

A MODEL OF NORTHERN PINTAIL PRODUCTIVITY AND POPULATION GROWTH RATE

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Abstract: Our objective was to synthesize individual components of reproductive ecology into a single estimate of productivity and to assess the relative effects of survival and productivity on population dynamics. We used information on nesting ecology, reneesting potential, and duckling survival of northern pintails (*Anas acuta*) collected on the Yukon-Kuskokwim Delta (Y-K Delta), Alaska, 1991-95, to model the number of ducklings produced under a range of nest success and duckling survival probabilities. Using average values of 25% nest success, 11% duckling survival, and 56% reneesting probability from our study population, we calculated that all young in our population were produced by 13% of the breeding females, and that early-nesting females produced more young than later-nesting females. Further, we calculated, on average, that each female produced only 0.16 young females/nesting season. We combined these results with estimates of first-year and adult survival to examine the growth rate (λ) of the population and the relative contributions of these demographic parameters to that growth rate. Contrary to aerial survey data, the population projection model suggests our study population is declining rapidly ($\lambda = 0.6969$). The relative effects on population growth rate were 0.1175 for reproductive success, 0.1175 for first-year survival, and 0.8825 for adult survival. Adult survival had the greatest influence on λ for our population, and this conclusion was robust over a range of survival and productivity estimates. Given published estimates of annual survival for adult females (61%), our model suggested nest success and duckling survival need to increase to approximately 40% to achieve population stability. We discuss reasons for the apparent discrepancy in population trends between our model and aerial surveys in terms of bias in productivity and survival estimates.

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Simple population models can be used as tools to guide management decisions, to assess management actions, or to identify data gaps (Cowardin and Johnson 1979, Caswell 1989, Carlson et al. 1993). Such models also can be used to combine individual components of reproductive performance into single estimates of productivity or reproductive success. For example, Carlson et al. (1993) developed a habitat-based model of productivity for northern pintails (hereafter, pintails) that synthesized information on nest success by habitat types into a single estimate of productivity. However, this habitat model lacks specific information on several aspects of pintail reproduction. While studies of pintails nesting on the Y-K Delta examined various components of reproductive performance (Flint and Grand 1996, Grand and Flint 1996a,b), none combined this information into a single measure of productivity.

In this paper, we develop an individual-based model that integrates estimates of various components of reproductive performance into a single measure of productivity. We then combine the estimate of productivity with estimates of first-year and adult survival to examine both the growth rate of the population and the relative contributions of productivity, first-year survival, and adult survival (Caswell 1989, Schmutz et al. 1997).

METHODS

Model Development

We developed 2 separate models. First, we developed a model that synthesized the separate components of productivity into 1 estimate. We then used the output from this first model in conjunction with published estimates of survival in a matrix-projection model of population dynamics.

Productivity Modeling.—We developed an individual-based model that simulated repro-

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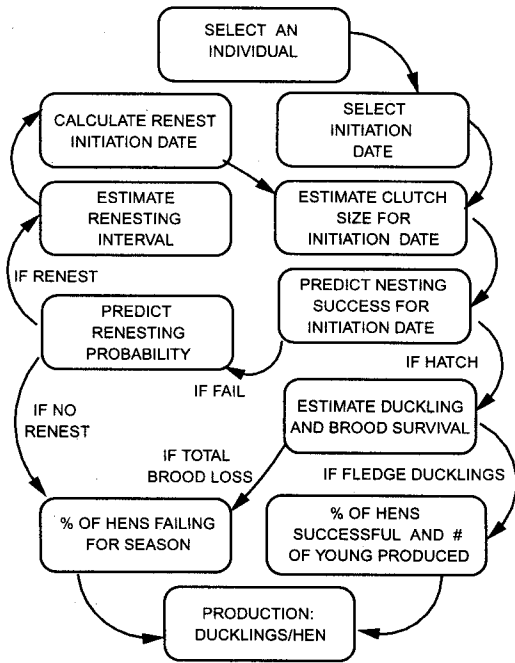


Fig. 1. Basic model structure used to simulate northern pintail productivity under a range of nest success and duckling survival probabilities.

ductive histories of females (Fig. 1) and estimated number of ducklings produced under a range of nest success (proportion of nests that hatch at least 1 egg) and duckling survival probabilities (proportion of ducklings that fledge). We used the approach of an individual-based model to easily incorporate the effect of correlations among reproductive parameters included in the model (Schmutz et al. 1997). For example, both clutch size and nest success vary with nest-initiation date (Flint and Grand 1996), and using an individual-based model allowed us to include a correlation between clutch size and nest success based on nest-initiation date. To construct our models, we used estimates of clutch size, nest-initiation date, and daily survival rates from Flint and Grand (1996), estimates of reneesting interval and propensity from Grand and Flint (1996b), and estimates of duckling survival from Grand and Flint (1996a). We randomly selected values from empirical distributions when available (e.g., reneesting interval), and we added random normal variation for values predicted from relationships (i.e., clutch size for a given nest-initiation date).

We did not know the actual distribution of

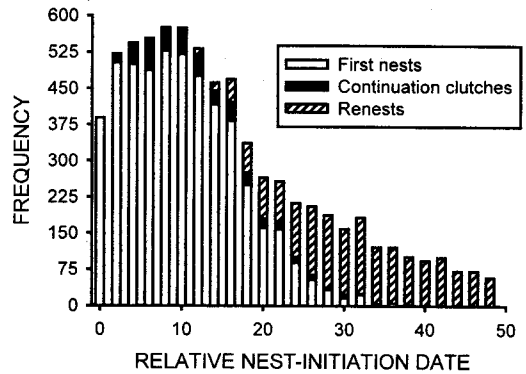


Fig. 2. Distribution of nest-initiation dates (open bars) used as input to the individual-based model. Combined distribution represents the realized distribution of nest-initiation dates for a simulated population of 5,000 individuals via an average value of 25% nest success.

initiation dates for first nests, because we could not classify nests discovered in the field by first or subsequent nesting attempt. In this model, we used a normal distribution with mean nest-initiation date coincident with the peak of nest initiations and truncated the left tail to match the left edge of the overall nest-initiation distribution (Fig. 2; compare with Fig. 1 in Flint and Grand 1996). We selected an initiation date for each individual's first nest from this left-truncated normal distribution. When we used this method, our model produced an overall distribution of nest-initiation dates (i.e., all nesting attempts combined) that closely matched our observations in the field (Fig. 2). Given the selected nest-initiation date, we predicted an appropriate clutch size from the relations between clutch size and initiation date (Flint and Grand 1996), using the integer from the equation

$$\text{clutch size} = 7.6475 + \alpha$$

$$+ (-0.0869)(\text{nest-initiation date}),$$

where α is a normally distributed random variable ($\bar{x} = 0$ and $\sigma^2 = 1$), and nest-initiation date is relative to the population mean. Daily nest survival probabilities were estimated for 10-day blocks of nest initiation and 5-day blocks of nest age (Table 1; Flint and Grand 1996). We then determined nest success by comparing a random number, uniformly distributed from 0 to 1, to the probability of nest survival for each day of incubation. The nest was considered destroyed if the random number was above the estimated survival probability for any day of incubation.

Table 1. Daily nest survival probabilities for northern pintails by nest age and relative initiation date from 1991 to 1993 on the Yukon-Kuskokwim Delta, Alaska.

Relative nest initiation date ^a	Nest age (days)						
	1-5	6-10	11-15	16-20	21-25	26-30	31-35
1-10	0.9672	0.9672	0.9672	0.9672	0.9813	0.9781	0.9860
11-20	0.9393	0.9553	0.9520	0.9551	0.9558	0.9768	0.9639
21-30	0.9504	0.9480	0.9497	0.9533	0.9682	0.9618	0.9584
31-40	0.9063	0.9154	0.9260	0.9272	0.9476	0.9303	0.9291
41-50	0.9355	0.8930	0.9044	0.9155	0.9350	0.8643	0.9545

^a Nest initiation dates are relative to first nests initiated in a given year.

If a nest with ≥ 5 eggs remaining to be laid failed during egg laying, we assumed females attempted to lay the remainder of the clutch in a new nest initiated on the day after first nest failure (i.e., a continuation clutch). If a nest failed with ≤ 4 eggs remaining to be laid, or failed during incubation, we examined the probability that the hen renested. Renesting probability was determined from the logistic regression equation

Renesting probability

$$= \frac{e^{0.5622 - (0.1532)(\text{nest-initiation date})}}{1 + e^{0.5622 - (0.1532)(\text{nest-initiation date})}}$$

where nest-initiation date is relative to the population mean (Grand and Flint 1996b). We compared this renesting probability to a uniformly distributed random number between 0 and 1 to determine if individual females re-nested. Females that did not attempt to re-nest were designated as finished with reproduction for the season. For females selected to re-nest, the interval between nest failure and subsequent re-nest initiation was randomly selected from the distribution of renesting intervals (Fig. 3 in Grand and Flint 1996b). The re-nest initiation date was determined by adding the se-

lected interval to the date of nest failure. We selected a new clutch size appropriate for the initiation date and determined nest success as described above. We constrained the range of nest-initiation dates to 45 days (Flint and Grand 1996), which functionally limited females to 1 renesting attempt.

For females determined to successfully hatch a clutch, we estimated brood size at hatch by accounting for eggs lost during incubation. The average number of eggs lost during incubation was 0.93 (Flint and Grand 1996). To approximate egg loss during incubation, we reduced the clutch size of 93% of successful nests by 1. We then selected a survival probability for each brood based on the relation between hatch date and duckling survival probabilities from Grand and Flint (1996b). We assumed all ducklings in a brood had the same underlying probability of survival, but we randomly varied survival probability among broods (Flint et al. 1995) via the equation

$$\text{Survival} = \beta - (0.006418)(\text{hatch date}),$$

where β is a normally distributed random variable ($\bar{x} = -0.05$ and $\sigma^2 = 0.35$). We did not know the true underlying variability in duckling survival probability among broods (i.e., the distribution of β). Thus, the distribution we used was obtained by iteratively adjusting the distribution of β until both duckling survival and brood success (proportion of females hatching a clutch that fledge ≥ 1 young) matched those measured in field studies (Grand and Flint 1996a).

Using the survival probability selected for each brood, we determined survival of each duckling separately by comparing survival probability to a uniformly distributed random number between 0 and 1, as we did with nest success and renesting probability, which provided estimates of total brood loss and number of

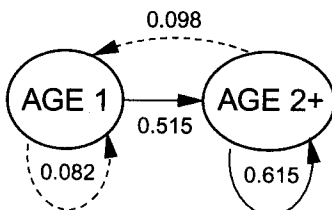


Fig. 3. Life-cycle diagram of basic population model structure used to predict population trends and relative elasticities of productivity, first-year survival, and adult survival of northern pintails. Individuals advance in age class immediately following reproduction. Numbers represent survival probabilities (solid lines) and contributions of young (dashed lines) by each age class.

ducklings fledged per female. Expected productivity for each simulated population was calculated as the total number of female ducklings fledged (assuming a sex ratio of 1:1 for ducklings) divided by population size of breeding females.

Population Modeling.—To examine the dynamics of the population, we used the estimated productivity from the above model with average values of nest success (25%), duckling survival (11%), and renesting propensity (56%), in conjunction with published estimates of adult and juvenile survival probability (Rienecker 1987). We used a 2-stage projection model depicted as a life cycle (Fig. 3), with classes corresponding to ages 0–1 and >1 years. We assumed a birth-pulse, post-breeding census model where individuals advance 1 age class immediately following reproduction, and annual mortality begins accruing as soon as an individual advances age class (Caswell 1989:10–14). We equated fledging with “birth” and used fledging as a point reference for reproductive output. We cast the life-cycle graph as a Leslie-style matrix and used standard methods of linear algebra to find the population growth rate λ . We used partial differentiation to calculate relative effects of the components of the life-cycle graph (technically, the lower-level elasticities of reproductive success, juvenile survival, adult survival) to evaluate how changes in each component affected our projection of λ (Caswell 1989, Schmutz et al. 1997). We examined the robustness of those elasticities by recalculating them over a wide range of estimates of the 3 parameters.

Analysis

Productivity Modeling.—We simulated the productivity of a single population of 5,000 females via average estimates of nest success, duckling survival, and renesting probability from the Y–K Delta (Flint and Grand 1996; Grand and Flint 1996a,b). The output from this model included the complete reproductive histories for each simulated female. From this output dataset, we calculated proportion of females hatching ≥ 1 egg (i.e., hen success), proportion of females fledging ≥ 1 duckling (i.e., breeding success), and average number of juvenile females fledged per breeding female (i.e., productivity). We used regression to examine the relation between date of first-nest initiation and

number of ducklings fledged (regardless of nesting attempt).

We simulated 625 populations of 1,000 individuals under a range of nest success and duckling survival probabilities (25 levels of both nest success and duckling survival). We allowed nest success and duckling survival to vary independently from 5 to 95%. Nest success was varied by adding or subtracting equally to all daily survival probabilities (within limits of 0 to 1), thus maintaining the pattern of nest survival within seasons (Table 1). Duckling survival was varied by adding or subtracting a constant to or from β , thereby altering the average probability of duckling survival without changing the variance in survival probability among broods. We examined standardized regression coefficients to determine the relative importance of nest success and duckling survival on the number of ducklings fledged per hen. We used second-order regression to examine the relation between nest success and average number of nesting attempts per female in each simulated population. We used regression to examine the relation between nest success and hen success.

Population Modeling.—We used average values of adult (0.615) and first-year (0.515) survival for pintails from Rienecker (1987). We calculated relative effects (i.e., elasticities) of survival and productivity on λ from the model of our study population. We then examined elasticities from parameter sets that included a range of estimates of adult survival (0.62, 0.80, 0.95), first-year survival (0.30, 0.52, 0.80), and productivity (0.16, 0.70, 1.25). These alternate parameter sets were chosen to demonstrate a wide range of parameter values that still maintained reasonable estimates of λ .

To link population trends directly to productivity, we predicted the annual adult female survival required to achieve a stable population size under different levels of nest success and duckling survival via the following equation from Cowardin and Johnson (1979):

$$(\text{young/hen})(R)(\text{sex ratio of ducklings}) = (1 - S)/S,$$

where R is the ratio of juvenile to adult survival, and S is annual survival of adult females. We used a value of $R = 0.85$ from Rienecker (1987), and we assumed a sex ratio of 1:1 for fledged ducklings.

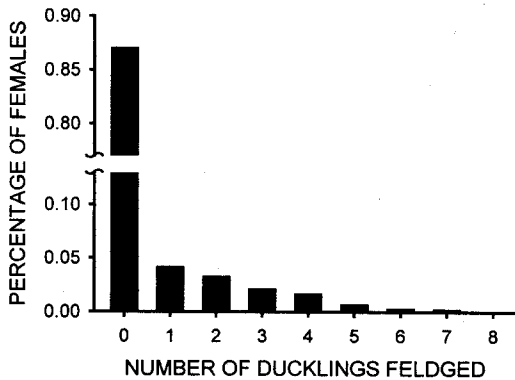


Fig. 4. Proportional frequency distribution of brood size at fledging based on a simulated population of 5,000 individuals with average values for nest success (25%), duckling survival (11%), and renesting probability (56%).

RESULTS

Our individual-based model of productivity predicted hen success of 39%, breeding success of 13%, and productivity of 0.16 female ducklings fledged/breeding female (Fig. 4) when we used distributions of nest success, clutch size, renesting potential, and duckling survival from our field studies. The number of ducklings fledged declined for females initiating nests later in the season ($F_{1,4998} = 94.06$, $P < 0.001$).

The influence of nest success ($b = 0.647$) and duckling survival ($b = 0.665$) on average number of ducklings produced per hen was similar when we used our individual-based model and a range of nest success and duckling survival probabilities. Hen success was positively related to nest success ($F_{1,623} = 59,642$, $P < 0.001$; Fig. 5). Additionally, the number of nest attempts by a population was inversely related to nest success ($F_{1,622} = 82,642$, $P < 0.001$; Fig. 6) as

$$\begin{aligned} \text{Number of nest attempts} \\ = 1.77 - (1.38)(\text{nest success}) \\ + (0.62)(\text{nest success}^2). \end{aligned}$$

The population-projection model suggested our breeding population was declining by >30%/year ($\lambda = 0.6969$). The relative effects indicated adult (i.e., age >1) survival had the greatest effect on λ (0.8825), compared to either first-year survival (0.1175) or productivity (0.1175). Further, this conclusion was robust over a range of survival and productivity values (Fig. 7). Both nest success and duckling survival

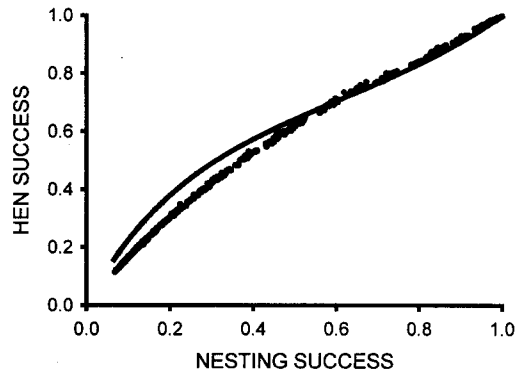


Fig. 5. Relation between nest success and hen success based on 625 simulated populations. Solid line represents levels of hen success predicted by the mathematical model developed by Cowardin and Johnson (1979).

of about 45% would be required to achieve population stability when adult female survival is 60% (Fig. 8).

DISCUSSION

Productivity Modeling

Both nest success and duckling survival had similar effects on productivity in our model. Similarly, both nest success and duckling survival were important determinants of productivity in the model developed by Carlson et al. (1993). Johnson et al. (1992) developed a general population model for waterfowl and concluded nest success had a slightly greater influence on productivity than duckling survival when applied to mallards (*Anas platyrhynchos*). The difference between our productivity model and the model of Johnson et al. (1992) is likely related to breeding season length and associated renesting probability. The breeding

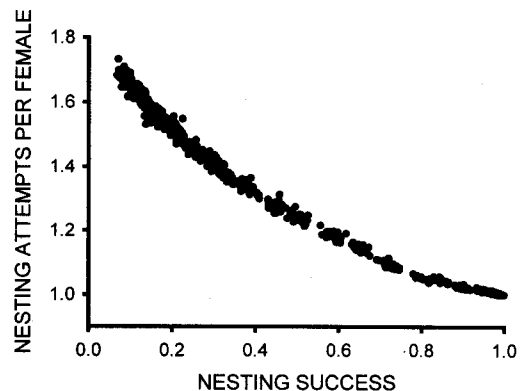


Fig. 6. Relation between nest success and number of nesting attempts per female based on 625 simulated populations.

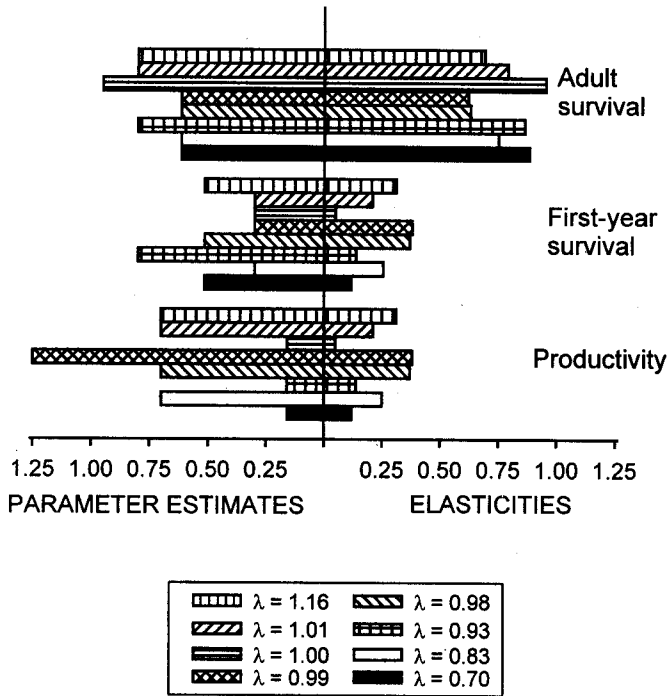


Fig. 7. Parameter estimates and associated elasticities for productivity, first-year survival, and adult survival under a range of different combinations of component estimates, and the resulting population growth rates (λ). The parameter estimates used were chosen to demonstrate a wide range of parameter estimates that still maintained reasonable estimates of λ .

season on the Y-K Delta is shorter than reported in other breeding areas (Flint and Grand 1996), which limits opportunities to re-nest. Thus, in populations of pintails with longer breeding seasons, nest success would likely

have a greater effect on productivity than our productivity model suggests for the Y-K Delta population.

The relation between hen success and nest success demonstrated renests contributed little to overall productivity for our study population. At best, hen success was 15% higher than nest success. This result is strongly influenced by the very low probability of success for late-initiated nests (Flint and Grand 1996). Cowardin and Johnson (1979) developed a simple theoretical model of hen success based on nest success. We applied their model to our estimates of nest success and compared the predictions of hen success with those produced by our productivity model. In general, the results of these 2 models are similar (Fig. 5). Thus, in the absence of data on re-nest rates, the model proposed by Cowardin and Johnson (1979) may approximate hen success.

Cowardin and Johnson (1979) suggested that when nest success is low, the proportion of hens attempting renests will be high because nests are more likely to be destroyed early in the reproductive attempt. Using this

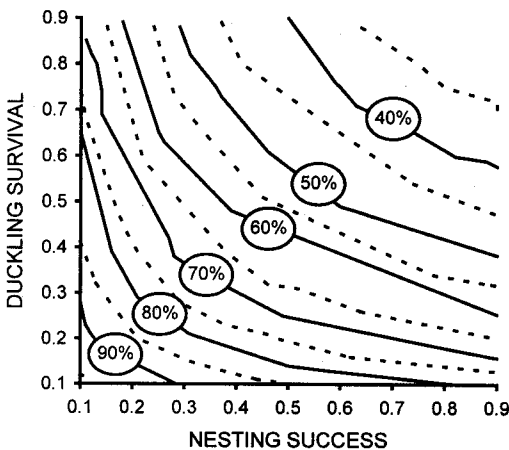


Fig. 8. Contour plot of the relation between nest success, duckling survival, and levels of adult female survival that lead to population stability. Contour lines represent levels of annual adult female survival that yield a stable population. This model assumes first-year survival is fixed at 85% of adult survival.

logic, we predicted the number of nest attempts per female would be inversely related to nest success. Accordingly, we predicted annual variation in nest density was related to breeding population size and nest success. We used the output from our individual-based model to develop the relation between nest success and number of nesting attempts per female (Fig. 6). Given this relation, we can predict the number of breeding females in a population from the number and success of nests. Flint and Grand (1996) provided 3 years of data on number of pintail nests located and nest success. Applying this correction factor to their data demonstrated that annual variation in breeding population size (range = 141–238) was not as extreme as indicated by the number of nests found (range = 197–368).

Our productivity model indicated early-breeding females fledge more young than later breeding females. Early-nesting pintails start reproduction with larger reserves, lay larger clutches, and are more likely to renest than late nesters (Esler and Grand 1994, Flint and Grand 1996, Grand and Flint 1996b). Additionally, early-nesting females on our study area had higher nest success, which is similar to the pattern of nest success reported by Klett and Johnson (1982) for several waterfowl species in the Prairie Pothole Region. Finally, early-hatching pintails had higher duckling survival on our study area (Grand and Flint 1996a). We suggest the seasonal pattern in productivity we found is related to some combination of female quality, age, or condition. Further, Carlson et al. (1993) concluded that productivity of pintails was positively related to body condition. Thus, a similar seasonal pattern in productivity may be found for other breeding populations of pintails.

Population Modeling

Our model predicts our study population of pintails is declining rapidly. Hence, our model disagrees with our data on nesting density, which suggests no consistent trend in size of our study population (Flint and Grand 1996; P. L. Flint and J. B. Grand, unpublished data). Further, our model disagrees with aerial survey data that indicates stable pintail populations on the Y–K Delta (Hodges et al. 1996). Similarly, other models of duck populations predicted declines that were inconsistent with population trends.

For example, Klett et al. (1988) concluded that most populations of ducks nesting in the Prairie Pothole Region did not have adequate production to achieve population stability. Further, Cowardin et al. (1985) examined productivity of mallards and concluded that populations were not declining at the 20% per year as predicted by their model.

Because our population is not declining as predicted by our model, 1 or more of our parameter estimates of productivity, first-year survival, and adult survival must be biased. Similar to the conclusion for emperor geese (*Chen canagica*; Schmutz et al. 1997) and lesser snow geese (*Anser caerulescens caerulescens*; Rockwell et al. 1997), our elasticity estimates demonstrated that adult survival has the greatest influence on population dynamics, and we showed this conclusion was valid over a wide range of survival and productivity estimates. As such, a small bias in adult survival will have a relatively large effect on λ compared to a similar bias in either first-year survival or productivity. The survival rates we used were based on pintails banded in California (Rienecker 1987), and thus may not apply to our study population. However, we note that survival required to obtain a stable population for our estimate of productivity (i.e., 94%) exceeds any survival value published for pintails.

Alternatively, the discrepancy between population trends and predictions from the model can be explained by bias in estimates of productivity. For the published levels of adult and first-year survival, both nest success and duckling survival would need to be about 45% to achieve population stability (Fig. 8), which is considerably higher than the 25% nest success and 13% duckling survival found during field studies. Similarly, Cowardin et al. (1985) demonstrated that nest success would have to double before they would predict a stable population. One explanation for the discrepancy between population trends and model predictions is that methods used in field studies yield biased estimates of productivity. Esler and Grand (1993) concluded that visitation of nests may affect surrounding vegetation and reduce nest success. Further, the influence on nest success from markers used to relocate study nests is equivocal (Greenwood and Sargeant 1995, Hein and Hein 1996). Additionally, radiotelemetry has commonly been used to measure duckling survival and renesting propensity

of hens, and several recent studies have demonstrated negative influences of transmitters on reproductive parameters (Peitz et al. 1995, Ward and Flint 1995, Paquette et al. 1997). These studies suggest published estimates of reproductive parameters may be biased low. However, the likelihood seems small that observer effects reduced estimates by the magnitude suggested by our models (i.e., >20%).

Finally, the discrepancy between predictions of population trends from our model and aerial surveys can be explained by a combination of relatively smaller biases in estimates of productivity, first-year survival, and adult survival. We would predict population stability if the estimates of nest success, duckling survival, and adult survival were all biased low by as little as 15% (Fig. 8). That is, our model would predict population stability if adult survival = 75%, nest success = 40%, and duckling survival = 26%. We believe this magnitude of bias is possible and suggest more than 1 of our model parameter estimates may be biased.

MANAGEMENT IMPLICATIONS

Regardless of the parameter set used, our model demonstrates that, of the 3 parameters considered, adult survival has the greatest influence on population dynamics. Therefore, managers seeking to alter population size could do so most efficiently by changing adult female survival. Our results also suggest published estimates of productivity (i.e., nest success, duckling survival) and adult female survival may be biased low for our population. Because of the larger elasticity of adult female survival in comparison to nest success or duckling survival, small biases in estimates of adult female survival would have a disproportionately greater effect on biasing projections of population growth. Most productivity studies, including our own, were conducted without controls or measurement of observer effects. We suggest observer effects or nonrandom sampling may influence estimates of survival and productivity. Whenever possible, we encourage researchers to assess bias of estimates and design studies with controls.

Managers hoping to enhance productivity could do so by increasing either nest success or duckling survival. However, our model suggests efforts to increase productivity should be concentrated early in the breeding season. Even if nest success and duckling survival were constant

within seasons, early-breeding females lay larger clutches and have more opportunities to re-nest, and thus will produce more young than later-breeding birds (Flint and Grand 1996, Grand and Flint 1996b).

Finally, our model demonstrates that a small percentage of the breeding population produces all the young in a given year (Fig. 4). If reproductive success is repeatable (as evidenced by high variation in lifetime reproductive success; Cooke et al. 1995), then management actions that affect survival of this subpopulation will have relatively large effects on population growth. Managers should consider methods of targeting harvest on nonreproductive or unsuccessful segments of the population (Clark et al. 1988).

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