (Wisdom et al. 2000). We regressed values of  $\lambda$  calculated for each replicate in a simulation on each parameter. Because  $\lambda$  was determined by model parameters, variation in  $\lambda$  was completely explained by variation in, and interactions among, parameters. The coefficient of determination ( $r^2$ ) for each regression indicated the proportion of variation in  $\lambda$  explained by each parameter. To assess robustness of ranking parameters based on  $r^2$  to uncertainty in estimates of process variation, we altered the process variation of each parameter to its upper and lower 90% confidence limits while other parameters remained unchanged. We then created new simulations and observed how ranks changed.

## RESULTS

At mean parameter values, the matrix took the form

$$\begin{pmatrix} 0.204 & 0.259 \\ 0.581 & 0.581 \end{pmatrix},$$

with  $\lambda = 0.824$ . The stable stage distribution vector ( $\mathbf{w}$ ) and relative reproductive value vector ( $\mathbf{v}$ ), scaled to 1 for the SY stage class, were

$$\mathbf{w} = \begin{pmatrix} 0.30 \\ 0.70 \end{pmatrix} \text{ and } \mathbf{v} = \begin{pmatrix} 1.00 \\ 1.07 \end{pmatrix}.$$

Table 4. Analytic sensitivities and elasticities of parameters at mean values of parameters and variation in sensitivities and elasticities across process variation in parameters for a demographic model of female midcontinent mallards.

Parameter	Analytic sensitivity <sup>a</sup>		Analytic elasticity <sup>b</sup>	
	Mean <sup>c</sup>	SD <sup>d</sup>	Mean <sup>c</sup>	SD <sup>d</sup>
Clutch size	0.05	0.04	0.29	0.12
Egg hatch	0.27	0.18	0.29	0.11
Nest success	1.66	0.79	0.26	0.09
Duckling survival	0.62	0.68	0.29	0.11
Breeding incidence	0.21	0.25	0.24	0.13
Renesting intensity	0.44	0.61	0.14	0.04
Breeding survival	1.13	0.24	1.00	0.00
Nonbreeding survival	1.06	0.23	1.00	0.00

<sup>a</sup> Relative  $\Delta\lambda$  resulting from an absolute and infinitesimal change in a vital rate when others were held constant.

<sup>b</sup> Relative proportional  $\Delta\lambda$  resulting from a proportional and infinitesimal change in a vital rate when others were held constant.

<sup>c</sup> From a model composed of mean values of parameters.

<sup>d</sup> SD from simulations of 5,000 replicates with process variation in all parameters.

**Analytic Perturbation Analyses.**—Sensitivity of  $\lambda$  at mean parameter values was highest for nest success, followed by breeding survival and nonbreeding survival (Table 4). Sensitivity was intermediate for duckling survival and low for other parameters. Elasticities were highest for breeding survival and nonbreeding survival, lowest for renesting intensity, and intermediate for other parameters. Sensitivities and elasticities of adult survival parameters showed little variation across process variation in parameters, but variation for other parameters often was substantial. Correlation of sensitivities and elasticities from each replicate with parameter values revealed that most variation in sensitivities was driven by process variation in nest success and duckling survival. Nest success (Fig. 4A) was negatively correlated with its own sensitivity ( $r = -0.40$ ), very strongly positively correlated with sensitivity of duckling survival ( $r = 0.87$ ), and strongly positively correlated ( $r > 0.72$  in all cases) with sensitivities of other parameters, except renesting intensity. Duckling survival (Fig. 4B) was positively correlated ( $r = 0.68$ ) with sensitivity of nest success. Similar patterns were apparent for elasticities. Nest success had high positive correlation ( $r > 0.57$  in all cases) with elasticities of all parameters except adult survival parameters, whose elasticities were invariant. Duckling survival also was positively related ( $r = 0.50$ ) to elasticity of nest success.

**Variance Decomposition Analyses.**—Nest success accounted for almost half of the variation in  $\lambda$  (Fig. 5A), with a  $r^2$  twice as large as any other

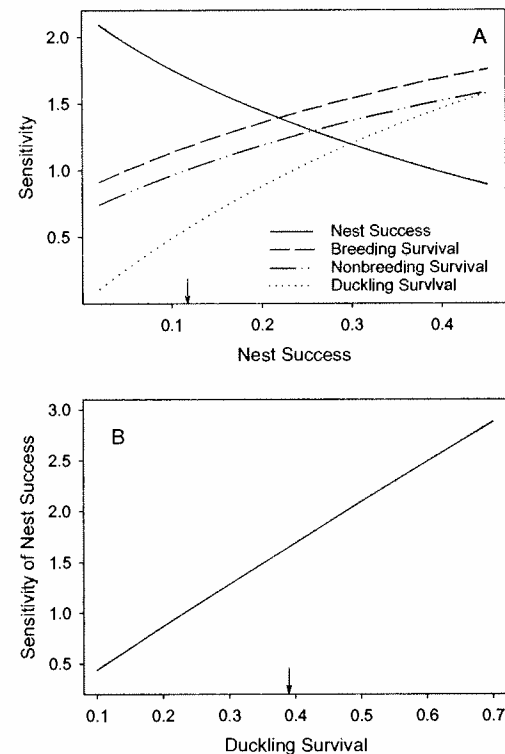


Fig. 4. Analytic sensitivities from a demographic model of female midcontinent mallards across the range of process variation in nest success (A) and duckling survival (B), while other parameters held at mean values. We present relationships for the 4 parameters with the highest sensitivities at mean values of parameters. Arrows denote mean values of parameters.

parameter. Breeding survival (Fig. 5B) and duckling survival (Fig. 5C) accounted for intermediate amounts of variation. The explanatory power of nonbreeding survival (Fig. 5D) and renesting intensity ( $r^2 = 0.052$ ) was small, and clutch size ( $r^2 = 0.022$ ), egg hatch ( $r^2 = 0.004$ ), and breeding incidence ( $r^2 = 0.004$ ) accounted for negligible amounts of variation. Nest success, breeding survival, and duckling survival together explained 76% of variation in  $\lambda$ . Main parameter effects explained 93% of variation in  $\lambda$ , and the remaining 7% was accounted for by interactions and non-linear response of  $\lambda$  to parameters. Ranks of parameter were moderately robust to uncertainty in estimates of process variation (Table 5). Even at its lower 90% confidence, process variation in nest success explained the most ( $r^2 = 0.38$ ) variation in  $\lambda$ . The rank of breeding survival was consistently high. At its lower 90% confidence inter-

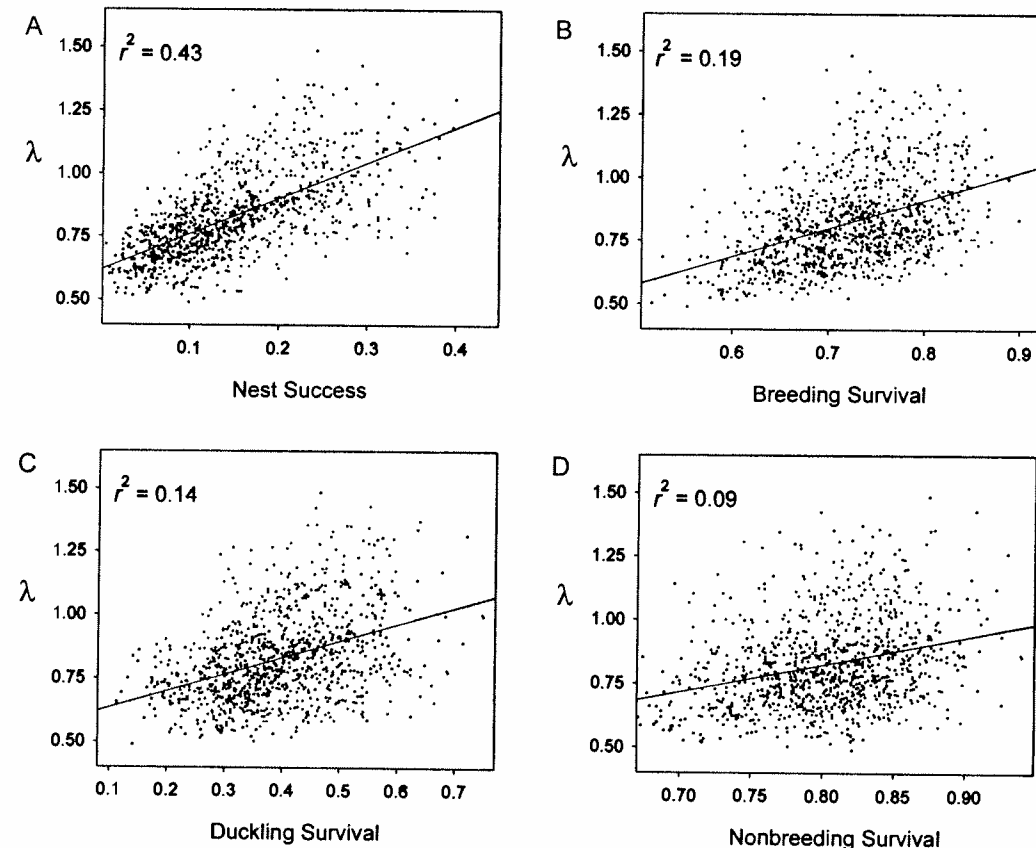


Fig. 5. Regressions of the finite rate of population growth ( $\lambda$ ) on the nest success (A), breeding survival (B), duckling survival (C), and nonbreeding survival (D) parameters of a demographic model of female midcontinent mallards. Data points show  $\lambda$  and parameter values for simulation replicates. Replicates were created by independently sampling from probability distribution defined from the estimated mean and process variation of each parameter. Regression lines show mean  $\lambda$  values across variation in each parameter, and regression slope coefficients are nearly equivalent to analytic sensitivities. Coefficients of determination ( $r^2$ ) indicate the proportion of variation in  $\lambda$  explained by variation in each parameter.

val, breeding survival explained 13% of variation in  $\lambda$ . Ranks of duckling survival and nonbreeding survival were less certain. At their upper 90% confidence intervals, both ranked second and explained 27% and 25% of variation in  $\lambda$ .

## DISCUSSION

**Analytic Perturbation Analyses.**—Formal perturbation analysis has not been published for mallards. However, a quantitative assessment of population dynamics of midcontinent mallards, which concluded that nest success and annual survival of females were important to  $\Delta\lambda$  (Cowardin and Johnson 1979), was consistent with our results. In contrast, studies of other ducks and geese have reported lower sensitivities and elasticities for nest success or reproductive success and have concluded that sensitivity of adult survival greatly

exceeded that of nest success (Rockwell et al. 1997, Schmutz et al. 1997, Flint et al. 1998).

Sensitivities are a function of model structure and all parameter values (Caswell 2001), but 2 factors largely explained the unusually high sensitivity of nest success for our model. First, when nest success approached 0, it was very limiting to  $\lambda$  because it created a demographic bottleneck. Increasing nest success from 0.13 to 0.21 resulted in  $\lambda$  becoming most sensitive to breeding survival. Second, persistent renesting magnified effects of nest success on fecundity transitions ( $F_i$ ) and hence on  $\lambda$ . With no renesting,  $\lambda$  was more sensitive to breeding and nonbreeding survival than to nest success.

Considering sensitivities and elasticities only at mean parameter values may yield misleading predictions of  $\Delta\lambda$  and lead to poorly informed man-



Table 5. Ranks of coefficient of determination ( $r^2$ ) values from variance decomposition analysis for the top 5 ranked parameters of a demographic model of female midcontinent mallards. Parameters with the highest ranks explained the most variation in  $\lambda$ . Ranks are shown for simulations when estimates of process variation were at mean values and when process variation ( $\hat{\sigma}$ ) for that parameter was set at the extremes of its 90% CI while other parameters were unchanged.

Parameter	$\hat{\sigma}^a$	90% CI of $\hat{\sigma}^b$	
		Upper	Lower
Nest success	1	1	1
Breeding survival	2	2	3
Duckling survival	3	2	5
Nonbreeding survival	4	2	8
Renesting intensity	5	3	5

<sup>a</sup> Ranks from original 5,000 simulations.

<sup>b</sup> Each rank based on 5,000 new simulations.

agement decisions because of variation in sensitivities and elasticities across space and time (Oostermeijer et al. 1996, Saether et al. 1999). Our analyses indicated that variation in sensitivities and elasticities primarily was influenced by process variation in nest success and duckling survival. Accurate estimates or predictions for these vital rates (Greenwood et al. 1995, Krapu et al. 2000) may improve predictions from perturbation analyses and optimize management prescriptions for specific situations. For example, as nest success increases, the influence of manipulating duckling survival increases dramatically, but the influence of nest success decreases (Fig. 4A). Therefore, management targets might be altered if nest success was predicted (e.g., based on landscape composition) to be high.

Predictions of  $\Delta\lambda$  resulting from large and simultaneous changes in parameters violates mathematical definitions of sensitivities and elasticities (e.g., infinitesimal change in 1 parameter). However, such predictions may be accurate if the effects of changes on  $\lambda$  are linear and additive (Mills et al. 1999, de Kroon et al. 2000). These assumptions were almost perfectly met for our model across the range of observed parameter values. Therefore, sensitivities and elasticities are useful for projecting and comparing predicted  $\Delta\lambda$  resulting from specific changes in parameters resulting from observed or hypothetical changes in vital rates. The predicted  $\Delta\lambda$  is the product of change in a parameter and its sensitivity (Caswell 2001:224); the predicted percent  $\Delta\lambda$  is a product of percent change in a parameter and its elasticity (Caswell 2001:242). The predicted effect of changes in multiple parameters is the sum of their individual effects. We stress that predictions

of expected  $\Delta\lambda$  are made in the context of variation in  $\lambda$  due to process variation in vital rates (Wisdom et al. 2000).

**Variance Decomposition Analyses.**—The contribution of a vital rate to variance of  $\lambda$  can be estimated as the product of the square of its sensitivity and its variance (Horvitz et al. 1997), assuming that  $\lambda$  is a linear function of vital rates. Because this assumption was nearly perfectly met for our model, analytic calculations provide insight to understanding  $r^2$  from simulations. Nest success and breeding survival had similar process variation, but nest success explained more variation in  $\lambda$  because of its relatively high sensitivity. Duckling survival had large variation but only moderate sensitivity, resulting in moderate contribution to variation in  $\lambda$ . Despite relatively high sensitivity, the contribution of nonbreeding survival was small because of its low variation.

Previous analyses of demographic models comparing the relative importance of reproductive vital rates to recruitment to the fall population concluded that nest success made the largest contribution to variation in recruitment, followed by survival of ducklings (Johnson et al. 1987, 1992). Our results were consistent with these analyses. However, correlations of annual change in breeding population size of midcontinent mallards with indices of breeding productivity and harvest rate were of comparable magnitude (Reynolds and Sauer 1991). These results suggest that reproductive vital rates and nonbreeding season mortality were of similar importance to annual population change. In contrast, our results emphasized the importance of vital rates during the breeding season. Differing conclusions may have resulted in part because Reynolds and Sauer (1991) pooled sexes, but we considered only females. Demographics differ substantially between males and females (Sargeant et al. 1984, Blohm et al. 1987), which limit population growth. For example, harvest is the primary source of male mortality, but most female mortality (>65%) typically has occurred during the breeding season (Cowardin and Johnson 1979, Cowardin et al. 1985, Reynolds et al. 1995). Furthermore, correlation of indices of productivity and harvest, which have unknown relationships to true parameters and unknown sampling error, along with change in breeding populations (Reynolds and Sauer 1991) may not have reflected relative strengths of true relationships between parameters.

Estimates of the relative contribution of parameters to variation in  $\lambda$  were subject to several

sources of uncertainty in deriving values for process variation. Because most of our breeding season estimates were collected over only 4 years, we did not capture the full spectrum of variation in these parameters. However, wetland conditions (indexed by May and Jul pond counts) and mallard breeding pair counts varied from below to well above long-term averages at sites used in this study (IWWR, unpublished data). Large error in estimates of process variation contributed to uncertainty in quantifying the contribution of parameters to variation in  $\lambda$ , but qualitative conclusions about ranks generally were robust.

The midcontinent population of mallards is characterized by high variation in recruitment and population size (Pospahala et al. 1974, Kaminski and Gluesing 1987). Effective management requires understanding the proximate factors that contribute to this variation. Positive correlations between indices to wetland conditions on the breeding grounds and indices to recruitment and population change have formed the cornerstone of understanding and predicting annual recruitment and population change in midcontinent mallards (Martin et al. 1979, Williams et al. 1999). One suggested mechanism for this relationship is that production rates increase in response to favorable wetland conditions (Leitch and Kaminski 1985, Kaminski and Gluesing 1987). Indices of breeding wetland conditions have been positively correlated with clutch size, nesting effort, and duckling survival (Krapu et al. 1983, Cowardin et al. 1985, Rotella and Ratti 1992, Greenwood et al. 1995). However, corresponding parameters in our model: clutch size, breeding incidence, renesting effort and duckling survival combined explained <20% of variation in  $\lambda$ .

Alternatively, the drought displacement hypothesis (Crissey 1969, Pospahala et al. 1974) suggests that during dry years breeding pairs are displaced to north of the PPR, where females are thought to exhibit lower reproductive effort and success (Hansen and McKnight 1964, Calverley and Boag 1977, Johnson and Grier 1988). In our analyses, measures of reproductive effort (i.e., breeding incidence and renesting intensity) made little contribution to explaining variation in  $\lambda$ . However, because our estimates of these parameters were derived solely from females in the PPR, we likely underestimated variation in reproductive effort and hence its influence on population dynamics. Further study is needed to explore low density-dependent displacement of breeding

pairs would add to our results. We note that, given the large proportion of variation in  $\lambda$  explained by nest success and its large spatial variation (Greenwood et al. 1995, Reynolds et al. 2001), displacement of pairs within the PPR could strongly influence population dynamics. Wetland conditions influence settling of pairs within the PPR (Johnson and Grier 1988, Krapu et al. 1997), and we hypothesize that displacement from areas of high to low nest success within the PPR may be an important mechanism linking variation in breeding wetland conditions to population change in midcontinent mallards.

Our estimate that nonbreeding survival explained <10% of variation in  $\lambda$  was consistent with studies (Burnham and Anderson 1984, Smith and Reynolds 1992) that failed to show a clear influence of harvest, the primary source of nonbreeding mortality, on annual survival of females in the midcontinent population. We assumed additive mortality, which maximized the potential influence of nonbreeding survival on  $\lambda$ . We emphasize that our results did not suggest that nonbreeding survival could not be influential to variation in  $\lambda$ . Rather, its influence was small because of its low variation, which may reflect bias against harvest of females and extensive management of migratory and wintering habitat to meet energetic needs of waterfowl (Williams et al. 1999).

Most variation in  $\lambda$  (62%) was explained by variation in nest success and breeding survival. Correlations between breeding wetland conditions in the PPR and both survival of adult females (Nichols et al. 1982) and nest success (Johnson et al. 1989, Beauchamp et al. 1996a) have been positive but weak, suggesting wetland conditions are not driving variation in  $\lambda$  among sites and years within the PPR (Bethke and Nudds 1995, Williams et al. 1999). At larger scales, wetland conditions could mediate the influence of local  $\lambda$  on population dynamics by altering densities of breeding pairs across sites. Predation is the primary proximate cause of both nest failure (Cowardin et al. 1985, Klett et al. 1988, Johnson et al. 1989) and mortality of adult females during the breeding season (Sargeant et al. 1984; IWWR, unpublished data) in midcontinent mallards and may therefore be driving variation in these vital rates. Abundance of individual predators and composition of predator communities have been linked to nest success (Johnson et al. 1989, Sovada et al. 1995, Beauchamp et al. 1996b, Garretson and Rohwer 2001). In addition, nest success is negatively correlated with percent

cropland in prairie regions of the PPR, perhaps as a result of altered predator communities and distributions (Greenwood et al. 1995, Reynolds et al. 2001). Both predator abundance and landscape composition vary more spatially than annually (Johnson et al. 1989) and thus better explain spatial than temporal variation in nest success. However, annual variation in nest success has exceeded spatial variation, and most variation in estimates of nest success remains unexplained (Greenwood et al. 1995, Sovada et al. 1995, Williams et al. 1999, Reynolds et al. 2001). Factors driving survival of breeding females have not been well-studied but may include predator composition and abundance (Sargeant et al. 1984), nesting effort (Reynolds et al. 1995), or nesting habitat (Murphy 1993). Temporal variation in the abundance or vulnerability of alternate prey such as microtine rodents or macroinvertebrates seems a plausible explanation for temporal variation in predation on both nests and breeding females. Despite some supporting evidence (Byers 1974, Weller 1979, Crabtree and Wolfe 1988), these hypotheses have received little investigation.

**Model Assumptions and Scope.**—Applying model predictions to actual population responses will be accurate only to the extent that model assumptions are valid. Calculation of  $\lambda$  from matrix models assumed a stable stage distribution. However, deviations from the stable stage distribution observed in the radiomarked samples (26% to 56% SY females) had negligible effects on our analyses because stage classes had similar reproductive values and hence similar influences on  $\lambda$ . We also assumed that effects of change in vital rates on  $\lambda$  were additive and density independent, with no covariation among vital rates. Some evidence supports compensatory responses (negative covariation) in midcontinent mallards (Pospahala et al. 1974, Burnham and Anderson 1984, Kaminski and Gluesing 1987), but the strength and mechanisms of compensation as well as the spatial scale at which it may occur are uncertain. We did not find compelling evidence of covariation among vital rates during the breeding season on our sites (Table 3). If present, positive covariation increases the influence of vital rates on  $\Delta\lambda$  and variation in  $\lambda$ , and negative covariation decreases their influence (van Tienderen 1995, Horvitz et al. 1997). The magnitude of the influence of this covariation is a function of their sensitivities and covariance. Because individual influence of each parameter is a function of related attributes (sen-

sitivity and variance), parameters that are individually influential have the highest potential to be influential through their covariation.

Our inferential scope was constrained by our sampling frame and data sources. Direct comparison of our results to breeding population surveys are invalid because we lacked clearly defined study populations, we did not incorporate spatial population structure, and estimates of  $\lambda$  may have been inaccurate. Our analyses incorporated parameter estimates across disjunct sites and years and therefore are not comparable to changes in breeding populations for specific sites and years. Our estimates of  $\lambda$  and its variation may not represent the midcontinent population as a whole because we did not account for spatial population structure within and beyond our sampling frame. We estimated parameters only for females breeding within the PPR and did not address effects of variation in breeding densities or source-sink population dynamics. In addition, our estimates of breeding season parameters were derived primarily from the Canadian PPR from 1993 to 1996, but the recent recovery of the midcontinent population appears to have been driven largely by production in the United States (Williams et al. 1999). Finally, we likely underestimated  $\lambda$  because parameters may have been underestimated (e.g., transmitter effects) and because of failure to account for covariation among parameters (Wisdom et al. 2000) or heterogeneity among individuals. Therefore, we prefer relative rather than absolute interpretations of estimates of  $\lambda$  (Beissinger and Westphal 1998).

#### MANAGEMENT IMPLICATIONS

Perturbation analysis frequently has been used to infer which vital rates are most important to  $\lambda$  and hence to management of populations. Often, management has focused on vital rates with the highest ranking sensitivities or elasticities at mean values of vital rates (Doak et al. 1994, Silvertown et al. 1996, Flint et al. 1998). Such recommendations may be ambiguous because ranks of parameters typically differ with respect to sensitivities versus elasticities (e.g., Table 4). These differences are not surprising because sensitivities and elasticities compare perturbations of different magnitudes (Caswell 2001:243). In addition, spatial and temporal variation in vital rates may substantially alter sensitivities and elasticities and hence their ranks (Oostermeijer et al. 1996, Wisdom et al. 2000). We recommend that, when possible, perturbation analyses should be inter-

preted in conjunction with consideration of the effectiveness and cost of manipulating different vital rates (Citta and Mills 1999, de Kroon et al. 2000, Cross and Beissinger 2001). Different vital rates are not equally susceptible to manipulation, and large change in a less sensitive vital rate may have a greater effect than small change in a more sensitive vital rate. In addition, the costs of implementing management, which may be monetary, sociopolitical, or ecological, can be assessed relative to predicted benefits. Sensitivities and elasticities at mean vital rates may be useful when better information is lacking. However, knowledge of deviations of vital rates from mean values can improve estimates of sensitivities and elasticities and hence predictions from sensitivity analyses.

Our perturbation analyses corroborate the historic focus on nest success and survival of adult females as potentially effective targets for management to increase  $\lambda$ . However, management of nesting habitat and predator communities often has yielded only modest or inconsistent increases in nest success (Greenwood 1986; Beauchamp et al. 1996b; McKinnon and Duncan 1999; Williams et al. 1999; IWWR, unpublished data; but see Garrettson and Rohwer 2001). Such results highlight the need for better knowledge of how habitat features and predator communities influence nest success and at which scale to implement management (Clark and Nudds 1991, Williams et al. 1999). Reducing harvest rates has not been convincingly demonstrated to increase female survival (Burnham and Anderson 1984, Smith and Reynolds 1992). We suggest that increasing survival of females during the breeding season has high potential to benefit  $\lambda$  because of the high sensitivity of breeding survival and because mortality during the breeding season accounted for >65% of annual mortality. Although survival of breeding females typically is not a target for management, practices focused on managing nest predation through management of predator communities or enhancement of nesting habitat also may decrease predation on females.

Improved knowledge of environmental conditions influencing survival of nests, ducklings, and breeding females is critical to understanding factors limiting population growth in midcontinent mallards. Because predation is the primary proximate source of mortality in each case, examination of the interaction of predator communities with other environmental conditions (e.g., alternate prey, weather, wetland conditions, nesting habitat) may elucidate mechanisms driving varia-

tion in these vital rates. Adaptive harvest management (Williams et al. 1996) seeks to optimize harvest strategies based on observed effects of harvest mortality on populations. Our results suggest that detecting such effects for females, over the observed range of harvest rates of the past several decades, may remain elusive. Increased variation in harvest rates may increase efficiency of adaptive management. Additionally, more accurate predictors of demographic processes on the breeding grounds may help control for natural variation and hence increase ability to detect effects of harvest on populations (Bethke and Nudds 1995, Williams et al. 1999). We strongly endorse ongoing efforts to broaden adaptive management to more fully include ecological processes on the breeding grounds.

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## APPENDIX

### Study Sites and Methods

Many parameter estimates were taken from unpublished data collected by the Institute for Wetlands and Waterfowl Research as part of the Prairie Habitat Joint Venture Assessment Program. In most cases, we used data collected from 11 sites that were 54 to 78 km<sup>2</sup> in area and widely distributed across prairie and parkland habitat in Canada. We studied 2 sites in 1993 and 3 each year during 1994-1996. Primary land use on all sites was production of cereal and oil-seed crops and pasture for beef cattle. Five sites received management treatments of habitat ( $\bar{x} \pm SD$ ; 590  $\pm$  135 ha at each site) to increase nest success and breeding pair densities (e.g., planted nesting cover, delayed haying, grazing systems); however, increases in nest success on treated sites were estimated to be modest (0.016  $\pm$  0.013). Pre-laying females were decoy-trapped (Sharp and Lokemoen 1987) and radiomarked during April and early May (median = 20 Apr). Females were marked primarily with abdominally implanted transmitters (Olsen et al. 1992), but at 5 sites, approximately 33% (see Paquette et al. 1997) of females received anchored backpack transmitters (Pietz et al. 1995). We classified females as SY or ASY based on feather characteristics. Radiotracking was conducted daily between 0630 and 1300 (see Paquette et al. 1997). After a female was located in nesting cover for 3 consecutive mornings, nesting status was verified by locating her nest while she was absent, which minimized nest abandonment due to investigator disturbance. We monitored nesting status and survival until females emigrated from the site. Broods of marked females successfully hatching a nest were used to estimate duckling survival. To increase samples, unmarked females were nest trapped approximately 6 days prior to hatching and were radiomarked with anchored backpack transmitters. We conducted nest searches 3 times per season at 3-week intervals beginning in early May. All habitats other than woodland, tilled cropland, and flooded emergent vegetation were intensively searched. Cable-chain drags (Klett et al. 1986) were used where possible, but hand drags, vehicle-mounted booms, and foot searches were used where necessary. In addition to all managed cover, randomly selected habitat was searched at sites with (1,260  $\pm$  420 ha,  $n = 5$ ) and without (3,150  $\pm$  740 ha,  $n = 6$ ) management treatments. We monitored nest fate after Klett et al. (1986).

### Analyses of IWWR Data

We estimated daily survival rates for nests (0.932  $\pm$  0.015,  $n = 11$ ) using the Mayfield method (Johnson 1979) from marked and unmarked females. We used the Kaplan-Meier (1958) method to estimate duckling survival to 30 days post-hatching (0.52  $\pm$  0.09,  $n = 11$ ). Because duckling survival within broods is not independent (Rotella and Ratti 1992), we assumed a binomial sampling variance ( $\hat{\pi}[1 - \hat{\pi}]/n$ , where  $\hat{\pi}$  is the estimated probability of 30-day survival and  $n$  is the number of broods).

We used records of nesting activity from marked females to estimate proportion of females initiating an  $x$ th nesting attempt if they were alive and previous nests failed. Nesting activity would be underestimated if nesting on site was not detected or if females nested off site. Therefore, we analyzed only females with no 5-day periods with  $<2$  locations before the last observed nest initiation on a site, unless a female was observed repeatedly in a flock of conspecifics and emigrated from a site. We assumed that these females did not breed off site. Decreased nesting activity for females with anchored backpack transmitters relative to females with abdominally implanted transmitters (Pietz et al. 1993, Rotella et al. 1993) probably led to underestimation of nesting activity at 5 sites where some females received backpack transmitters. We estimated breeding incidence for each site to be the proportion of females initiating at least 1 nest (0.968  $\pm$  0.040,  $n = 11$ ), and we assumed binomial sampling variance. Breeding incidence was higher for ASY ( $\bar{x} \pm SE$ ; 0.984  $\pm$  0.009,  $n = 11$ ) than for SY females (0.945  $\pm$  0.022,  $n = 11$ ). We estimated renesting intensity ( $\bar{x} \pm SD$ ; -0.26  $\pm$  0.11,  $n = 11$ ) by regressing the proportion of females initiating an  $x$ th nesting attempt (where  $2 \leq x \leq 6$ ) on the attempt number, with the intercept forced through a probability of 1 for the first nesting attempt (because females must initiate a first nest before renesting). The proportion nesting for each attempt was weighted by sample size; such weighting was justified because earlier attempts had larger samples (and hence less sampling error) and greater biological significance. Regressions explained most of the variation in the data (mean  $r^2 = 0.94$ , range 0.85-1.00). At sites ( $n = 8$ ) with sufficient samples for both age classes, we estimated that renesting intensity was higher for ASY females ( $\bar{x} \pm SE$ ; -0.188  $\pm$  0.020) than for SY females (-0.243  $\pm$  0.037).

We used known-fate models (White and Garrott 1990) to estimate weekly survival rates for breeding females radiomarked with abdominally implanted transmitters ( $\bar{x} \pm \text{SD}$ ;  $n = 118 \pm 21$ ) for 19 sites studied from 1993 to 1998. These sites included the original 11 sites with 4 additional sites in each 1997 and 1998. Survival was estimated for the period from marking until 13 weeks post-marking (median = 20 Apr to 20 Jul). Right-censored females were assumed to have survived. If transmitter loss or failure was associated with mortality, survival would be overestimated. Analy-

ses did not support differences in survival between age classes, so classes were pooled in estimates of period survival ( $0.762 \pm 0.063$ ,  $n = 19$ ). These estimates did not account for additional mortality occurring between (20 Jul) and the end of the breeding season (15 Aug). Therefore, we applied the estimated mean weekly survival ( $0.987 \pm 0.004$ ,  $n = 19$ ) for 10–13 weeks post-attachment, when breeding activity was low and survival was relatively high, to the following 4 weeks. We estimated the sampling variance of the resulting estimates using the Delta Method (Seber 1982).