THE RELATIONSHIP BETWEEN BODY MASS AND SURVIVAL OF WINTERING CANVASBACKS

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ABSTRACT.—Mass and recapture histories of 6,000 Canvasbacks (*Aythya valisineria*) banded in upper Chesapeake Bay were used to test two hypotheses: (1) early-winter body mass is associated with the probability of surviving the winter, and (2) early-winter body mass is associated with annual survival probability. Data were analyzed by a binary regression method that treated mass as a continuous variable and estimated parameters to describe a general relationship between body mass and survival probability. Results for adult males, which provided our largest data sets, presented strong evidence that birds with high relative early-winter masses had both greater overwinter and annual survival probabilities. Results of overwinter analyses necessarily are qualified by the alternative explanation of mass-dependent emigration, i.e. the possibility that lighter birds move south in response to cold weather and leave only heavy birds for recapture. Such a phenomenon remains to be documented. Results concerning annual survival probabilities are not vulnerable to this alternative explanation because of the strong fidelity of Canvasbacks at the banding site. Because of small sample size, data were inadequate to permit mass/survival inferences for adult females. Sample sizes were adequate for young Canvasbacks, but the results were less consistent than for adult males. Although early-winter body mass was associated positively with overwinter as well as annual survival for young Canvasbacks in some years, we suspect that the lack of established wintering patterns among these birds may underlie the less consistent result. Received 11 February 1985, accepted 9 January 1986.

FOR several species of waterfowl, evidence now exists for a relationship between the physiological state or "condition" of an individual and its subsequent reproductive performance (e.g. Ankney and MacInnes 1978; Raveling 1979; Krapu 1979, 1981). It is also reasonable to expect that the "physiological condition" of an individual at some time t is related to its probability of surviving some subsequent period (t, $t + \Delta$), especially if the period is one in which food resources are limited or environmental conditions are energetically stressful, or both. This expectation has been accepted in the literature not only for waterfowl, but for birds and mammals in general, and it is now a tacit assumption of most published studies dealing with physiological condition during nonbreeding periods. We are aware of few efforts that use birds, however, to test the hypothesis that particular physiological characteristics are related to survival probability. There is considerable speculation and some evidence for several bird species that food supplies may be limited during winter and that both food availability and winter weather are related to survival probability (Lack 1966; Fretwell 1968, 1972; Goss-Custard 1979; North and Morgan 1979; Pulliam and Parker 1979; van Balen 1980; Ekman et al. 1981; Jansson et al. 1981). Winter is thus a logical time to look for a relationship between physiological condition and survival within many Temperate Zone birds.

Two general approaches have been used to draw inferences about the relationship between condition and survival in wintering birds. The first involves comparisons of variables believed to reflect condition (e.g. body mass, percentage of fat or lipid in the body, percentage of protein in the body) between two groups: (1) birds found dead during periods of severe winter weather, and (2) birds collected during "normal" or mild winter weather and believed to be representative of live wintering birds. There are large differences between these two groups for Eurasian Coots (*Fulica atra*; Visser 1978), Common Redshanks (*Tringa totanus*; Davidson and Evans 1982), and Eurasian Oystercatchers (*Haematopus ostralegus*; Davidson and Evans 1982, Swennen and Duiven 1983). Thus, these results provided evidence that lipid and

protein reserves are mobilized during periods of severe weather and may be important to winter survival. Nevertheless, these studies did not demonstrate that variation in survival probability is associated with variation in body mass or nutrient reserves.

The second general approach permits stronger inferences about this relationship. Birds are captured and weighed (or assigned to a condition category by some other means) at the beginning of a winter period. Recaptures or resightings of the birds at the end of the period are then used to draw inferences about variation in survival probabilities for birds of different masses or condition categories. We are aware of two such studies on wintering birds. In a 2-yr study, Fretwell (1968) captured and banded 85 Field Sparrows (*Spizella pusilla*) in early winter and assigned them to two fat categories (above and below average). The proportion of birds seen later in winter was significantly greater for the above-average category in 1 of 2 years. In another study, Kikkawa (1980) weighed and color-banded 388 first-year Gray-backed White-eyes (*Zosterops lateralis*) at the beginning of winter over a 3-yr period. Resightings at the end of each winter showed no significant difference between the proportion of birds above vs. below average in initial mass.

We use an approach similar to the second described above with Canvasbacks (*Aythya valisineria*) wintering on Chesapeake Bay. Winter weather conditions on Chesapeake Bay are frequently subfreezing, and prolonged ice cover may limit food availability for Canvasbacks. In addition, resource-related differences in winter mortality associated with behavioral dominance or fasting endurance may be important selective forces in the evolution of winter distribution patterns in this species (Nichols and Haramis 1980, Alexander 1983, Haramis et al. 1985). In ducks, there is generally a good correlation between body mass and both fat (Owen and Cook 1977, Bailey 1979) and total nutrient (lipid + protein) reserves (Wishart 1979). Therefore, we expect high body masses to reflect good reserves and possibly confer a greater probability of surviving the winter. In our study, masses and recapture histories of Canvasbacks were used to test two hypotheses: (1) Canvasback body mass in early winter is associated with the probability of surviving that

winter, and (2) Canvasback body mass in early winter is associated with subsequent annual survival probability.

METHODS

We used masses and recapture histories of winter-banded Canvasbacks caught from December through March, 1978–1983, in upper Chesapeake Bay. Birds were captured in wire traps baited with corn and held in modified poultry crates until dry. Birds were then sexed, aged, banded, weighed to the nearest 5 g, and released (see Haramis et al. 1982 for detailed methods).

Body masses of individual birds could not be compared directly because birds were held for different periods of time before weighing. Because greater numbers of birds generally were captured at dawn and dusk, two times for weighing were chosen: those birds captured in early morning and held 3–8 h before weighing and those birds captured in late afternoon and held overnight (13–18 h) before weighing. We inspected the gullet of each bird for corn content before weighing and separated birds into those with corn and those with little or no corn. Thus, each bird was classified in 1 of 4 categories, depending on the time delay before weighing and the corn content.

A mean mass was computed for each of the 4 categories, and a "normalized" mass (x_i) was computed for each individual as:

$$x_i = (w_i - \bar{w})/\bar{w},$$

where w_i is the mass of individual i and $\bar{w}$ is the arithmetic mean mass of birds in the appropriate category. Thus, normalized masses expressed the mass of each individual relative to all other birds with similar corn content and time delay before weighing. Separate analyses were conducted for adult males, adult females, and young of both sexes.

To determine whether a bird's mass at capture was related to the probability of catching that bird in a sample at some later time, we let θ_i denote the probability that individual i, from a particular banded sample, is recaptured at some later time. θ_i is the product of two probabilities, $\theta_i = \phi_i p$, where ϕ_i denotes the probability that marked bird i will survive until the subsequent recapture period and p is the probability that a bird alive during the recapture period will be captured. If we assume a priori that p is the same for each duck regardless of body mass at initial capture (or perhaps just that p does not depend on body mass, regardless of whether or not it is a constant for all birds), then a test of the hypothesis that θ_i is not related to body mass is also a test of the hypothesis that ϕ_i is not related to body mass.

In the first analysis, we determined whether ducks in a banded sample were recaptured in the same winter (e.g. banded in December 1979 and recaptured in

January–March 1980). In a second analysis, we determined whether banded birds were recaptured during the winter following the winter of banding (e.g. banded in December 1978 and recaptured December 1979 to March 1980). In both analyses we were not interested in multiple recaptures, but simply in whether a bird was recaptured at least once in the sampling period of interest.

For both analyses the recapture data were binary (i.e. a bird either was recaptured or not), and we applied a binary regression model (see Cox 1970: 87–91). The following linear-logistic model provides a reasonable and flexible form (see discussion in Cox 1970) for the relationship between θ_i and body mass:

$$\theta_i = \frac{\exp(B_0 + B_1 x_i)}{1 + \exp(B_0 + B_1 x_i)}, \tag{1}$$

where B_0 and B_1 are parameters to be estimated and x_i is the normalized mass. We further define the random variable y_i, which assumes a value of 0 if individual i is not recaptured and 1 if it is recaptured. We then write the probability distribution function for a vector of y_i from a banded sample of n individuals as:

$$P(y_1, y_2, \ldots y_n) = \frac{\displaystyle\prod_{i=1}^{n} \exp(B_0 + B_1 x_i) y_i}{\displaystyle\prod_{i=1}^{n} [1 + \exp(B_0 + B_1 x_i)]} . \tag{2}$$

The logarithm of Eq. 2 is the log likelihood; first and second derivatives of this, with respect to the parameters of interest (B_0 and B_1), were used with the iterative "method of scoring" (see Brownie et al. 1978: 212) to obtain the maximum likelihood estimates, $\hat{B}_0$ and $\hat{B}_1$, and their asymptotic variances and covariances, $\widehat{\text{var}}(\hat{B}_0)$, and $\widehat{\text{var}}(\hat{B}_1)$, $\widehat{\text{cov}}(\hat{B}_0, \hat{B}_1)$.

One approach to testing the significance of the relationship between mass and recapture probability uses a simple model that does not contain B_1. In this model θ_i is written as:

$$\theta_i = \frac{\exp(B_0)}{1 + \exp(B_0)} . \tag{3}$$

Thus, each individual is assumed to have the same recapture probability (which does not depend on body mass). Closed-form estimators of B_0 and $\text{var}(\hat{B}_0)$ are available. If we call this model M_0, and the previous model (Eqs. 1 and 2) M_1, then the likelihood ratio test of M_0 vs. M_1 provides a test of the hypothesized mass relationship.

A quadratic-logistic model (M_2) with greater flexibility than M_1 also was tested. In this model θ_i is written as:

$$\theta_i = \frac{\exp(B_0 + B_1 x_i + B_2 x_i^2)}{1 + \exp(B_0 + B_1 x_i + B_2 x_i^2)} . \tag{4}$$

Maximum likelihood estimates of B_0, B_1, and B_2 were obtained using the method of scoring, and likelihood ratio tests for M_1 vs. M_2 and for M_0 vs. M_2 were conducted. A computer program was written to compute the parameter estimates using all three models. The three described likelihood ratio test statistics and their associated probability levels were computed.

Another means of judging the significance of the relationship between mass and recapture probability in the above model is to compute a z statistic [$z = \hat{B}_1 / \widehat{\text{SE}}(\hat{B}_1)$]. z is approximately distributed as Normal (0,1) under the null hypothesis of no relationship between mass and survival.

We also used the nonparametric Wilcoxon rank sum test (see Dietz 1983) to test for a relationship between recapture probability and mass without the assumption of a specific model such as Eqs. 1–4. In this procedure, we ranked birds in specified samples by mass (greatest to least) and asked whether recaptured birds were clumped in certain portions of this distribution or were distributed uniformly throughout the distribution.

Test statistics were computed for a number of banded samples, each representing a specific age-sex class and a specific month and year of banding. Composite test statistics also were computed over all banded samples for each age-sex class and banding month, and for both banding months (December and January) combined. The likelihood ratio test statistics are distributed as chi-square, so the composite statistic was obtained by summing these individual statistics and their associated degrees of freedom to obtain an overall statistic distributed as chi-square under the null hypothesis. For the Wilcoxon rank sum statistics, the composite was obtained by computing

$$-2 \sum_{i=1}^{n} \ln P_i,$$ where P_i is the probability associated

with the test statistic for data set i and n is the total number of data sets. This statistic is distributed as chi-square with $2n$ degrees of freedom under the null hypothesis. A composite Z statistic was computed as

$$\sum_{i=1}^{n} z_i / \sqrt{n},$$ where z_i is the z statistic for data set i and

n is again the number of data sets. Z is distributed as Normal (0,1) under the null hypothesis. We treated the likelihood ratio and Wilcoxon tests as two-tailed; however, the sign of the z statistic indicates the direction of the relationship between body mass and recapture probability, so we use one-tailed z tests with positive B_1 and z representing the alternative hypothesis of interest.

RESULTS

The first set of tests used bandings and subsequent recaptures occurring later the same winter. Only recaptures occurring at least 2 weeks after initial banding were included in

TABLE 1. Parameter estimates and test statistics for adult Canvasbacks banded in December and January at Gibson Island, Maryland and recaptured later the same winter.[a,b]

Sex Banding period	Recapture period	No. bandings	No. recaptures	M_1 parameter estimates				z statistic		M_1 vs. M_0			Wilcoxon test	
				$\hat{B}_0$	SÊ $(\hat{B}_0)$	$\hat{B}_1$	SÊ $(\hat{B}_1)$	z	P	χ^2	df	P	T	P
Male														
Dec 1978	Dec 1978–Mar 1979	193	37	−1.50	0.19	7.52	3.10	2.43**	0.01	6.16*	1	0.01	2.44*	0.01
Dec 1979	Dec 1979–Mar 1980	163	13	−2.54	0.32	7.99	5.10	1.57	0.06	2.61	1	0.11	1.83	0.07
Dec 1980	Dec 1980–Mar 1981	313	18	−2.80	0.24	0.16	3.53	0.05	0.48	0.00	1	0.96	0.26	0.79
Dec 1981	Dec 1981–Mar 1982	961	73	−2.51	0.12	2.12	1.94	1.09	0.14	1.19	1	0.27	1.07	0.28
Means and totals		1,630	141	−2.34	0.11	4.45	1.80	2.57**	0.01	9.96*	4	0.04	$\chi^2_8 = 17.55$*	0.02
Jan 1979	Jan 1979–Mar 1979	552	49	−2.33	0.15	2.03	2.74	0.74	0.23	0.55	1	0.46	0.62	0.54
Jan 1980	Jan 1980–Mar 1980	361	15	−3.14	0.26	−0.60	4.30	−0.14	0.56	0.02	1	0.89	0.53	0.60
Jan 1982	Jan 1982–Mar 1982	478	14	−3.50	0.27	1.30	4.07	0.32	0.37	0.10	1	0.75	0.43	0.67
Means and totals		1,391	78	−2.99	0.13	0.91	2.17	0.53	0.30	0.67	3	0.88	$\chi^2_6 = 3.05$	0.80
Means and totals (Dec + Jan bandings)		3,021	219	−2.62	0.09	2.39	1.39	2.29*	0.01	10.63	7	0.16	$\chi^2_{14} = 20.60$	0.11
Female														
Dec 1981	Dec 1981–Mar 1982	207	17	−2.42	0.25	1.32	3.44	0.38	0.35	0.15	1	0.70	0.35	0.73

[a] Analyses were restricted to recaptures occurring at least 2 weeks after banding.
[b] Likelihood ratio and Wilcoxon tests are two-tailed; z statistic probabilities are one-tailed. * = $0.01 < P < 0.05$, ** = $P < 0.01$.

the analyses. These analyses thus deal with the relationship between initial body mass and the probability of surviving the subsequent 2–12-week (in most cases 4–6-week) wintering period). Seven data sets for adult males, 1 for adult females, and 5 for young Canvasbacks met our arbitrary minimum requirement of at least 9 recaptures (Tables 1 and 2). Six of 7 adult-male data sets had positive $\hat{B}_1$'s, and the relationship was significant ($P < 0.05$) for all three tests for birds banded in December 1978 (Table 1), a winter with the coldest combined January and February period during the study. The composite statistics were significant ($P < 0.05$) for birds banded in December, but not for birds banded in January. For December and January bandings combined, the directional composite Z statistic was significant (1-tailed, $P < 0.05$; Table 1). Only one data set for adult females was sufficiently large for analysis, and the resulting $\hat{B}_1$ was positive but nonsignificant (Table 1). For young Canvasbacks, 3 of 5 $\hat{B}_1$'s were positive; 2 of these yielded significant ($P < 0.05$) test statistics using all three tests (Table 2). The composite test statistics for December bandings and December and January bandings combined were significant ($P < 0.05$).

The second set of tests used recaptures occurring during the winter following the winter of banding, and thus concerned the relationship between winter mass and annual survival. Six data sets for adult males, 2 for adult females, and 6 for young Canvasbacks met our minimum arbitrary sample-size requirement of at least 9 recaptures (Tables 3 and 4). For adult males, $\hat{B}_1$ was positive for all data sets, which suggested a positive relationship between winter body mass and annual survival (Table 3). Significant test statistics were obtained for a number of the individual adult-male data sets, and results were consistent for the three test statistics. All three composite statistics for December bandings and December and January bandings combined were highly significant ($P < 0.01$; Table 3). Sample sizes were small for the two adult-female data sets. One $\hat{B}_1$ was positive, the other negative. None of the individual or composite test statistics was significant.

Among young Canvasbacks, 3 of the data sets had positive $\hat{B}_1$'s and 3 had negative, although the two strongest relationships had positive $\hat{B}_1$'s (Table 4). For December, January, and combined bandings, the composite M_1 vs. M_0 test statistics were significant ($P < 0.05$) and the

TABLE 2. Parameter estimates and test statistics for young Canvasbacks (sexes combined) banded in December and January at Gibson Island, Maryland and recaptured later the same winter.[a,b]

Banding period	Recapture period	No. band-ings	No. recap-tures	M_1 parameter estimates				z statistic		M_1 vs. M_0			Wilcoxon test		
				$\hat{B}_0$	$\text{SÊ}(\hat{B}_0)$	$\hat{B}_1$	$\text{SÊ}(\hat{B}_1)$	z	P	χ^2	df	P	T	P
Dec 1978	Dec 1978–Mar 1979	404	60	−1.75	0.14	−1.23	2.07	−0.59	0.72	0.35	1	0.55	0.64	0.52
Dec 1979	Dec 1979–Mar 1980	726	76	−2.17	0.12	3.50	1.61	2.17*	0.02	4.77*	1	0.03	2.19*	0.03
Dec 1980	Dec 1980–Mar 1981	475	20	−3.40	0.29	10.15	3.25	3.12**	0.00	10.64*	1	0.00	2.92**	0.00
Means and totals		1,605	156	−2.44	0.11	4.14	1.39	2.71**	0.00	15.76	3	0.00	$\chi^2_6 = 19.36$**	0.00
Jan 1979	Jan 1979–Mar 1979	535	46	−2.38	0.16	−2.82	2.20	−1.28	0.90	1.67	1	0.20	1.29	0.20
Jan 1980	Jan 1980–Mar 1980	347	25	−2.58	0.21	3.09	2.95	1.05	0.15	1.11	1	0.29	1.20	0.23
Means and totals		882	71	−2.48	0.13	0.14	1.84	−0.16	0.56	2.78	2	0.25	$\chi^2_4 = 6.16$	0.19
Means and totals (Dec and Jan bandings)		2,487	227	−2.46	0.09	2.54	1.11	2.00*	0.02	18.54**	5	0.00	$\chi^2_{10} = 25.52$**	0.00

[a] Analyses were restricted to recaptures occurring at least 2 weeks after banding.
[b] Likelihood ratio and Wilcoxon tests are two-tailed; z statistic probabilities are one-tailed. * $= 0.01 < P < 0.05$, ** $= P < 0.01$.

TABLE 3. Parameter estimates and test statistics for adult Canvasbacks banded in December and January at Gibson Island, Maryland and recaptured the following winter.[a]

Sex Banding period	Recapture period	No. bandings	No. recaptures	M_1 parameter estimates				z statistic		M_1 vs. M_0			Wilcoxon test	
				$\hat{B}_0$	$\text{SÊ}(\hat{B}_0)$	$\hat{B}_1$	$\text{SÊ}(\hat{B}_1)$	z	P	χ^2	df	P	T	P
Male														
Dec 1978	Dec 1979–Mar 1980	193	20	-2.22	0.25	6.63	3.91	1.70*	0.04	2.94	1	0.09	1.89	0.06
Dec 1979	Dec 1980–Mar 1981	163	16	-2.35	0.30	9.74	4.76	2.05*	0.02	4.54*	1	0.03	2.08*	0.04
Dec 1980	Dec 1981–Mar 1982	313	29	-2.30	0.20	2.76	2.89	0.96	0.17	0.92	1	0.34	1.05	0.29
Dec 1981	Dec 1982–Mar 1983	961	13	-4.68	0.37	14.38	4.59	3.13**	0.00	10.19**	1	0.00	3.09**	0.00
Means and totals		1,630	78	-2.89	0.14	8.38	2.05	3.92**	0.00	18.59**	4	0.00	$\chi^2_8 = 26.97$**	0.00
Jan 1979	Dec 1979–Mar 1980	552	33	-2.80	0.19	5.78	3.34	1.73*	0.04	3.05	1	0.08	1.30	0.19
Jan 1981	Dec 1981–Mar 1982	827	51	-2.73	0.15	2.08	1.96	1.06	0.14	1.12	1	0.29	1.28	0.20
Means and totals		1,379	84	-2.77	0.12	3.93	1.94	1.97*	0.02	4.17	2	0.12	$\chi^2_4 = 6.54$	0.16
Means and totals (Dec and Jan bandings)		3,009	162	-2.85	0.10	6.90	1.51	4.34**	0.00	22.76**	6	0.00	$\chi^2_{12} = 33.51$**	0.00
Female														
Jan 1980	Dec 1980–Mar 1981	88	10	-2.06	0.34	-1.91	4.96	-0.39	0.65	0.15	1	0.70	0.44	0.66
Jan 1981	Dec 1981–Mar 1982	286	12	-3.16	0.30	3.47	3.87	0.90	0.18	0.81	1	0.37	1.10	0.27
Means and totals		374	22	-2.61	0.23	0.78	3.15	0.36	0.36	0.96	2	0.62	$\chi^2_4 = 1.45$	0.79

[a] Likelihood ratio and Wilcoxon tests are two-tailed; z statistic probabilities are one-tailed. * = $0.01 < P < 0.05$, ** = $P < 0.01$.

composite Wilcoxon statistics approached significance. Both positive and negative relationships between body mass and survival, however, contribute to the magnitude of these test statistics. For this reason, when some individual data sets show positive and others negative $\hat{B}_1$'s, the most informative composite test statistic is the Z. For young Canvasbacks, the composite Z statistics were positive but nonsignificant (Table 4).

We also estimated parameters and computed likelihoods under a more flexible quadratic-logistic model, M_2. The M_1 vs. M_2 likelihood ratio test statistic was significant ($P < 0.05$) for only 4 of the 27 individual data sets, however, and we concluded that the additional complexity of the M_2 model was not necessary for these data.

DISCUSSION

Adult males with high relative body mass had greater overwinter survival probabilities than lightweight birds (Table 1). When actual body masses are used in Eq. 1 in conjunction with the parameter estimates under model M_1, extremely heavy individuals have estimated overwinter survival probabilities that are substantially larger than those of extremely lightweight birds. Body mass in early winter is also associated with the annual survival probability of adult males (Table 3). Thus, the overwinter survival advantage associated with large mass is not eliminated by any mass-associated disadvantages occurring at some other time of the year.

There was no evidence in adult females for a relationship between early-winter body mass and either overwinter (Table 1) or annual (Table 3) survival. Sample sizes were very small for this category, however, and we conclude that the data simply were not adequate to permit inferences about the presence or absence of a mass effect on survival.

The small sample size for young Canvasback females and inconsistent results of sex-specific tests prompted combining data for the sexes for final analyses. Although the estimated B_1 coefficients were negative in some years and positive in others, 4 of 5 significant ($P < 0.05$) test statistics indicated a positive relationship between early-winter body mass and both overwinter (Table 2) and annual (Table 4) survival. Results for young Canvasbacks are presumably

TABLE 4. Parameter estimates and test statistics for young Canvasbacks (sexes combined) banded in December and January at Gibson Island, Maryland and recaptured the following winter.[a]

Banding period	Recapture period	No. bandings	No. recaptures	M_1 parameter estimates				z statistic		M_1 vs. M_0			Wilcoxon test	
				$\hat{B}_0$	$\hat{SE}(\hat{B}_0)$	$\hat{B}_1$	$\hat{SE}(\hat{B}_1)$	z	P	χ^2	df	P	T	P
Dec 1978	Dec 1979–Mar 1980	404	9	-3.82	0.35	-4.43	4.93	-0.90	0.18	0.80	1	0.37	0.64	0.52
Dec 1979	Dec 1980–Mar 1981	726	24	-3.39	0.21	-2.02	2.75	-0.73	0.23	0.54	1	0.46	0.79	0.43
Dec 1980	Dec 1981–Mar 1982	475	19	-3.36	0.27	8.29	3.24	2.56**	0.01	6.98**	1	0.01	2.43	0.02
Means and totals		1,605	52	-3.52	0.16	1.84	2.17	0.54	0.29	8.32*	3	0.04	$\chi^2_6 = 10.82$	0.09
Jan 1979	Dec 1979–Mar 1980	535	14	-3.73	0.30	-6.98	3.93	-1.78*	0.04	3.23	1	0.07	1.75	0.08
Jan 1980	Dec 1980–Mar 1981	347	13	-3.40	0.32	8.21	4.06	2.02*	0.02	4.16*	1	0.04	1.29	0.20
Jan 1981	Dec 1981–Mar 1982	254	14	-2.86	0.28	2.48	3.37	0.74	0.23	0.54	1	0.46	0.85	0.40
Means and totals		1,136	41	-3.33	0.17	1.24	2.19	0.57	0.28	7.39*	3	0.05	$\chi^2_6 = 10.10$	0.12
Means and totals (Dec and Jan bandings)		2,741	93	-3.42	0.12	0.93	1.54	0.78	0.22	16.25**	6	0.01	$\chi^2_{12} = 20.92$	0.05

[a] Likelihood ratio and Wilcoxon tests are two-tailed; z statistic probabilities are one-tailed. * = $0.01 < P < 0.05$, ** = $P < 0.01$.

less consistent than for adult males because the young lack an established wintering pattern.

A critical assumption in our analysis was that the probability of catching a bird, given that it is alive (p), is independent of initial body mass. Our results indicated a positive relationship between body mass and θ_i. We interpret this as indicative of a positive relationship between body mass and survival rate, ϕ_i. Because $\theta_i = \phi_i p$, however, this result could reflect a positive relationship between body mass and p. We have no evidence to suggest that such a relationship between body mass and p existed. Not only were large numbers of Canvasbacks trapped at Gibson Island, but there was substantial variation in body masses of the birds in all samples. Weatherhead and Ankney (1984) speculated that bait trapping may result in higher capture probabilities for lightweight birds. If this was true for Canvasbacks, however, then our tests would be conservative and the true relationship between body mass and survival probability would be even stronger than indicated by our results.

We note also that the complement of our survival probability ($1 - \phi_i$) includes not only mortality but emigration from the Gibson Island banding site. Generally, large numbers of females and young pass through Chesapeake Bay in November and December to winter in North Carolina. Males remain in the upper Bay and commonly outnumber females 4 to 1 or more by midwinter. This general migration pattern has been supported by the observation of increased male-to-female sex ratios from late fall through midwinter on Chesapeake Bay (Welling and Sladen 1979). A midwinter latitudinal gradient in flyway distribution of the sexes was confirmed by aerial photography (Haramis et al. 1985). Finally, a decline in the number of juveniles and an increase in adult male Canvasbacks captured with the advent of cold weather imply a change (Haramis unpubl. data). Emigration will not influence our results if it is independent of mass (i.e. condition) within an age-sex class. Mass-dependent emigration, i.e. light birds moving south with the advent of cold weather and leaving only the heavy birds for recapture, could explain the results of our same-winter analyses. We have no evidence to support this explanation but currently are studying this possibility.

Unlike the same-winter analyses, the between-winter analyses are not vulnerable to possible effects of a mass-dependent emigration because of the strong fidelity of Canvasbacks in the upper Bay. For instance, about 95% of the Canvasbacks recovered in the Atlantic Flyway from 1929 to 1977 had been banded during winter in the Atlantic Flyway (Nichols and Haramis 1980: table 2). In addition, our trap site is located strategically at a traditional arrival and departure area for Canvasbacks using the Chesapeake Bay migration corridor, and thus provides access over three months of trapping to a majority of Canvasbacks wintering from Chesapeake Bay south to coastal North Carolina. These characteristics are the foundation for the assumption of equal catchability of previously marked birds.

Because birds with larger fat reserves should be able to survive longer during periods of food shortage and cold stress (Calder 1974: 114) and because body mass and fat reserves are positively correlated in ducks (Owen and Cook 1977, Bailey 1979, Wishart 1979), heavy Canvasbacks are expected to better survive winter periods of food shortage. The between-winter recapture analyses indicate that heavy Canvasbacks in the upper Chesapeake Bay have higher survival probabilities, at least during some years. The apparent absence of this relationship during some years may result from mild winter weather and the availability of food resources. Results of the same-winter analyses also support these findings, but are contingent on the independence of body mass and emigration probabilities.

The majority of studies of wintering waterfowl have assumed a relationship between condition/mass and survival. Except for the contrasting results of Fretwell (1968) and Kikkawa (1980), however, we know of no other tests of this hypothesized relationship. Our study indicates that Canvasback body mass in early winter is related to survival probability, and thus provides evidence that this commonly assumed relationship does exist in wintering waterfowl.

LITERATURE CITED

ALEXANDER, W. C. 1983. Differential sex distributions of wintering diving ducks (Aythyini) in North America. Amer. Birds 37: 26–29.

ANKNEY, C. D., & C. D. MacINNES. 1978. Nutrient reserves and reproductive performance of female Lesser Snow Geese. Auk 95: 459–471.

BAILEY, R. O. 1979. Methods of estimating total lipid content in the Redhead Duck (*Aythya americana*) and an evaluation of condition indices. Can. J. Zool. 57: 1830–1833.

VAN BALEN, J. H. 1980. Population fluctuations of the Great Tit and feeding conditions in winter. Ardea 68: 143–164.

BROWNIE, C., D. R. ANDERSON, K. P. BURNHAM, & D. S. ROBSON. 1978. Statistical inference from band recovery data: a handbook. U.S. Fish Wildl. Serv., Resour. Publ. No. 131.

CALDER, W. A. 1974. Consequences of body size for avian energetics. Pp. 86–144 *in* Avian energetics (R. A. Paynter, Jr., Ed.). Publ. Nuttall Ornithol. Club No. 15.

COX, D. R. 1970. The analysis of binary data. London, Chapman and Hall.

DAVIDSON, N. C., & P. R. EVANS. 1982. Mortality of Redshanks and Oystercatchers from starvation during severe weather. Bird Study 29: 183–188.

DIETZ, E. J. 1983. Distribution free tests in binary regression models. Inst. Statistics Mimeo Ser. No. 1633. Raleigh, North Carolina State Univ.

EKMAN, J., G. CEDERHOLM, & C. ASKENMO. 1981. Spacing and survival in winter groups of Willow Tit *Parus montanus* and Crested Tit *P. cristatus*—a removal study. J. Anim. Ecol. 50: 1–9.

FRETWELL, S. D. 1968. Habitat distribution and survival in the Field Sparrow (*Spizella pusilla*). Bird-Banding 39: 293–306.

———. 1972. Populations in a seasonal environment. Princeton, New Jersey, Princeton Univ. Press.

GOSS-CUSTARD, J. D. 1979. Effect of habitat loss on the numbers of overwintering shorebirds. Pp. 167–177 *in* Shorebirds in marine environments (F. A. Pitelka, Ed.). Stud. Avian Biol. 2.

HARAMIS, G. M., E. L. DERLETH, & D. G. MCAULEY. 1982. Techniques for trapping, aging, and banding wintering Canvasbacks. J. Field Ornithol. 53: 342–351.

———, J. R. GOLDSBERRY, D. G. MCAULEY, & E. L. DERLETH. 1985. An aerial photographic census of Chesapeake Bay and North Carolina Canvasbacks. J. Wildl. Mgmt. 49: 449–454.

JANSSON, C., J. EKMAN, & A. VON BROMSSEN. 1981. Winter mortality and food supply in tits *Parus* spp. Oikos 37: 313–322.

KIKKAWA, J. 1980. Winter survival in relation to dominance classes among Silvereyes *Zosterops lateralis chlorocephala* of Heron Island, Great Barrier Reef. Ibis 122: 437–446.

KRAPU, G. L. 1979. Nutrition of female dabbling ducks during reproduction. Pp. 59–70 *in* Waterfowl and wetlands—an integrated review (T. A. Bookhout, Ed.). LaCrosse, Wisconsin, LaCrosse Printing Co.

———. 1981. The role of nutrient reserves in Mallard reproduction. Auk 98: 29–38.

LACK, D. 1966. Population studies of birds. Oxford, Clarendon Press.

NICHOLS, J. D., & G. M. HARAMIS. 1980. Sex-specific differences in winter distribution patterns of Canvasbacks. Condor 82: 406–416.

NORTH, P. M., & B. J. T. MORGAN. 1979. Modelling heron survival using weather data. Biometrics 35: 667–681.

OWEN, M., & W. A. COOK. 1977. Variations in body weight, wing length and condition of Mallard *Anas platyrhynchos platyrhynchos* and their relationship to environmental changes. J. Zool. 183: 377–395.

PULLIAM, H. R., & T. A. PARKER III. 1979. Population regulation of sparrows. Fortschr. Zool. 25: 137–147.

RAVELING, D. G. 1979. The annual cycle of body composition of Canada Geese with special reference to control of reproduction. Auk 96: 234–251.

SWENNEN, C., & P. DUIVEN. 1983. Characteristics of Oystercatchers killed by cold-stress in the Dutch Wadden Sea area. Ardea 71: 155–159.

VISSER, J. 1978. Fat and protein metabolism and mortality in the Coot *Fulica atra*. Ardea 66: 173–183.

WEATHERHEAD, P. J., & C. D. ANKNEY. 1984. A critical assumption of band-recovery models may often be violated. Wildl. Soc. Bull. 12: 198–199.

WELLING, C. H., & W. J. L. SLADEN. 1979. Canvasback sex ratios on Rhode and West rivers, Chesapeake Bay, 1972–78. J. Wildl. Mgmt. 43: 811–813.

WISHART, R. A. 1979. Indices of structural size and condition of American Wigeon (*Anas americana*). Can. J. Zool. 57: 2369–2374.