

DO RESTRICTIVE HARVEST REGULATIONS RESULT IN HIGHER SURVIVAL RATES IN MALLARDS? A COMMENT

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Abstract: Smith and Reynolds (1992) analyzed recovery and survival rates for mallards (*Anas platyrhynchos*) during periods of liberal (1979–84) and restrictive (1985–88) harvest regulations to examine the relationships between harvest and survival. Using a model explicitly relating survival to recovery rates, Smith and Reynolds (1992) concluded that restrictive harvest resulted in higher survival rates for mallards. We reanalyzed these data to examine relationships between survival rates and both harvest and population size. Mallard population size declined ($P = 0.038$) over the interval in question. Therefore, the apparent relationship between harvest and survival found by Smith and Reynolds (1992) is potentially spurious because kill rates and population size declined from 1979 to 1988. In our analyses, the hunting-mortality model failed to provide an explanation of variation in annual survival rates of mallards substantially superior to models of density dependence or constancy in survival rates. We conclude that there is little evidence that restrictive harvest regulations improved mallard survival, and we renew the call for experimental harvest regulations necessary to address the relationship between these 2 variables.

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Debate continues over the forces that influence waterfowl survival rates. A contribution to that research is a paper by Smith and Reynolds (1992). Smith and Reynolds (1992) analyzed harvest and survival rates for mallards during periods of liberal (1979–84) and restrictive (1985–88) harvest regulations. They observed significant declines in recovery rates between the 2 periods in 28 of 32 banding reference area-age-sex combinations (banding ref. areas from Anderson and Henny [1972]). Using Model H_{02} (Brownie et al. 1985), which assumes constant survival within periods, Smith and Reynolds also determined that adult males survived at higher rates under restrictive regulations in 3 of 7 reference areas (Z-tests) and overall (composite Z-test). Survival of adult females improved in only 1 reference area (061, south. Manit.), while survival of immature females improved in only 2 reference areas (031 and 041, south. Alta. and south. Sask.), although composite Z-statistics were significant for adult and immature females. Smith and Reynolds also analyzed the relationship between harvest and survival using the model of Anderson et al. (1982) and Barker et al. (1991). The model is $S_i = S_0(1 - \beta K_i)$, where S_i is the overall survival rate in year i , S_0 is survival in the absence of harvest, K_i is the kill rate in year i and β is the slope of the relationship

between kill rate and survival. Currently it is impossible to precisely estimate kill because of uncertainty about crippling loss. Smith and Reynolds (1992), therefore, estimated a hunting mortality factor (R) in the equation $S_i = S_0(1 - R_i f_i)$, where f_i is the band recovery rate. The hunting mortality factor, R , is related to β by the following equation: $R = \beta / (1 - u)\lambda$, where u and λ are the estimated crippling loss and band reporting rate, respectively (Barker et al. 1991). By averaging estimates across reference areas, Smith and Reynolds' estimate of β differed from zero across the entire range of crippling loss. On the basis of this analysis and the difference in mallard survival for some reference areas between periods of liberal and restrictive harvest regulations, Smith and Reynolds (1992:315) concluded that "restrictive regulations, can under certain conditions, result in increased survival rates of mallards."

We believe it is premature to conclude that restrictive regulations resulted in higher survival rates for mallards, especially for females and both sexes in the Pacific Flyway. We believe there are 2 potential problems with Smith and Reynolds' (1992) analyses. First, to increase power in their analysis of the relationship between harvest and survival, they averaged parameter estimates across reference areas. Pos-

We used the breeding-population estimate rather than midwinter surveys as an index of population size because the latter are notoriously variable for ducks, owing to factors unrelated to population dynamics. The breeding-population surveys were most strongly influenced by mallards contributing to the Central and Mississippi flyways (76 and 79% of the mallard indices in 1991 and 1992, respectively, were in strata contributing predominantly to the Central and Mississippi flyways [Munro and Kimball 1982, Caithamer et al. 1992]). Breeding-population surveys have failed historically to estimate mallards in the Pacific Flyway (6 and 7% of mallard indices in 1991 and 1992, respectively, were in Alas., while 17 and 15% were in north. Alta. and Northwest Territor., from which only 20% of recoveries occur in the Pacific Flyway [Munro and Kimball 1982, Caithamer et al. 1992]). Therefore, we anticipated weak association between mallard survival and population size for reference area 101 (because mallard numbers in this area were poorly estimated) even if mallard density influenced survival.

Power of tests contrasting constancy of R across flyways, and of tests differentiating models containing only density dependence, only influence of hunting, and both density dependence and hunting mortality was calculated. This was done by simulating data under the most complex model of interest, fitting complex and reduced models to the data, and using the resulting χ^2 statistic from the likelihood-ratio test as a non-centrality parameter from which power may be computed (Rexstad and Anderson 1992).

RESULTS

The breeding-population estimate declined ($t = -0.58$, $t = -2.03$, 8 df, $P = 0.038$) between 1979 and 1988. The likelihood-ratio test for geographic variation in R for males was nearly significant ($\chi^2 = 2.635$, 1 df, $P = 0.105$) despite low power (see below) to distinguish differences in R as large as estimated for California ($R = 0.93$) and the midcontinent ($R = 3.91$). From AIC values, the simplest model describing variation in survival rate, $\{f_{i,\alpha}, S_{0A}, \alpha = 0, R = 0\}$, was the preferred model for 2 of 6 datasets for males and 5 of 6 datasets for females (Table 2). One hunting-mortality model $\{f_{i,\alpha}, S_{0A}, \alpha = 0, R\}$ was selected for 2 male datasets and 1 female dataset. A model including density-dependent and hunting-mortality mechanisms $\{f_{i,\alpha}, S_0 = 1, \alpha, R_A\}$ was selected for 1 male dataset.

Table 1. Models used in analysis of 2 age classes of male and female mallards banded in reference areas 031, 041, 051, 061, 101, and 131-133 (Anderson and Henny 1972) during 1979-88.

Model ^a	Description
$\{f_{i,\alpha}, S_{0A}, \alpha = 0, R = 0\}$	Survival rate constant by age class.
$\{f_{i,\alpha}, S_{0A}, \alpha = 0, R\}$	Survival rate dependent on hunting mortality, with relationship equal across ages.
$\{f_{i,\alpha}, S_{0A}, \alpha, R = 0\}$	Survival rate is density dependent, with relationship equal across ages.
$\{f_{i,\alpha}, S_{0A}, \alpha = 0, R_A\}$	Survival rate dependent on hunting mortality; relationship is age specific.
$\{f_{i,\alpha}, S_{0A}, \alpha_A, R = 0\}$	Survival rate is density dependent; relationship is age specific.
$\{f_{i,\alpha}, S_{0A} = 1, \alpha_A, R_A\}$	Survival rate is density dependent and dependent on hunting mortality. Both relationships are age specific. S_0 is constrained at 1.0 for both ages.
$\{f_{i,\alpha}, S_{0A}, \alpha_A, R_A\}$	Survival rate is density dependent and dependent on hunting mortality. Both relationships and S_0 are age specific.

^a Recovery rates (f) are independently year and age specific for all models as indicated by the $i \cdot A$ subscript. S_{0A} , as defined in the equation

$$S_i = S_0 \left(1 - \frac{\alpha N_i}{N_{max}} - Rf_i \right)$$

is assumed to be age specific for all models as indicated by the subscript A. α , the density-dependent term, is either fixed at 0 ($\alpha = 0$), age specific (α_A), or constant with respect to age (α). R, the hunting mortality factor, is either fixed at 0 ($R = 0$), age specific (R_A), or constant with respect to age (R).

Because the contrast between the density-dependent model $\{f_{i,\alpha}, S_{0A}, \alpha_A, R = 0\}$ and hunting mortality model $\{f_{i,\alpha}, S_{0A}, \alpha = 0, R_A\}$ are not hierarchical, likelihood-ratio tests cannot be used for statistical comparisons. Nonetheless, AIC values can be used for relative comparisons. In 5 of the 12 datasets, the hunting-mortality model had AIC values >2 units smaller than the density-dependent model (Table 2). In no instance, however, was the pure density-dependent model $\{f_{i,\alpha}, S_{0A}, \alpha_A, R = 0\}$ rejected by likelihood-ratio test over the model including both factors $\{f_{i,\alpha}, S_{0A}, \alpha_A, R_A\}$ (Table 3), nor was the model containing only hunting mortality. Furthermore, in only 2 of 12 datasets did a

Table 2. Akaike Information Criterion (AIC) values for density-dependent and hunting-mortality models for mallards. Model (Table 1) with lowest AIC from those shown is also shown for each dataset.

Sex-area ^a	AIC: density dependence	AIC: hunting	Δ AIC	Model with lowest AIC
Males				
031	630.86	628.85	2.01	$\{f_{i,t}, S_{0,t}, \alpha = 0, R = 0\}$
041	725.36	722.36	3.00	$\{f_{i,t}, S_{0,t}, \alpha = 0, R\}$
051	591.84	589.40	2.44	$\{f_{i,t}, S_{0,t} = 1, \alpha, R\}$
061	707.83	708.00	-0.17	$\{f_{i,t}, S_{0,t}, \alpha, R = 0\}$
101	651.49	651.49	0.00	$\{f_{i,t}, S_{0,t}, \alpha = 0, R\}$
131-133	679.33	678.52	0.81	$\{f_{i,t}, S_{0,t}, \alpha = 0, R = 0\}$
Females				
031	335.88	334.78	1.10	$\{f_{i,t}, S_{0,t}, \alpha = 0, R = 0\}$
041	489.09	486.69	2.40	$\{f_{i,t}, S_{0,t}, \alpha = 0, R = 0\}$
051	404.99	405.71	-0.72	$\{f_{i,t}, S_{0,t}, \alpha = 0, R\}$
061	507.64	507.62	0.02	$\{f_{i,t}, S_{0,t}, \alpha = 0, R = 0\}$
101	533.02	529.04	3.98	$\{f_{i,t}, S_{0,t}, \alpha = 0, R = 0\}$
131-133	527.32	526.14	1.18	$\{f_{i,t}, S_{0,t}, \alpha = 0, R = 0\}$

^a Banding reference areas (Anderson and Henry 1972).

harvest-only model have the lowest overall AIC value. We also were unable to differentiate either of the models containing a single mortality factor (hunting mortality or density dependence) from the simplest model of constant survival (Table 3). These analyses demonstrate that neither the density-dependent nor hunting-mortality models are preferable to the simplest model, but the hunting-mortality model possibly was slightly more appropriate for males than for females.

We had low power to detect differences in R for adult males between reference area 101 and areas 041, 051, and 061. In simulations using $R_{101} = 0.93$ and $R_{041,051,061} = 3.91$, the power of the test of equality of R across reference areas was 0.37. Exaggerating this difference by diminishing R_{101} to 0.3, while holding $R_{041,051,061}$ at 3.91, increased test power to only 0.51.

Restricting our power calculation only to males in reference area 041, we simulated data under parameter estimates derived from our analyses, $R_h = 3.16$, $\alpha_h = 0.117$. The power of the tests (Table 3) to distinguish between $\{f_{i,t}, S_{0,t}, \alpha, R\}$ and $\{f_{i,t}, S_{0,t}, \alpha = 0, R = 0\}$ was 0.72. Power of the test between $\{f_{i,t}, S_{0,t}, \alpha, R = 0\}$ and $\{f_{i,t}, S_{0,t}, \alpha, R_h\}$ was 0.60, while power of the test between $\{f_{i,t}, S_{0,t}, \alpha = 0, R_h\}$ and $\{f_{i,t}, S_{0,t}, \alpha, R_h\}$ was 0.21. Increasing the magnitude of R_h would increase power to detect existence of hunting effects, similarly increasing α_h would increase power to detect density-dependent mechanisms.

DISCUSSION

Mallard Survival and Population Size

Midcontinent mallard populations declined between 1979 and 1988. Moreover, a model relating mallard survival to population size performed almost as well as a model relating survival to harvest, suggesting that density-related mortality is a viable hypothesis compared with a hypothesis invoking hunting mortality to explain observed temporal patterns in survival. Indirect evidence also is consistent with a density-dependent mortality hypothesis for mallards in the midcontinent. Delnicki and Reinecke (1986) showed that mallards in the Mississippi Alluvial Valley were in better condition during midwinter in years of greater rainfall. Furthermore, a smaller proportion of mallards wintered in the Mississippi Alluvial Valley during dry years (when presumably fewer wetlands were available) or when population size was larger (Nichols et al. 1983). These observations are consistent with the hypothesis that habitat use and physiological condition of mallards are influenced by per capita habitat availability. Physiological condition is correlated with survival probability (Haramis et al. 1986, Conroy et al. 1989) and we, therefore, conclude that change in density-dependent mortality, alone, is a viable hypothesis explaining higher mallard survival rates in the late 1980s, when population sizes were smaller. Although the hunting mortality model was selected slightly more often

Table 3. Likelihood-ratio tests for density-dependent models (Table 1) containing terms α and R , and models containing only

Models compared	df	Likelihood-ratio test
$\{f_{i,t}, S_{0,t}, \alpha, R\}$ vs. $\{f_{i,t}, S_{0,t}, \alpha = 0, R = 0\}$	2	12.1
$\{f_{i,t}, S_{0,t}, \alpha, R\}$ vs. $\{f_{i,t}, S_{0,t}, \alpha = 0, R\}$	1	12.1
$\{f_{i,t}, S_{0,t}, \alpha, R = 0\}$ vs. $\{f_{i,t}, S_{0,t}, \alpha, R_h\}$	1	12.1
$\{f_{i,t}, S_{0,t}, \alpha = 0, R_h\}$ vs. $\{f_{i,t}, S_{0,t}, \alpha, R_h\}$	1	12.1

^a All tests 12 df.

than the density-dependent model, there is no evidence to suggest the density-dependent model was inappropriate for explaining annual survival rates. Because population size in the midcontinent between 1979 and 1988, we were unable to distinguish between survival to either harvest or density-dependent processes by analyzing banding data. Reynolds and Sedinger (1992) and Sedinger and Reynolds stated (1992) "The decline in mallard populations had a density-dependent native hypothesis [of] density-dependent mortality may be possible." Therefore, we conclude that restrictive harvest regulations may improve mallard survival.

Pooling Data to Assess

Even if a hypothesis of density-dependent mortality was true under some conditions, we believe low statistical power would prevent us from applying their conclusions to mallards than was justifiable. Sedinger (1992) pooled across reference areas to increase power to detect density-dependent mortality, but this was completely additive or multiplicative mortality. Therefore, geographic variation in mortality relationship between harvest and survival may have differed between California and midcontinent areas. Sedinger (1992) found mallards in California generally responded weakly to restrictive harvest regulations. Estimates of survival of mallards in California were actually higher than estimates of survival of mallards in the midcontinent (311-312). Unlike midcontinent mallard populations breeding in the Sacramento Fish and Game, Sacramento River, wintering in California, Sedinger (1992) found that survival of mallards in California, Oreg. unpubl. 1992.

Table 3 Likelihood-ratio tests pooled across banding reference areas (Anderson and Henny 1972) contrasting mallard survival models (Table 1) containing terms relating harvest and population density to survival with models containing only one of these terms, and models containing only a single term (e.g., population density) against a model of constant survival.

Models contrasted	Males		Females	
	χ^2	P	χ^2	P
$\{f_{i,t}, S_{i,t}, \alpha_{i,t}, R_{i,t}\}$ vs. $\{f_{i,t}, S_{i,t}, \alpha = 0, R_{i,t}\}$	7.01	0.857	3.49	0.991
$\{f_{i,t}, S_{i,t}, \alpha_{i,t}, R_{i,t}\}$ vs. $\{f_{i,t}, S_{i,t}, \alpha_{i,t}, R = 0\}$	15.29	0.226	11.18	0.514
$\{f_{i,t}, S_{i,t}, \alpha_{i,t}, R = 0\}$ vs. $\{f_{i,t}, S_{i,t}, \alpha = 0, R = 0\}$	8.70	0.729	6.10	0.911
$\{f_{i,t}, S_{i,t}, \alpha = 0, R_{i,t}\}$ vs. $\{f_{i,t}, S_{i,t}, \alpha = 0, R = 0\}$	16.98	0.150	13.79	0.314

^aAll tests 12 d.f.

than the density-dependent model, we found no evidence to suggest the density-dependent model was inappropriate for explaining patterns in annual survival rates. Because harvest and population size in the midcontinent declined between 1979 and 1988, however, power is reduced to distinguish between hypotheses relating survival to either harvest or density-dependent processes by analyzing band recoveries. As Smith and Reynolds stated (1992:315), however, "If mallard populations had declined . . . an alternative hypothesis [of] density dependence could be possible." Therefore, we believe the conclusion that restrictive harvest regulations could improve mallard survival is premature.

Pooling Data to Assess Harvest Effects

Even if a hypothesis of additive hunting mortality was true under some conditions, we believe low statistical power led Smith and Reynolds to apply their conclusions to a broader class of mallards than was justified. Smith and Reynolds (1992) pooled across age and sexes and averaged parameter estimates across geographic areas to increase power to reject hypotheses of completely additive or completely compensatory hunting mortality. The likelihood-ratio test for geographic variation in R suggests that the relationship between harvest and survival may have differed between California (ref. area 101) and midcontinent areas, and we note that mallards in California generally responded most weakly to restrictive harvest regulations; point estimates of survival of male and female immatures were actually lower under restrictive harvest regulations (Smith and Reynolds 1992: 311-312). Unlike midcontinent populations, mallard populations breeding (California Dep. Fish and Game, Sacramento, unpubl. data) and wintering in California (J. C. Bartonek, Portland, Oreg. unpubl. 1992 Pac. Flyway briefing

mater.) did not decline in the late 1980s. Relatively constant density-dependent effects in California may explain the lack of improvement in survival under restrictive regulations in California during the late 1980s.

Recent analyses have indicated heterogeneity in recovery and survival rates for mallards among reference areas 041, 051, and 061 (J. D. Nichols, Patuxent Wildl. Res. Cent., Laurel, Md., pers. commun.). In our analysis of differences between the midcontinent and California in the relationship between harvest and survival we pooled data from reference areas 041, 051, and 061, thereby implicitly assuming constant survival and recovery rates across these areas. In our analysis, we were primarily concerned with differences between the midcontinent (areas 041, 051, and 061) and California in estimates of R, the parameter relating recovery rates to survival. Our estimates of R (0.93 and 3.91 for Calif. and the pooled midcontinent sample, respectively) were similar to those reported by Smith and Reynolds (1992:313). Furthermore, our pooling of the midcontinent sample should have increased our power to detect differences in the estimate of R between California and the midcontinent. Despite pooling, the power to detect geographic variation in R remained relatively low.

There are numerous reasons to expect that survival of different age and sex classes might respond differently to harvest. Adult males are typically dominant to unpaired females and juveniles (Hepp and Hair 1984, Hepp 1989), and their corresponding access to higher quality habitats may reduce the importance of density-related mortality for adult males relative to other age and sex classes at a given population size. Conversely, females and juveniles may be more susceptible to density-related mortality, and females incur high rates of mortality during the



breeding season (Sargeant et al. 1984) as noted by Smith and Reynolds (1992). When males and females were considered separately, Smith and Reynolds (1992) were unable to reject either a model of completely compensatory or completely additive mortality for females, while they could reject a model of completely compensatory mortality for males. Differences between the sexes in response to harvest also were suggested by our result that, on the basis of AIC values, a model containing harvest performed better than a model of constant survival in 3 of 6 male datasets but in only 1 of 6 female datasets. We suggest that pooling across age and sex classes to examine the relationship between harvest and survival was not appropriate.

Generality of Patterns of Harvest and Survival

Smith and Reynolds (1992:310) showed that recovery rates declined coincident with restrictive harvest regulations. On the basis of composite Z-statistics, Smith and Reynolds concluded that survival was higher under restrictive regulations, although this was true for females only in the analyses with the greatest statistical power (survival rates were assumed constant within periods [Smith and Reynolds 1992:311]). Survival for adult females improved only in southern Manitoba (out of 6 ref. areas), while survival of immature females improved only in southern Alberta and southern Saskatchewan (Smith and Reynolds 1992:311). Removal of these areas from the composite Z-calculations for adult and immature females, respectively, renders the composite Z-values nonsignificant ($Z = -1.2717$, $P = 0.1017$ for adult F and $Z = -0.858$, $P = 0.195$, for immature F).

We recognize that removal of the effects of a few reference areas represents selective data editing. Significant composite Z-statistics for female mallards in Smith and Reynolds (1992:311), however, resulted from the contributions of a few geographically contiguous areas. We conclude only that survival of female mallards improved during the late 1980s for segments of the population breeding in midcontinent prairies. We caution that because of the confounding with population size (see above) even the significant increases in survival in southern Canada during the late 1980s cannot be completely attributed to reduced harvest. Even so, we do not believe the analyses support the conclusion

that survival of female mallards increased continent wide in the late 1980s.

MANAGEMENT IMPLICATIONS

Despite the general inability to establish a functional relationship between harvest and mallard survival, restrictive harvest regulations have been implemented continent wide in response to low numbers of mallards. Continental harvest regulations are consistent with the principle of parsimony; harvest regulations are not more detailed than justified by the data (J. D. Nichols, Patuxent Wildl. Res. Cent., Laurel, Md., pers. commun.). Philosophically, however, this practice is equivalent to acceptance of the null hypothesis in statistics. We do not believe that analyses with low statistical power provide a sound justification for applying restrictive regulations to all classes of mallards across all flyways.

Restrictive regulations combined with low duck population numbers are associated with a steady decline in hunter participation through the 1980s (Martin et al. 1990). The potential advantages of conservative harvest management (i.e., restrictive harvest regulations) must be weighed against the decline in numbers of hunters potentially associated with such management.

Restrictive harvest regulations usually are implemented in response to declining populations (Nichols and Johnson 1989), resulting in substantial confounding of harvest and density-dependent effects on survival. Only when harvest is manipulated in an experimental fashion will it be possible to separate the numerous confounding factors that have existed in previous assessments of the relationship between harvest and survival (Nichols and Johnson 1989). Such manipulations of harvest regulations have been suggested in the past (Anderson and Burnham 1976, Burnham et al. 1984, Anderson et al. 1987, Nichols and Johnson 1989) and we renew the call for experimental harvest manipulations here.

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HUNTING AND MALLARD SURVIVAL: A REPLY

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Abstract: Sedinger and Rexstad (1994) objected to the model selection procedures in our analysis of mallard (*Anas platyrhynchos*) survival (Smith and Reynolds 1992), especially in our analysis of the additive and compensatory nature of hunting mortality. Sedinger and Rexstad (1994) disagreed with pooling data over age-sex classes and the averaging over banding reference areas that was part of our ultrastructural analysis. We believe these objections are unfounded and are based on a misinterpretation of the principle of parsimony. Sedinger and Rexstad (1994) proposed the addition of a density-dependent term to the ultrastructural model to explain observed changes in survival patterns. Their analysis suggested, as we also believe, that density dependence may be a viable alternative. Certainly density-dependent mortality should be investigated further using appropriate mechanistic models. However, a comparison of the 2 models indicates that the hunting hypothesis fits historical data better, and therefore is the more appropriate model. We disagree with Sedinger and Rexstad's (1994) call for implementing differing management actions in the absence of supporting information.

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Key words: *Anas platyrhynchos*, density dependence, harvest, hunting, mallard, survival, ultrastructural model.

The purpose of our Reply is to respond to the comments of Sedinger and Rexstad (1994), in which they objected to our pooling of data over age-sex classes and averaging over banding reference areas that were part of our ultrastructural analysis (Smith and Reynolds 1992). We examine the principle of parsimony and how it should be used in model selection and present an additional analysis that considers whether pooling over reference areas was appropriate. We also correct an error in our 1992 paper (Smith and Reynolds 1992).

Much of the discussion by Sedinger and Rexstad (1994) involved their interpretation of the principle of parsimony. Appropriate model selection is critical for valid inference when analyzing data (Burnham and Anderson 1992). Fundamental to this issue is the concept that data will only support limited inference. A model should be selected that has enough structure and parameters to account for the variability in the data but not so much structure or so many parameters that precision is unnecessarily lost and effects that are not justified by the data are inferred.

For the ultrastructural model (Anderson et al. 1982), the relevant question is whether data for various age and sex classes and reference areas should be pooled. The principle of parsimony supports pooling when data do not support ad-

ditional structure or additional effects. In the absence of other biological information a series of models ranging from the most specific to the most general are analyzed. The model with the fewest parameters that adequately describes the data is chosen; more specific models do not explain the observed variation any better.

Sedinger and Rexstad (1994) argued that the model we selected was underparameterized, which led to inappropriate pooling and biased estimates. We disagree with their assessment and their interpretation of parsimony. Their misinterpretation forms the basis for their objections to our procedures of pooling age and sex classes and averaging across reference areas. It also is the crux of their argument about statistical power and how likely their density-dependent model is as an alternative explanation to the hunting model.

For the ultrastructural model (Smith and Reynolds 1992) no compelling evidence suggested that density-dependent mechanisms that likely regulated the compensatory response to hunting were acting differently among age and sex classes or reference areas. Differences existed in the geographical distribution of recoveries and in recovery, harvest, and survival rates, as we noted, but these should not be confused with differences in compensatory processes. Lacking any previous knowledge about differences

Table 1. Goodness-of-fit of estimates of R by reference area.

Reference area	χ^2	df
031	120.46	129
041	174.33	172
051	142.44	149
061	188.08	177
101	184.61	179
131-133	171.52	176
\bar{x}		

^a After Anderson and Henny (1991).
^b All age-sex classes combined.
 kill rates is R (Barker et al. 1991).

among ages, sexes, or selection process established. To conduct an analysis based on the belief that ≥ 1 of the classes had any evidence of such a process, the a priori belief is strong enough to conduct the analysis.

Sedinger and Rexstad (1994) argued that their analysis of power and error rates for analyses of Smith and Reynolds (1992) especially as related to banding reference areas. Their objection to conducting this analysis in California as being different from other regions would provide a rationale for California to have hunting regulations different from other regions. Sedinger and Rexstad (1994: 576) stated: "Despite the fact that we cannot establish a functional relationship between harvest and mallard survival, our regulations have been widely in response to local conditions." They continued: "Philosophically, this practice is equivalent to the null hypothesis in statistical analyses with low statistical power. A sound justification for applying the same regulations to all classes of data is not possible." We argue that the null hypothesis, but rather a certain probability of occurrence based on available data. Their objection suggested that management actions differently if they were different. Different management actions should not be applied when there is no evidence with relevant data. It is reasonable to build patterns of management in the absence of relevant information.



Table 1. Goodness-of-fit of the ultrastructural model and estimates of R by reference area^a for mallards, 1979-88.

Reference area	Model goodness of fit				
	χ^2	df	P	R ^b	SE(R)
031	120.46	129	0.691	-0.001	2.924
041	174.33	172	0.440	3.970	0.934
051	142.44	149	0.616	4.346	1.508
061	188.08	177	0.272	3.049	1.150
101	184.61	179	0.374	1.862	0.816
131-133	171.52	176	0.585	2.941	1.121
\bar{x}				2.694	0.644

^a After Anderson and Henny (1972).
^b All age-sex classes combined. The relationship between survival and kill rates is R (Barker et al. 1991).

among ages, sexes, or areas, we let the model selection process establish appropriate pooling. To conduct an analysis on the basis of an a priori belief that ≥ 1 of these factors differ without any evidence of such differences is improper. If the a priori belief is strong, then there is no need to conduct the analysis in the first place.

Sedinger and Rexstad (1994) conducted an analysis of power and discussed the lack of power for analyses of Smith and Reynolds (1992), especially as related to differences among reference areas. Their apparent motivation for conducting this analysis was to identify California as being different from other areas, which would provide a rationale for permitting California to have hunting regulations that differ from other regions. Sedinger and Rexstad (1994:576) stated: "Despite the general inability to establish a functional relationship between harvest and mallard survival, restrictive harvest regulations have been implemented continent wide in response to low numbers of mallards." They continued: "Philosophically, however, this practice is equivalent to acceptance of the null hypothesis in statistics. We do not believe that analyses with low statistical power provide a sound justification for applying restrictive regulations to all classes of mallards across all flyways." We argue that one never accepts the null hypothesis, but rather fails to reject it with a certain probability of being correct, given the available data. Their analyses and arguments suggested that managers should manage areas differently if they believe that the areas are different. Different management tactics should not be applied when their use cannot be justified with relevant data. We do not believe it reasonable to build patterns of variation in the absence of relevant information.

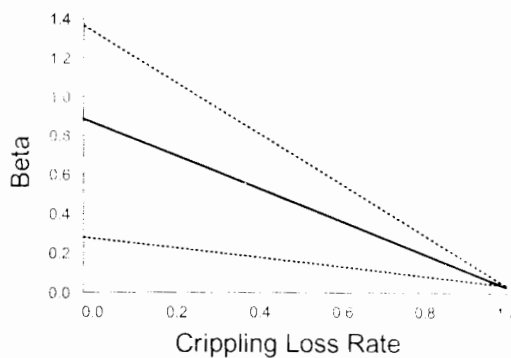


Fig. 1. The relationship between survival and kill rates, β , (Anderson et al. 1982), and upper and lower 95% confidence interval boundaries plotted as a function of crippling loss for mallards, 1979-88.

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REEVALUATION OF OUR ULTRASTRUCTURAL ANALYSIS

Reviewing analyses we conducted for our 1992 manuscript we found an error in programming of the EST.FOR subroutine for program SURVIV (White 1983) for the ultrastructural analysis. The correction did not change our conclusions. The model is $S_i = S_0(1 - \beta K_i)$, where S_i = survival in year i , S_0 = survival in the absence of hunting, K_i = kill rate in year i ($K_i = f_i / (1 - u)\lambda$, where f_i = recovery rate in year i , u = crippling loss, and λ = band reporting rate), and β = the slope of the linear relationship between survival rate and the respective kill rate. For analysis, the model was reparameterized as $S_i = S_0(1 - R f_i)$, where $R = \beta / (1 - u)\lambda$ (Barker et al. 1991). Adult male recovery rates were mistakenly substituted for adult female recovery rates in the ultrastructural relationship defining adult female survival. The correct analysis resulted in a slightly higher value (Table 1) for the average value of R in Table 6 of Smith and Reynolds (1992:313). No differences were observed for the values of R among reference areas (program CONTRAST, Hines and Sauer 1989, $\chi^2 = 4.85$, 5 df, $P = 0.43$). A revised figure of β as a function of crippling loss, u (Fig. 1), still leads to the rejection of the completely compensatory model over all values of u .

To formally evaluate whether averaging across reference areas was appropriate, we conducted

Table 2. Akaike Information Criterion (AIC^a) values for ultrastructural models for mallards. Values of R^b were calculated for the most specific model and for a series of reduced models. Recovery rates were estimated annually for each age-sex class by reference area. Survival in the absence of hunting was estimated for each age-sex class by reference area.

Model	AIC
Specific - R sex/age/areas separately	7,725.73
M _{A=1} ^c , areas separate	7,715.76
M _{A=1} , areas pooled	7,708.87
F _{A=1} , areas separate	7,727.96
F _{A=1} , areas pooled	7,722.65
M _{A=1} , F _{A=1} , areas separate	7,717.99
M _{A=1} , F _{A=1} , areas pooled	7,705.78
M _{A=1} = F _{A=1} , areas separate	7,710.63
M _{A=1} = F _{A=1} , areas pooled	7,704.68

^a Burnham and Anderson (1992).

^b The relationship between survival and kill rates is R (Barker et al. 1991).

^c Value of R for adult and immature birds constrained equal.

a new analysis using the ultrastructural model. We combined all reference areas (031, 041, 051, 061, 101, and 131+) into a single analysis. The most specific model estimated annual recovery rates, survival in the absence of hunting, and R separately for each age-sex class in each area. A hierarchical series of reduced models combining ages, sexes, and areas for the estimation of R were compared. We were unable to conduct this analysis in 1992 due to the limited computing resources available at that time (the most specific model has 312 parameters).

The Akaike Information Criterion (AIC) (Burnham and Anderson 1992) was used to choose among models. The most reduced model (i.e., where R was estimated pooling over sex, age, and reference area; S₀ was estimated for each age-sex class and area; and f was estimated for each age-sex class, year, and area) was the model with the lowest AIC value (Table 2). We conclude that a single R is most appropriately estimated from the data. This analysis yielded a value of R = 2.81 (SE[R] = 0.443); a value that is somewhat greater than the average value of R = 2.69 (SE[R] = 0.644) (Table 1). There is some evidence that the heterogeneity within the data for females is not well explained.

REVIEW OF SEDINGER AND REXSTAD ANALYSIS

Sedinger and Rexstad (1994) pooled males from reference areas 041, 051, and 061 prior to analysis, and then compared this combination to males in area 101. This pooling was inappro-

appropriate because our previous analyses suggested that recovery rates differed among reference areas. In a formal test of the pooling we constructed the equivalent model and compared it with the most specific model with recovery rates specified by age, sex, area, and year. The AIC value (7,768.69) for the pooled data model was greater than that for the specific model (7,725.73). Inappropriate pooling can result in precise but biased estimates. Inferences from subsequent statistical tests also could be incorrect.

The purpose of our manuscript (Smith and Reynolds 1992) was not intended to be a comparison of northern California versus Prairie Canada. To reduce the analysis to such a comparison ignores our previous continental analyses that included Quebec and Wisconsin. Subsequently we tested if a model with R estimated for northern California (area 101) and for the other areas pooled fit the data better than the model for all areas pooled. The AICs for these analyses (model with a different R for Calif., sexes separate and ages pooled AIC = 7,707.79; model with a different R for Calif., sexes and ages pooled AIC = 7,705.95) suggest that the value of R for northern California did not differ from that of the other areas (most reduced model AIC = 7,704.68; Table 2).

Sedinger and Rexstad (1994) proposed density dependence as an alternative explanation for the observed changes in survival rates. Their explanation is not as likely as the ultrastructural model involving only hunting mortality on the basis of data used. In only 1 of the 12 comparisons presented is the AIC for the density-dependent model less than the AIC for the ultrastructural model. The hunting model fits the data better than does the density-dependence model.

CONCLUSION

Sedinger and Rexstad's (1994) analysis has heightened our awareness that density dependence may be an alternative explanation for the pattern of changes observed in survival. However, we prefer to incorporate density as a determinant of survival differently. The Sedinger and Rexstad (1994) model is somewhat confusing. We do not understand why it was necessary to include both a density-dependent (α) and a hunting (R) portion. A response to hunting probably cannot occur other than through density-dependent mechanisms. Also, the Sedinger and

Rexstad (1994) model values. The high value regression relationship Rexstad (1994) did not show *n* birds/unit of limiting the span of years are shown was that the May declined from never measured. Different from population unaware of any appropriate and correct regions. We believe the density-dependence Rexstad (1994) and independent discussion in Both the hunting and (1994) density-dependence and not (1993). Phenomenological relationships and stochastic models, do not biological mechanism examining more density dependence modeled.

Sedinger and Rexstad hunter participation discussion about population with the need for experimental that political and social experimentation diverse means of gaining resource management

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Rexstad (1994) model was not robust to outlier values. The high value for 1979 was driving the regression relationship. In addition, Sedinger and Rexstad (1994) did not show that density (i.e., n birds/unit of limiting resource) decreased over the span of years analyzed. All that could be shown was that the abundance of mallards in May declined from 1979–88; resources were never measured. Density is fundamentally different from population numbers, and we are unaware of any measures of density that are appropriate and consistent among geographic regions. We believe that we can improve upon the density-dependent analysis of Sedinger and Rexstad (1994) and on our previous density-dependent discussion in Smith and Reynolds (1992). Both the hunting and the Sedinger and Rexstad (1994) density-dependent models are phenomenological and not mechanistic (Johnson et al. 1993). Phenomenological models define statistical relationships and, compared with mechanistic models, do not incorporate underlying biological mechanisms. We currently are examining more mechanistic models where density dependence can be more realistically modeled.

Sedinger and Rexstad's (1994) discussion about hunter participation was not germane to the discussion about population dynamics. We agree with the need for experimentation but recognize that political and sociological constraints make experimentation difficult. A promising alternative means of gaining knowledge is adaptive resource management (Johnson et al. 1993).

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