

## HUNTING AND MALLARD SURVIVAL, 1979-88

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**Abstract:** A recent pattern of changes in hunting regulations offered a unique opportunity to further investigate the relationship between hunting and survival rates of mallards (*Anas platyrhynchos*). Consequently, we used 2 approaches to study the effects of hunting on survival of mallards banded on the Canadian prairie and the northcentral United States. First we compared recovery and survival rates during 1979-84, when regulations were stable and relatively liberal, with rates during 1985-88, when regulations were restrictive. Recovery rates declined between the 2 periods, suggesting that harvest rates declined. Survival rates for all age-sex classes were greater during the second period. Second, we analyzed the additive and compensatory nature of hunting mortality, for the same data, using the ultrastructural model of Anderson et al. (1982), as extended by Barker et al. (1991). We were able to reject both the completely additive and completely compensatory models for the years 1979-88, although our rejection of the compensatory model was much stronger. We conclude that, under certain conditions, restrictive regulations can successfully increase survival rates of mallards.

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Anderson and Burnham (1976) specified 2 hypotheses that represent extremes of the effect of hunting on annual survival rates. The first hypothesis assumes that hunting mortality is additive to other forms of mortality during the rest of the year. The second hypothesis assumes that as hunting mortality increases, there is a compensatory decrease in non-hunting mortality. With complete compensation, survival rate remains constant as long as hunting mortality is below some threshold. At harvest rates above the threshold, some portion of hunting mortality becomes additive.

There have been a number of approaches to testing predictions from the 2 hypotheses (summarized in Nichols et al. 1984). Nichols and Hines (1983), Caswell et al. (1985), and Trost (1987) suggested that, for some age-sex classes, harvest and survival were inversely related. Nevertheless, the bulk of available evidence tends to favor the compensatory, rather than the additive, hypothesis (Anderson and Burnham 1976, Rogers et al. 1979, Anderson et al. 1982, Nichols and Hines 1983, Burnham and Anderson 1984, Burnham et al. 1984, Nichols et al. 1984, Trost 1987).

From 1979 to 1984, hunting regulations were held constant at relatively liberal levels (Brace et al. 1987). In 1985 regulations became restrictive and in subsequent years even more restrictive. This pattern of regulations, and accom-

panying banding and recovery data, presented an opportunity to investigate the relationship between harvest and survival rates. This opportunity, although unplanned, fits the pattern of manipulation of hunting regulations to produce substantial variation in hunting mortality proposed by Anderson et al. (1987), Conroy and Kremenetz (1990), Nichols (1991), and others, to test the effects of hunting on duck population dynamics.

We tested whether hunting affected mallard survival rates using banding and recovery data during 1979-89. First, we compared survival and band-recovery rates between 1979-84 and 1985-88. Second, we used the procedures described in Anderson et al. (1982), Burnham et al. (1984), and Barker et al. (1991) to assess whether harvest was additive or compensatory.

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### METHODS

Mallard banding and recovery data for 1979-89 were obtained from the U.S. Fish and Wildlife Service, Bird Banding Laboratory. We used only records of normal, wild birds banded during July-September and shot or found dead from 1 September through 15 February. Bandings and recoveries were tallied by minor reference area (Fig. 1, Anderson and Henny 1972). We examined minor reference areas with bandings



Fig. 1. Reference areas.

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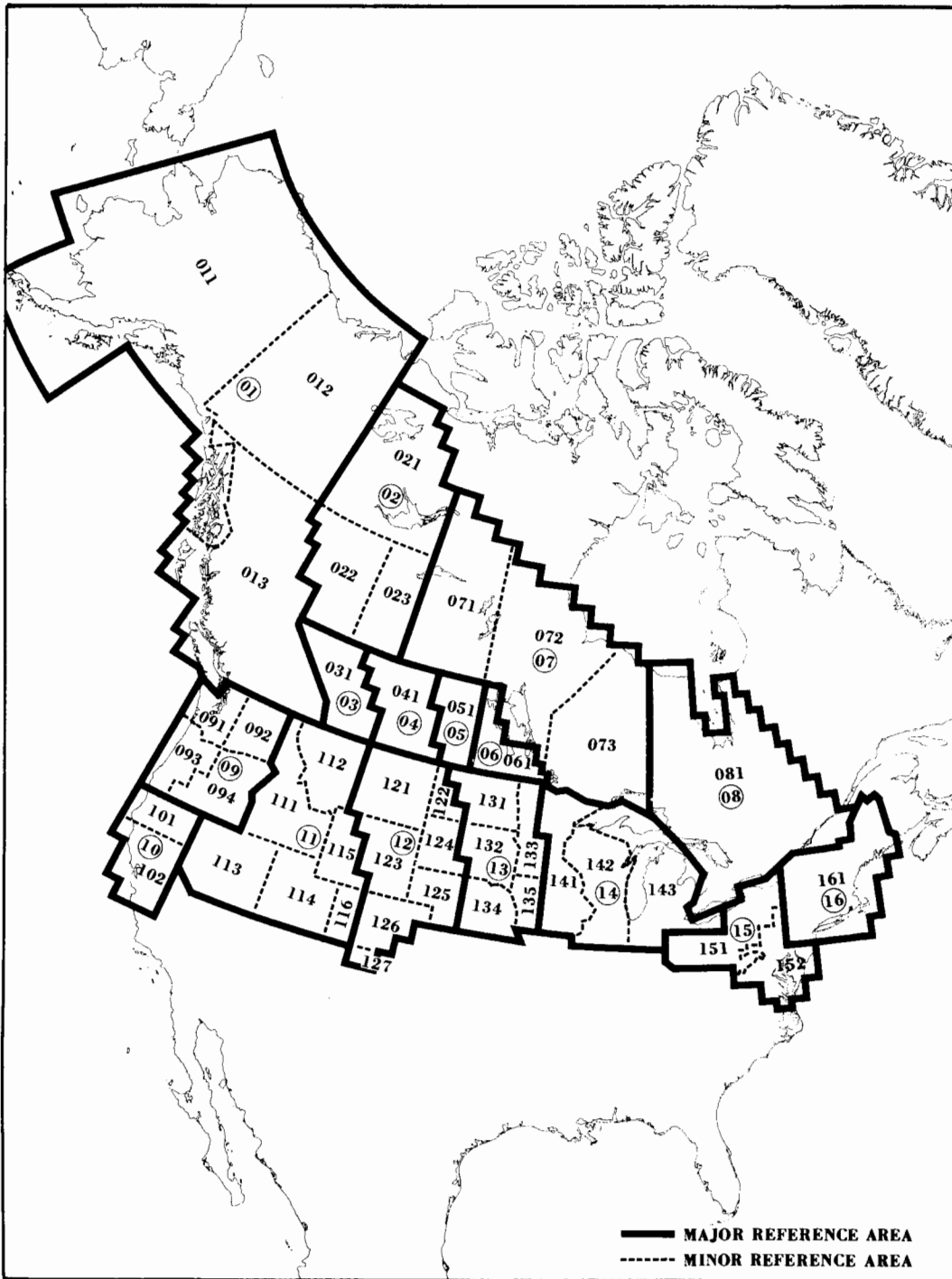


Fig. 1. Reference areas for breeding mallards in North America (Anderson and Henny 1972). Circled numbers are major reference areas.

of all age-sex classes (adult and immature birds of both sexes) in all years and with  $\geq 200$  adults banded each year. Minor reference areas 131, 132, and 133 were combined to overcome the problems of missing years and inadequate sample sizes.

Annual recovery and survival rates were estimated for minor reference areas under model  $H_1$  (Brownie et al. 1985) using program SURVIV (White 1983). Recovery and survival rates are assumed to be year-specific using this model. Our hypothesis was that recovery rates were higher, and survival was lower during 1979-84 than during 1985-89. When goodness-of-fit tests indicated that model  $H_1$  did not fit, data were analyzed using program BROWNIE (Brownie et al. 1985). We also tested the hypothesis (model  $H_{02}$ ) that survival during each of these periods was constant. We tested our hypotheses using a series of hierarchical models and likelihood ratio tests. Overall tests were made by summing Chi-square values and associated degrees of freedom across minor reference areas. Akaike's Information Criterion (AIC) was used for selecting the appropriate model (Burnham and Anderson 1992). The constant survival rate for 1979-84 was compared to the constant survival rate for 1985-88 for reference areas where the reduced model was appropriate.

Survival rates were compared using Z-statistics, and the statistics then were pooled using the composite Z-test described by Anderson and Burnham (1976). Annual estimates of recovery and survival rates from the appropriate models were averaged for each period and then compared using 1-tailed Z-test procedures.

We used Barker et al.'s (1991) 2-age extension of the model of Anderson et al. (1982) and Burnham et al. (1984) to examine the effect of hunting on annual survival rates. The model is  $S_i = S_o(1 - \beta K_i)$  and  $S'_i = S'_o(1 - \beta' K'_i)$  where  $S_i$  and  $S'_i$  = adult and immature survival in year  $i$ ;  $S_o$  and  $S'_o$  = adult and immature survival rates in the absence of hunting;  $K_i$  and  $K'_i$  = adult and immature kill rate in year  $i$  (i.e., the proportion of birds alive at banding in year  $i$  killed by hunters during hunting season  $i$ ); and  $\beta$  and  $\beta'$  = the slope of the linear relationship between adult and immature survival rates and the respective kill rate. The annual kill rate ( $K_i$ ) can be estimated as

$$\hat{K}_i = \frac{\hat{f}_i}{(1 - \hat{u})\hat{\lambda}}$$

where  $\hat{f}_i$  = band recovery rate,  $\hat{u}$  = crippling loss, and  $\hat{\lambda}$  = band reporting rate. Barker et al. (1991) parameterized the model as  $S_i = S_o(1 - Rf_i)$ , where  $R = \frac{\beta}{(1 - \hat{u})\hat{\lambda}}$ .

Given values of  $u$  and  $\lambda$ ,  $\beta$  can be estimated as  $\hat{\beta} = \hat{R}(1 - \hat{u})\hat{\lambda}$  and

$$\widehat{\text{Var}}(\hat{\beta}) = \hat{R}^2(1 - \hat{u})^2\widehat{\text{Var}}(\hat{\lambda}) + [\hat{\lambda}^2 - \widehat{\text{Var}}(\hat{\lambda})] \\ [(1 - \hat{u})^2\widehat{\text{Var}}(\hat{R}) + \hat{R}^2\widehat{\text{Var}}(\hat{u}) - \\ \widehat{\text{Var}}(\hat{R})\widehat{\text{Var}}(\hat{u})].$$

The null hypothesis for the completely compensatory model is  $H_0: \beta = 0$ , and the test statistic  $Z = (\hat{\beta} - 0)/\widehat{\text{SE}}(\hat{\beta})$ . The null hypothesis for the completely additive model is  $H_0: \beta = 1$ , and the test statistic  $Z = (\hat{\beta} - 1)/\widehat{\text{SE}}(\hat{\beta})$  (Burnham et al. 1984).

We used program SURVIV to estimate  $S_o$ ,  $R$ ,  $f_i$ ,  $S'_o$ ,  $R'$ , and  $f'_i$ .  $R$  and  $R'$  were estimated separately for the periods 1979-84 and 1985-88. Estimates of  $R$  and  $R'$  were restricted to the range (-5, 15). A separate analysis was conducted for each reference area. Within these analyses, parameters for all age-sex classes were estimated simultaneously. We tested age-, sex-, and time-specificity of  $R$  by comparing unconstrained models with the appropriate constrained models using likelihood ratio tests available in SURVIV.

Because reliable estimates of the crippling loss and its precision do not exist, we calculated the value of  $\beta$  over the range of possible crippling loss values. These values were then evaluated as tests of the completely compensatory and additive models.

## RESULTS

### Model Selection

The goodness-of-fit tests (Table 1) indicated that model  $H_{02}$ , with different survival rates for each period, fit all reference areas except male and female mallards in minor reference area 081 ( $P \leq 0.021$ , primarily Que.), and female mallards in minor reference area 142 ( $P = 0.001$ , primarily Wis.). Model  $H_1$  also did not fit for these 3 cases. Subsequent goodness-of-fit tests (program BROWNIE) indicated that model  $H_2$  was appropriate for these cases. Model  $H_2$  is an extension of  $H_1$  with first-year recovery rates differing from those in subsequent years. Because neither model  $H_{02}$  nor  $H_1$  was appropriate, these birds were excluded from the analysis

Table 1. Goodness-of-fit of the survival rates were constant, 1

Reference area <sup>a</sup>	$\chi^2$
031	77.
041	99.
051	86.
061	112.
081	116.
101	101.
131-133	91.
142	86.
Total	771.

<sup>a</sup> After Anderson and Henny (1976).

where survival was assumed constant during 1979-84 and 1985-88 and additive-compensatory hypothesis were included in estimates of recovery and survival rates. Because for these cases, estimates of survival in 1988 and adult survival were not available.

The SURVIV analyses assumed the supposition that survival was constant during the individual periods 1979-84 and 1985-88. All individual tests for constant survival models ( $H_{02}$  Period 1 [survival rates differing for adult and immature birds] for 1979-84),  $H_{02}$  Period 2 [survival rates for 1985-88], and  $H_{02}$  Period 3 [survival rates for 1979-84 and 1985-88]) were conducted.

Table 2. Likelihood ratio tests

Reference area <sup>b</sup>	Sex	Model	
		$\chi^2$	Period
031	M	9.305	1
	F	9.394	1
041	M	15.775	1
	F	11.529	1
051	M	6.614	1
	F	11.109	1
061	M	11.059	2
	F	11.869	1
101	M	13.427	1
	F	8.045	1
131-133	M	5.196	1
	F	14.890	1
142	M	8.482	1
	F	66.858	7
Total	M	69.858	7
	F	66.836	6

<sup>a</sup> Period 1 = 1979-84; Period 2 = 1985-88; Period 3 = 1979-84 and 1985-88.  
<sup>b</sup> After Anderson and Henny (1976).

Table 1. Goodness-of-fit of the model (model  $H_{02}$  Periods 1 and 2) for which recovery rates varied annually and for which survival rates were constant, 1979–84 and 1985–88.

Reference area <sup>a</sup>	M			F		
	$\chi^2$	df	P	$\chi^2$	df	P
031	77.118	89	0.812	85.788	106	0.923
041	99.825	103	0.575	65.321	61	0.334
051	86.083	89	0.573	47.309	53	0.694
061	112.402	101	0.207	65.592	68	0.667
081	116.676	88	0.020	94.454	69	0.021
101	101.313	102	0.505	76.655	72	0.336
131–133	91.683	96	0.610	69.808	72	0.557
142	86.558	86	0.468	109.775	69	0.001
Total	771.658	754	0.320	614.702	570	0.095

<sup>a</sup> After Anderson and Henny (1972); see Fig. 1.

where survival was assumed constant during 1979–84 and 1985–88 and from tests of the additive-compensatory hypotheses. However, they were included in estimating average recovery and survival rates. Because model  $H_2$  was used for these cases, estimates of adult and immature survival in 1988 and adult recovery rates in 1979 were not available.

The SURVIV analyses supported our a priori supposition that survival was constant during the individual periods 1979–84 and 1985–88. All individual tests for comparison of reduced models ( $H_{02}$  Period 1 [survival rates constant but differing for adult and immature age–sex classes for 1979–84],  $H_{02}$  Period 2 [the same model but for 1985–88], and  $H_{02}$  Periods 1 and 2 [the pre-

vious 2 models merged into 1 model with different survival parameters for the 2 periods], vs. model  $H_1$ ) were not significant ( $P > 0.05$ ) (Table 2). However, the composite test suggested that model  $H_{02}$  Period 2 fit poorly for females. In part, this was due to the near significance of reference area 101 (northern Calif., an area outside the geographic range of the other reference areas [Fig. 1]). Without this area, the composite test was not significant ( $\chi^2_{30} = 38.62$ ,  $P = 0.13$ ). The composite test of model  $H_1$  versus model  $H_{02}$  Periods 1 and 2 for females was significant ( $\chi^2_{96} = 121.61$ ,  $P = 0.04$ ), suggesting that survival was not constant for Period 2 females. However, the AIC analysis supported the selection of  $H_{02}$  Periods 1 and 2 for both males (model  $H_1 =$

Table 2. Likelihood ratio tests among models used in the analyses of mallard recovery and survival rates, 1979–88.

Reference area <sup>b</sup>	Sex	Model $H_1$ vs. model $H_{02}$ Period 1 <sup>a</sup>			Model $H_1$ vs. model $H_{02}$ Period 2 <sup>a</sup>			Model $H_1$ vs. model $H_{02}$ Periods 1 and 2			Model $H_{02}$ Periods 1 and 2 vs. model All Equal		
		$\chi^2$	df	P	$\chi^2$	df	P	$\chi^2$	df	P	$\chi^2$	df	P
031	M	9.305	10	0.503	3.074	6	0.800	11.156	16	0.800	0.164	2	0.921
	F	9.394	10	0.495	11.486	6	0.075	20.849	16	0.184	2.397	2	0.302
041	M	15.775	10	0.106	2.753	6	0.839	19.271	16	0.255	12.224	2	0.002
	F	11.529	10	0.318	5.012	6	0.542	22.897	16	0.117	4.531	2	0.104
051	M	6.614	10	0.761	1.929	6	0.926	8.281	16	0.940	5.621	2	0.060
	F	11.109	10	0.349	4.129	6	0.659	15.533	16	0.486	3.268	2	0.195
061	M	11.059	10	0.353	10.066	6	0.122	21.358	16	0.165	2.555	2	0.279
	F	11.869	10	0.294	7.600	6	0.269	19.233	16	0.257	7.036	2	0.030
101	M	13.427	10	0.201	4.966	6	0.548	18.623	16	0.289	2.525	2	0.283
	F	8.045	10	0.625	12.482	6	0.052	20.496	16	0.199	2.527	2	0.283
131–133	M	5.196	10	0.878	1.668	6	0.948	7.008	16	0.973	5.553	2	0.062
	F	14.890	10	0.136	10.400	6	0.109	22.605	16	0.125	0.584	2	0.747
142	M	8.482	10	0.582	6.757	6	0.344	15.992	16	0.454	1.575	2	0.455
	F	69.858	70	0.482	31.213	42	0.889	101.689	112	0.747	30.217	14	0.001
Total	M	69.858	70	0.482	31.213	42	0.889	101.689	112	0.747	30.217	14	0.001
	F	66.836	60	0.254	51.109	36	0.049	121.613	96	0.040	20.343	12	0.061

<sup>a</sup> Period 1 = 1979–84; Period 2 = 1985–88.

<sup>b</sup> After Anderson and Henny (1972); see Fig. 1.

Table 3. Mallard recovery rates<sup>a</sup> during years of liberal regulations (1979–84) and years of restrictive regulations (1985–88).

Sex Age	Reference area <sup>b</sup>	$\hat{r}(SE)$ 1979–84	$\hat{r}(SE)$ 1985–88	Test statistics	
				Z	P
<b>Male</b>					
Adult	031 <sup>c</sup>	0.0425 (0.0017)	0.0368 (0.0015)	2.514	0.0060
	041 <sup>c</sup>	0.0496 (0.0012)	0.0326 (0.0010)	10.883	<0.0001
	051 <sup>c</sup>	0.0524 (0.0072)	0.0373 (0.0022)	2.006	0.0220
	061 <sup>c</sup>	0.0580 (0.0012)	0.0427 (0.0026)	5.343	<0.0001
	081 <sup>d</sup>	0.0647 (0.0048)	0.0433 (0.0045)	3.253	0.0006
	101 <sup>c</sup>	0.0693 (0.0020)	0.0569 (0.0026)	3.780	<0.0001
	131–133 <sup>e</sup>	0.0579 (0.0018)	0.0426 (0.0016)	6.353	<0.0001
	142 <sup>e</sup>	0.0738 (0.0031)	0.0432 (0.0027)	7.444	<0.0001
	Mean	0.0585 (0.0012)	0.0419 (0.0009)	14.699 <sup>e</sup>	<0.0001
	Immature	031 <sup>c</sup>	0.0557 (0.0046)	0.0444 (0.0041)	1.835
041 <sup>c</sup>		0.0591 (0.0025)	0.0463 (0.0023)	3.768	0.0001
051 <sup>c</sup>		0.0670 (0.0051)	0.0497 (0.0040)	2.669	0.0038
061 <sup>c</sup>		0.0868 (0.0030)	0.0650 (0.0050)	3.739	0.0001
081 <sup>d</sup>		0.1081 (0.0024)	0.0890 (0.0026)	5.398	<0.0001
101 <sup>c</sup>		0.1204 (0.0043)	0.1205 (0.0064)	-0.013	0.4948
131–133 <sup>e</sup>		0.0889 (0.0032)	0.0728 (0.0035)	3.395	0.0003
142 <sup>e</sup>		0.1269 (0.0034)	0.0846 (0.0037)	8.418	<0.0001
Mean		0.0891 (0.0013)	0.0715 (0.0015)	10.326 <sup>e</sup>	<0.0001
<b>Female</b>					
Adult	031 <sup>c</sup>	0.0313 (0.0047)	0.0913 (0.0031)	2.131	0.0165
	041 <sup>c</sup>	0.0268 (0.0025)	0.0165 (0.0017)	3.407	0.0003
	051 <sup>c</sup>	0.0279 (0.0029)	0.0196 (0.0026)	2.131	0.0165
	061 <sup>c</sup>	0.0361 (0.0017)	0.0198 (0.0017)	6.780	<0.0001
	081 <sup>d</sup>	0.0490 (0.0056)	0.0416 (0.0054)	0.951	0.1707
	101 <sup>c</sup>	0.0462 (0.0023)	0.0316 (0.0025)	4.298	<0.0001
	131–133 <sup>e</sup>	0.0386 (0.0019)	0.0221 (0.0013)	7.167	<0.0001
	142 <sup>d</sup>	0.0457 (0.0041)	0.0275 (0.0045)	2.990	0.0014
	Mean	0.0377 (0.0012)	0.0248 (0.0011)	10.555 <sup>e</sup>	<0.0001
	Immature	031 <sup>c</sup>	0.0376 (0.0049)	0.0317 (0.0047)	0.869
041 <sup>c</sup>		0.0457 (0.0026)	0.0278 (0.0023)	5.157	<0.0001
051 <sup>c</sup>		0.0463 (0.0039)	0.0415 (0.0044)	0.816	0.2071
061 <sup>c</sup>		0.0639 (0.0032)	0.0319 (0.0041)	6.153	<0.0001
081 <sup>d</sup>		0.0926 (0.0026)	0.0804 (0.0028)	3.193	0.0007
101 <sup>c</sup>		0.0877 (0.0041)	0.0662 (0.0052)	3.247	0.0006
131–133 <sup>e</sup>		0.0602 (0.0026)	0.0361 (0.0025)	6.682	<0.0001
142 <sup>d</sup>		0.0951 (0.0029)	0.0599 (0.0031)	8.292	<0.0001
Mean		0.0611 (0.0012)	0.0469 (0.0013)	12.165 <sup>e</sup>	<0.0001

<sup>a</sup> Means of annual estimates from model H<sub>1</sub> or H<sub>2</sub>.  
<sup>b</sup> After Anderson and Henny (1972); see Fig. 1.  
<sup>c</sup> Model H<sub>1</sub>.  
<sup>d</sup> Model H<sub>2</sub>.  
<sup>e</sup> Composite Z-test.

4,652.8, model H<sub>02</sub> Period 1 = 4,594.2, model H<sub>02</sub> Period 2 = 4,605.3, and model H<sub>02</sub> Periods 1 and 2 = 4,546.5) and females (model H<sub>1</sub> = 3,247.5, model H<sub>02</sub> Period 1 = 3,194.3, model H<sub>02</sub> Period 2 = 3,226.6, and model H<sub>02</sub> Periods 1 and 2 = 3,177.1) as the appropriate model for the analysis.

The composite test of model H<sub>02</sub> Periods 1 and 2 versus the model in which survival rates for each age-sex class were constant from 1979–88 (model All Equal) provided evidence that survival rates for males changed over the 2 periods of study. Survival rates increased in ref-

erence area 041 for males and in 061 for females. An increase was suggested for males in areas 051 and 131–133, and for females in 041 (P = 0.10).

**Recovery and Survival Rates**

Recovery rates declined between the 2 periods in all reference areas for all age-sex classes, except for immature males in reference area 101, adult females in area 081, and immature females in areas 031 and 051 (Table 3). All composite Z-statistics for recovery rates were highly significant.

Table 4. Mallard survival rates<sup>a</sup> during

Sex Age	Reference area <sup>b</sup>	Survival rate
<b>Male</b>		
Adult	031	0.01
	041	0.01
	051	0.01
	061	0.01
	101	0.01
	131–133	0.01
	Mean	0.01
Immature	031	0.01
	041	0.01
	051	0.01
	061	0.01
	Mean	0.01
<b>Female</b>		
Adult	031	0.01
	041	0.01
	051	0.01
	061	0.01
	Mean	0.01
Immature	031	0.01
	041	0.01
	051	0.01
	061	0.01
	Mean	0.01

<sup>a</sup> Survival rates were assumed constant.  
<sup>b</sup> After Anderson and Henny (1972).  
<sup>c</sup> Composite Z-test.

Adult male survival rates were constant with periods, increased (P < 0.05) in 041 (P < 0.12), of the 7 reference areas. Composite Z was highly significant (P < 0.0001, Table 4). No increases (P > 0.05) were observed in immature males occurring in reference areas, although there were increases (P < 0.11) in reference areas 051 and 131–133. The composite Z-test was highly significant (P < 0.0001) for males, increases in survival rates were observed in 031 (P < 0.01), and possibly 051 (P < 0.05) in reference areas. The composite Z-test was highly significant (P = 0.002). Survival rates for immature males increased in areas 031 (P < 0.08), and overall (P < 0.0001). In the second analysis, survival rates were estimated annually.

Table 4. Mallard survival rates<sup>a</sup> during years of liberal regulations (1979–84) and restrictive regulations (1985–88).

Sex Age	Reference area <sup>b</sup>	$\hat{S}_i$ (SE) 1979–84	$\hat{S}_i$ (SE) 1985–88	Covariance	Test statistics		
					Z	P	
<b>Male</b>							
Adult	031	0.680 (0.012)	0.676 (0.019)	-0.00005052	0.1882	0.5746	
	041	0.673 (0.007)	0.728 (0.014)	-0.00002668	-3.2422	0.0006	
	051	0.654 (0.011)	0.722 (0.025)	-0.00005650	-2.3038	0.0106	
	061	0.636 (0.007)	0.665 (0.021)	-0.00003168	-1.2437	0.1068	
	101	0.649 (0.010)	0.656 (0.019)	0.00004917	-0.2860	0.3874	
	131–133	0.639 (0.010)	0.685 (0.017)	-0.00004090	-2.1261	0.0167	
	142	0.593 (0.013)	0.630 (0.025)	-0.00006707	-1.2134	0.1125	
	Mean	0.646 (0.004)	0.679 (0.008)		-3.8654	0.0001	
	Immature	031	0.650 (0.043)	0.676 (0.066)	0.00005203	-0.3399	0.3670
		041	0.650 (0.025)	0.718 (0.041)	0.00003274	-1.5422	0.0615
051		0.582 (0.033)	0.627 (0.066)	0.00002990	-0.6031	0.2732	
061		0.558 (0.021)	0.641 (0.062)	0.00002117	-1.2664	0.1027	
101		0.602 (0.025)	0.521 (0.046)	0.00002724	1.5343	0.9375	
131–133		0.573 (0.024)	0.641 (0.045)	0.00003057	-1.3381	0.0904	
142		0.511 (0.024)	0.545 (0.049)	0.00004753	-0.6460	0.2591	
Mean		0.589 (0.011)	0.624 (0.021)		-1.5880	0.0559	
<b>Female</b>							
Adult	031	0.595 (0.041)	0.563 (0.069)	-0.00046661	0.3665	0.6430	
	041	0.602 (0.022)	0.614 (0.037)	-0.00020232	-0.2536	0.3999	
	051	0.567 (0.026)	0.652 (0.055)	-0.00033380	-1.2887	0.0988	
	061	0.537 (0.016)	0.655 (0.043)	-0.00014735	-2.4771	0.0066	
	101	0.542 (0.016)	0.590 (0.034)	-0.00011223	-1.1947	0.1161	
	131–133	0.542 (0.016)	0.562 (0.025)	-0.00007510	-0.4720	0.3185	
	Mean	0.565 (0.010)	0.606 (0.019)		-2.1717	0.0150	
Immature	031	0.460 (0.077)	0.691 (0.159)	0.00588900	-1.6743	0.0470	
	041	0.600 (0.052)	0.803 (0.090)	0.00042558	-2.0226	0.0216	
	051	0.630 (0.072)	0.846 (0.139)	0.00083053	-1.4271	0.0765	
	061	0.646 (0.046)	0.702 (0.122)	0.00018041	-0.4335	0.3323	
	101	0.594 (0.040)	0.523 (0.078)	0.00004919	0.8105	0.7912	
	131–133	0.613 (0.039)	0.664 (0.067)	0.00009403	-0.6655	0.2529	
	Mean	0.591 (0.023)	0.705 (0.047)		-2.2105	0.0136	

<sup>a</sup> Survival rates were assumed constant within each period and estimated with model H<sub>02</sub>.  
<sup>b</sup> After Anderson and Henny (1972); see Fig. 1.  
<sup>c</sup> Composite Z-test.

Adult male survival rates, for the case where survival was constant within each of the 2 periods, increased ( $P < 0.05$ ) in 3, and possibly 5 ( $P < 0.12$ ), of the 7 reference areas. The composite Z was highly significant ( $P = 0.0001$ ) (Table 4). No increases ( $P > 0.05$ ) in survival of immature males occurred in individual reference areas, although there were marginal increases ( $P < 0.11$ ) in reference areas 041, 061, and 131–133. The composite test suggests biological significance ( $P = 0.06$ ). Among adult females, increases in survival occurred in 1 ( $P = 0.01$ ), and possibly 3 ( $P < 0.12$ ), of the 6 reference areas. The composite Z was highly significant ( $P = 0.002$ ). Survival of immature females increased in areas 031, 041, 051 ( $P < 0.08$ ), and overall ( $P = 0.01$ ).

In the second analysis, where survival rates were estimated annually (model H<sub>1</sub> or H<sub>2</sub>) and

then averaged for each of the time periods (Table 5), adult male survival increased only in reference area 041; however, the composite Z was highly significant ( $P = 0.002$ ). Survival rates in 081 and 131–133 increased marginally ( $P < 0.10$ ). For immature males, the increase in survival in reference area 081 (model H<sub>2</sub>) was significant ( $P = 0.02$ ), as was the composite test ( $P = 0.033$ ). Survival in reference areas 131–133 and 142 increased marginally ( $P < 0.07$  and  $0.10$ , respectively). The composite tests for both adult and immature females were not significant.

### Survival as a Function of Kill Rate

We found no evidence of age-specificity in  $\hat{R}$  for either sex (males  $\chi^2_{18} = 11.654$ ,  $P = 0.865$ ; females  $\chi^2_{18} = 20.267$ ,  $P = 0.318$ ). Using a con-

Table 5. Mallard survival rates<sup>a</sup> during the years of liberal regulations (1979–84) and years of restrictive regulations (1985–88).

Sex Age	Reference area <sup>b</sup>	$\hat{S}(\widehat{SE})$ 1979–84	$\hat{S}(\widehat{SE})$ 1985–88	Covariance	Test statistics	
					Z	P
<b>Male</b>						
Adult	031 <sup>c</sup>	0.678 (0.013)	0.690 (0.024)	-0.000057	-0.3906	0.3481
	041 <sup>c</sup>	0.685 (0.010)	0.731 (0.018)	-0.000065	-1.9301	0.0268
	051 <sup>c</sup>	0.666 (0.013)	0.710 (0.034)	-0.000077	-1.1165	0.1321
	061 <sup>c</sup>	0.638 (0.009)	0.687 (0.043)	-0.000052	-1.0808	0.1399
	081 <sup>d</sup>	0.578 (0.024)	0.682 (0.062)	-0.000577	-1.3974	0.0812
	101 <sup>c</sup>	0.643 (0.012)	0.647 (0.024)	-0.000009	-0.1234	0.4509
	131–133 <sup>c</sup>	0.646 (0.013)	0.683 (0.023)	-0.000063	-1.3023	0.0964
	142 <sup>c</sup>	0.605 (0.026)	0.638 (0.041)	-0.000191	-0.6218	0.2670
	Mean	0.642 (0.006)	0.684 (0.013)		-2.8153 <sup>e</sup>	0.0024
	Immature	031 <sup>c</sup>	0.665 (0.049)	0.685 (0.081)		-0.2074
041 <sup>c</sup>		0.643 (0.126)	0.726 (0.237)		-0.3579	0.3602
051 <sup>c</sup>		0.570 (0.040)	0.654 (0.087)		-0.8753	0.1907
061 <sup>c</sup>		0.565 (0.022)	0.540 (0.073)		0.3245	0.6272
081 <sup>d</sup>		0.474 (0.031)	0.692 (0.098)		-2.1350	0.0164
101 <sup>c</sup>		0.581 (0.027)	0.528 (0.052)		0.9002	0.8160
131–133 <sup>c</sup>		0.571 (0.025)	0.660 (0.052)		-1.5421	0.0615
142 <sup>c</sup>		0.508 (0.026)	0.601 (0.066)		-1.3197	0.0935
Mean		0.572 (0.019)	0.636 (0.039)		-1.8429 <sup>e</sup>	0.0327
<b>Female</b>						
Adult	031 <sup>c</sup>	0.651 (0.071)	0.514 (0.077)	-0.001134	1.1924	0.8835
	041 <sup>c</sup>	0.590 (0.032)	0.613 (0.049)	-0.000667	-0.3455	0.3648
	051 <sup>c</sup>	0.583 (0.046)	0.663 (0.093)	-0.001362	-0.6891	0.2454
	061 <sup>c</sup>	0.532 (0.023)	0.621 (0.058)	-0.000402	-1.2970	0.0973
	081 <sup>d</sup>	0.509 (0.031)	0.595 (0.089)	-0.000376	-0.8775	0.1901
	101 <sup>c</sup>	0.537 (0.020)	0.616 (0.055)	-0.000146	-1.2933	0.0979
	131–133 <sup>c</sup>	0.600 (0.028)	0.553 (0.032)	-0.000202	1.0078	0.8432
	142 <sup>c</sup>	0.520 (0.029)	0.578 (0.072)	-0.000588	-0.6820	0.2476
	Mean	0.565 (0.014)	0.594 (0.024)		-1.0551 <sup>e</sup>	0.1457
	Immature	031 <sup>c</sup>	0.544 (0.121)	0.572 (0.161)		-0.1407
041 <sup>c</sup>		0.608 (0.066)	0.655 (0.084)		-0.4460	0.3278
051 <sup>c</sup>		0.592 (0.088)	0.791 (0.168)		-1.0494	0.1470
061 <sup>c</sup>		0.636 (0.048)	0.688 (0.161)		-0.3066	0.3796
081 <sup>d</sup>		0.490 (0.051)	0.461 (0.075)		0.3232	0.6267
101 <sup>c</sup>		0.606 (0.046)	0.520 (0.084)		0.9001	0.8160
131–133 <sup>c</sup>		0.641 (0.044)	0.634 (0.069)		0.0832	0.5332
142 <sup>c</sup>		0.556 (0.049)	0.572 (0.097)		-0.1518	0.4397
Mean		0.584 (0.024)	0.612 (0.042)		-0.2786 <sup>e</sup>	0.3903

<sup>a</sup> Estimated using model H<sub>1</sub> or H<sub>2</sub> and are means of annual estimates.  
<sup>b</sup> After Anderson and Henny (1972); see Fig. 1.  
<sup>c</sup> Model H<sub>1</sub>.  
<sup>d</sup> Model H<sub>2</sub>.  
<sup>e</sup> Composite Z-test.

strained model with equal  $R$  for the 2 ages, we found no evidence of sex-specificity ( $\chi^2_{12} = 33.276, P = 0.830$ ). The data from all reference areas fit the ultrastructural model of Anderson et al. (1982) as modified by Barker et al. (1991) (Table 6). The parameter  $\hat{R}$  did not change between 1979–84 and 1985–88 (Table 7). We constrained  $R$  to be equal over all age–sex classes and time periods. Values of  $\hat{R}$  did not differ among reference areas (Table 6). All pair-wise comparisons of  $\hat{R}$  using the Bonferroni multiple comparisons procedure were nonsignificant (Sokal and Rohlf 1981:241).

We calculated the values of  $\hat{\beta}$ , and its 95% confidence intervals, over all possible values (0–1) of  $u$ , using  $\hat{\lambda} = 0.3174$  and  $\widehat{SE}(\hat{\lambda}) = 0.0625$  (Nichols et al. 1991). For this simulation we used the formula

$$\widehat{Var}(\hat{\beta}) = (1 - u)\{R^2(\widehat{Var}\hat{\lambda}) + \hat{\lambda}^2(\widehat{Var}\hat{R}) - (\widehat{Var}\hat{\lambda} \widehat{Var}\hat{R})\}$$

We can reject the completely compensatory model over all values of  $u$  (Fig. 2). We also can reject the completely additive model over most reasonable values of  $u$ , although this rejection

Table 6. Goodness-of-fit (G-O-F) and estimates of  $R$  by reference area.

Reference area <sup>a</sup>	Model G-O-F	
	$\chi^2$	df
031	114.46	119
041	166.55	166
051	137.49	144
061	182.18	173
101	180.01	175
131–133	164.41	172
Mean		

<sup>a</sup> After Anderson and Henny (1972).  
<sup>b</sup> All age–sex classes combined.

is not nearly as strong a compensatory model.

DISCUSSION

In order for changes have affected survival demonstrated that changes in affected harvest rates are a reflection of harvest

(Anderson and Burnham) recovery rates can be used harvest rates have changed the reporting rates are Conroy and Blandin (19) was no evidence of change over time or among species. The statistically significant average recovery rates are of mallards in all but 5 study (Table 4) are consistent in harvest between the by Nichols et al. 1984:5

Table 7. The likelihood ratio  $R$  was estimated separately for RALL, where  $R$  was estimated 88.<sup>a</sup>

Reference area <sup>b</sup>	$\chi^2$
031	0.000
041	0.466
051	3.461
061	1.721
101	1.193
131–133	2.311
Total	9.152

<sup>a</sup> All age–sex classes were combined.  
<sup>b</sup> After Anderson and Henny (1972).

Table 6. Goodness-of-fit (G-O-F) of the ultrastructural model and estimates of R by reference area for mallards, 1979-88.

Reference area <sup>a</sup>	Model G-O-F			$\hat{R}^b$	$SE(\hat{R})$
	$\chi^2$	df	P		
031	114.46	119	0.604	0.186	2.886
041	166.55	166	0.477	4.345	0.887
051	137.49	144	0.640	4.406	1.428
061	182.18	173	0.304	2.835	1.156
101	180.01	175	0.385	1.092	0.786
131-133	164.41	172	0.651	2.692	1.157
Mean				2.593	0.634

<sup>a</sup> After Anderson and Henny (1972); see Fig. 1.  
<sup>b</sup> All age-sex classes combined.

is not nearly as strong as is our rejection of the compensatory model.

**DISCUSSION**

In order for changes in hunting intensity to have affected survival rates, it must first be demonstrated that changes in hunting intensity have affected harvest rates. Because recovery rates are a reflection of harvest rates (H),

$$H = \frac{f}{\lambda}$$

(Anderson and Burnham 1976:2), changes in recovery rates can be used to evaluate whether harvest rates have changed. This assumes that the reporting rates are constant through time. Conroy and Blandin (1984) concluded that there was no evidence of changes in reporting rate over time or among species.

The statistically significant decreases in average recovery rates among all age-sex classes of mallards in all but 3 reference areas of our study (Table 4) are consistent with a reduction in harvest between the 2 periods (see discussion by Nichols et al. 1984:544). The U.S. Waterfowl

Table 7. The likelihood ratio test between models R12, where R was estimated separately for 1979-84 and for 1985-88, and RALL, where R was estimated for the complete period 1979-88.<sup>a</sup>

Reference area <sup>b</sup>	$\chi^2$	df	P
031	0.000	1	0.986
041	0.466	1	0.495
051	3.461	1	0.063
061	1.721	1	0.190
101	1.193	1	0.275
131-133	2.311	1	0.129
Total	9.152	6	0.165

<sup>a</sup> All age-sex classes were combined for the analysis.  
<sup>b</sup> After Anderson and Henny (1972); see Fig. 1.

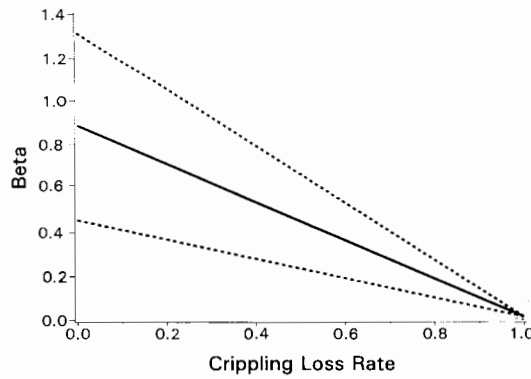


Fig. 2.  $\hat{\beta}$  and upper and lower 95% confidence interval boundaries plotted as a function of crippling loss for mallards, 1979-88.

Harvest Survey (U.S. Fish Wildl. Serv., Preliminary Estimates of Waterfowl Harvest and Hunter Activity, unpubl. data) also shows that mallard harvest declined between the 2 periods.

The likelihood ratio tests (Table 2), the goodness of fit test of model H<sub>02</sub> Periods 1 and 2 (Table 1), and the AIC analysis support our hypothesis that use of a model, with survival independently constant during the stabilized regulations and the post-stabilized regulations periods, was appropriate. By using a model in which survival rates were constant for each of the individual periods, 1979-84 and 1985-88, we calculated survival rates with better precision than if we had used a model in which survival rates were estimated annually.

A more conservative approach, averaging annual survival rates from model H<sub>1</sub> or H<sub>2</sub> for the 2 periods (Table 5) produced similar results, but was less conclusive for females. As expected, the precision of the average of the year-specific survival rates was lower than the constant survival rate for each time period for model H<sub>02</sub> Periods 1 and 2 (Table 5 vs. Table 4).

The use of averages from models H<sub>1</sub> or H<sub>2</sub> for testing between periods of years of "liberal" and "restrictive" regulations is unlikely to be fruitful with females. Point estimates lack precision and tests have such low power that differences in survival between the time periods are difficult to detect.

A number of other analyses examined survival during years of "liberal" versus "restrictive" regulations. Anderson and Burnham (1976) selected 1962, 1965, and 1968 as years of "restrictive" regulations and 1964 and 1970 as years of "liberal" regulations. Their examination of harvest and band recovery data indicated that

harvest rates differed between the sets of years, but survival rates were the same. Rogers et al. (1979) repeated Anderson and Burnham's (1976) analysis of using the same "restrictive" years but designating 1970, 1974, and 1975 as "liberal" years. This analysis also provided no evidence that survival was higher during the years of restrictive regulations. Nichols and Hines (1983) variously grouped years from the 1960's and 1970's and suggested that survival and harvest rates were inversely related for immature females. Caswell et al. (1985) found higher survival for both adult males and adult females associated with restrictive regulations for southern Manitoba (roughly, minor reference area 061).

Burnham et al. (1984) caution that their ultrastructural model could be criticized because  $S_{t+1}$  may not be constant but may vary yearly. They concluded, however, that yearly variation in  $S_{t+1}$  would not bias the estimates of  $\beta$  as long as  $S_{t+1}$  and  $K_t$  are independent over years. Barker et al. (1991) demonstrated, using simulation, that this is true and that the model is robust to temporal variation in  $S_{t+1}$ .

Pooling age classes in our ultrastructural model analysis increased the power of the test. Barker et al. (1991) stated that inclusion of immatures reduced the variance of  $\hat{R}$  in their analysis by 25–40%. Our pooling of sex classes also increased the precision of the estimates. Without pooling sex classes, we could reject the completely compensatory model ( $\hat{R} = 2.803$ ,  $\widehat{SE}(\hat{R}) = 0.665$ ), but not the completely additive model for males, and could not reject either model ( $\hat{R} = 1.667$ ,  $\widehat{SE}(\hat{R}) = 1.865$ ) for females.

One criticism of our analysis is that pooling sex classes was not appropriate if males and females have different parameter values. Parameters could be estimated with such poor precision that the power of the tests to detect differences between sexes is low. There are biological reasons and sufficient evidence that male and female classes have different recovery and survival patterns; however, this does not necessarily translate to expected differences in density dependence or in response to hunting.

For compensation to occur, some non-hunting mortality must be density dependent, and such mortality would probably have to account for a sizable portion of total annual mortality. For female mallards, the nesting season appears to be a period when high mortality occurs (Blohm et al. 1987); although no density-dependent

mortality factors have been identified. It also is possible that little or no compensation occurs, but that the magnitude and variation of non-hunting mortality during the nesting period mask the effect of hunting mortality. This could explain the inability to detect additivity due to hunting using correlation analyses that have been popular in the past (reviewed in Nichols et al. 1984:546). Despite these caveats, the data give us no justification to analyze sexes separately. The likelihood ratio tests indicate that the reduced model with a single  $R$  parameter for all age-sex classes adequately explains the variability in the data.

Burnham et al. (1984) had difficulty in obtaining reasonable estimates of  $\beta$  (some lay outside the possible 0–1 range) and suggested that annual recovery rates with small coefficients of variation could cause  $\beta$  to have poor properties. This occurs because the analysis is basically regression, and if the recovery rates vary little, then the slope estimate,  $\hat{R}$  scaled to  $\hat{\beta}$ , tends to be imprecise (Burnham et al. 1984:357). We did not have these difficulties, probably due to the large change in recovery rates between the 2 time periods (Table 3).

Crippling losses for the United States, calculated from harvest survey data, are around 20% (Anderson and Burnham 1976). Recent observational investigations in Canada (Neiman et al. 1987) suggest hunter estimates of crippling loss there may lie between 20 and 45%. If crippling loss is above 0.21 we can reject ( $P < 0.05$ ) the completely additive model (Fig. 2).

Our analysis using Anderson et al.'s (1982) model is the first to reject thoroughly the completely compensatory model for mallards. Previous analyses supported the belief that hunting mortality was mostly compensated by other sources of mortality (Burnham et al. 1984). Trost (1987) was unable to reject either hypothesis. Earlier forms of the analysis by Anderson and Burnham (1976) and alternate methods of analysis by Burnham and Anderson (1984) had similar results; i.e., rejection of the completely additive model for males and inconclusive results for females. Most previous analyses included only adult birds.

Most likely, our results differ from those of previous analyses because we analyzed different sets of years. Population abundance, weather, habitat conditions, recruitment, regulations, harvest rates, and other factors differed. During the 1960's and 1970's, it is possible that harvest

was mostly compensatory mortality. During the 1980's, compensation may have

If mallard populations the 2 periods then an a relating population size, density dependence co this hypothesis, as densi rying capacity, survival are able to obtain more remaining individual. V esis unlikely because we mallard populations dec Breeding mallard num Serv., Annu. Status of W Forecast, unpubl. data) different between the 2 0.65, Fisher's randomiz Mid-winter mallard sur differ ( $t = 0.98$ ,  $P = 0.33$  Manage., U.S. Fish Wil However, we cannot dis critical resources were the later period, effect density.

## MANAGEMENT IMPL

The evidence from that a portion of harve period 1979–89 was ad restrictive regulations, ditions, result in increa lards. However, even i isted, compensatory re still be possible via d ductive rates. The exis not mean necessarily rates are translated in size. Our analyses sug ulations may be most when recruitment is depressed.

Our findings suppo ulation dynamics of m than the simple depi additive and complete Conroy and Krentz discussion of why the could be expected to both additive and cor

It is important to k process in proper pti tions became even m have remained there s

was mostly compensatory to other forms of mortality. During the 1980's, it appears that less compensation may have occurred.

If mallard populations had declined between the 2 periods then an alternate hypothesis relating population size, carrying capacity, and density dependence could be possible. Under this hypothesis, as densities declined below carrying capacity, survival could increase as birds are able to obtain more critical resources per remaining individual. We believe this hypothesis unlikely because we found no evidence that mallard populations declined during the study. Breeding mallard numbers (U.S. Fish Wildl. Serv., Annu. Status of Waterfowl and Fall Flight Forecast, unpubl. data) were not significantly different between the 2 periods ( $t = 0.54$ ,  $P = 0.65$ , Fisher's randomization test, Green 1977). Mid-winter mallard survey indices also did not differ ( $t = 0.98$ ,  $P = 0.35$ , Office Migratory Bird Manage., U.S. Fish Wildl. Serv., unpubl. data). However, we cannot discount the possibility that critical resources were more available during the later period, effectively reducing mallard density.

#### MANAGEMENT IMPLICATIONS

The evidence from our 2 analyses suggests that a portion of harvest sometime during the period 1979-89 was additive. We conclude that restrictive regulations can, under certain conditions, result in increased survival rates of mallards. However, even if complete additivity existed, compensatory responses to hunting could still be possible via density-dependent reproductive rates. The existence of additivity does not mean necessarily that changes in harvest rates are translated into changes in population size. Our analyses suggest that restrictive regulations may be most beneficial during periods when recruitment is low and populations are depressed.

Our findings support the idea that the population dynamics of mallards are more complex than the simple depictions of the completely additive and completely compensatory models. Conroy and Kremenetz (1990) present an in-depth discussion of why the mortality process in ducks could be expected to be a mixed model with both additive and compensatory components.

It is important to keep the hunting mortality process in proper perspective. Hunting regulations became even more restrictive in 1988 and have remained there since. The number of hunt-

ers and harvest rates have decreased dramatically. Despite low harvest rates, mallard populations have not increased, suggesting that recruitment rates are insufficient to maintain population levels (Cowardin et al. 1985, Greenwood et al. 1987). While increased survival may improve population status, long-term gains appear unlikely unless recruitment rates increase.

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## ULNAR LIPID AND FAT RESERVES

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**Abstract:** We wanted to determine if body lipid, because many waterfowl are euthanized 12 mallards at a time, was constant when total body lipid was constant. With these criteria, we examined the lipid of 1987 and 1988 in the same birds ( $n = 31.0\%$ ) for mallards with lipid reserves between immature and adult. A screen for starved birds was used to determine if the ulnar content was constant. The classification error rate was determined for wings for depleted body lipid.

Bones of some waterfowl species are rich in lipids in addition to calcium and mineral. Ankney (cited in Ringelman et al. 1984) found lipid in the ulna of mallards and geese (*Chen caerulescens*). Lipids are stored in the ulna of cackling Canada geese (*Nyroca nympha*; Raveling et al. 1984). Owen (1984) reported lipid deposits (1.64 g) in the ulna of mallards (*A. rubripes*). They concluded that lipids were one of the first to be depleted before depletion of medullary lipid.

During a study of waterfowl in the San Luis Valley, we banded hundreds of ducks for unknown causes. Because we consumed the flesh, most ducks were only by wings. The g

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