SOURCES OF VARIATION IN WATERFOWL SURVIVAL RATES

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ABSTRACT.—Because of the need to manage hunted populations of waterfowl (Anatidae), biologists have studied many demographic traits of waterfowl by analyzing band recoveries. These analyses have produced the most extensive and best estimates of survival available for any group of birds. Using these data, we examined several factors that might explain variation among annual survival rates to explore large-scale patterns that might be useful in understanding waterfowl population dynamics. We found that geography, body mass, and tribe (i.e. phylogeny) were important in explaining variation in average waterfowl survival rates. Received 22 April 1996, accepted 18 September 1996.

ALTHOUGH MODERN METHODS for estimating survival rates have been available for 30 years (Cormack 1964, Jolly 1965, Seber 1965), these estimators have not been applied evenly among all groups of birds. Modern estimation procedures have been put to their fullest use in only one order, the Anseriformes. One reason for this emphasis is the need to understand the relationship between hunter harvest and changes in population parameters (e.g. Anderson and Burnham 1976). Another is that band recoveries reported by hunters provide intensive and extensive samples of birds that otherwise would not be available to researchers. These samples have promoted the development of new estimation procedures and have provided the often "data hungry" methods with sufficient numbers of recoveries for analysis. The estimation of survival rates for many waterfowl species, as well as the thorough documentation of basic biology on those species, provide a unique opportunity for investigating variation in life-history traits. The accessibility of this large data base allowed us to examine factors that might influence average annual survival rates. Previous attempts to understand such relationships (e.g. Zammuto 1986) have been hampered by the use of poor metrics to represent survival rates, e.g. maximum lifespan. Krementz et al. (1989) demonstrated that these metrics should be avoided in such applications.

Our primary interest was to explain variation in average annual survival rates based on a variety of ecological, genetic, and evolutionary factors. Previous work in this area has focused on factors such as geography, body mass, phylogeny, behavior, and reproductive effort (Roff 1992, Stearns 1992). We investigated a subset of these factors: geography, body mass, and phylogeny.

Geography.—Analyses of variation in avian survival rates within geographic strata (continents) have demonstrated an effect of location (Krementz et al. 1987, Nichols and Hines 1987, Nichols et al. 1990). One drawback of these studies has been the restricted range (e.g. North America) over which these comparisons have been made. Our data set represents the first sample for birds that covers a wide geographic range (many continents). Laurila (1988) examined variation in age at maturity (which is a correlate of average annual survival rate) in waterfowl across a broad geographic range and concluded that on average, waterfowl with northern breeding ranges began breeding at an older age than waterfowl breeding in temperate and equatorial regions. Gaillard et al. (1989) found that age at first breeding and adult life expectancy tended to covary in birds. Hence, we predicted that in geographic strata more distant from the equator, average annual survival rates should increase, even after controlling for body mass.

Phylogeny.—Phylogenetic history influences many life-history characteristics, including various measures of lifespan (Laurila 1988, Gaillard et al. 1989, but see Brawn et al. 1995). Our sample includes 31 species among 6 tribes in the

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order Anseriformes, with an additional 15 cases of replicate estimates for a species/tribe/geographic stratum. After controlling for the effects of body mass on variation in life-history traits, it is possible to examine differences among tribes in average annual survival rates. Previous work along these lines has produced conflicting results. Laurila (1988), Saether (1987, 1989), Gaillard et al. (1989), and Dobson (1990) found that phylogeny covaries with lifespan, whereas Brawn et al. (1995) determined that phylogeny was unrelated to lifespan. This apparent difference may have resulted in part because Brawn et al. (1995) examined only a single order, Passeriformes, whereas the other researchers examined many orders. Based on the findings of Laurila (1988), Saether (1987, 1989), and Gaillard et al. (1989), we predicted that anseriform phylogeny would explain a significant amount of the residual variation in average annual survival rates, after we controlled for body mass. However, we could not predict the direction of these differences.

Body mass.—Body mass relates to many biological characteristics (Western and Ssemakula 1982; Boyce 1984; Saether 1985, 1987, 1989; Laurila 1988; Brawn et al. 1995). Relationships between body mass and phylogeny have suggested that among orders, anseriforms tend to have both late age at first reproduction and high fecundity (Gaillard et al. 1989). Within orders, Saether (1987) found evidence of a "slow-fast continuum" contrasting at the slow end with large eggs, small clutch sizes, long incubation periods, delayed fledging, and delayed maturation, with the opposite traits at the fast end. Thus, we predicted that body mass would explain a large amount of the variation in average annual survival rates, and that waterfowl with larger body masses would have greater survival rates than waterfowl with smaller body masses.

DATA AND METHODS

We confined our analyses to data from adult females because of their high philopatry to nesting areas (Bellrose 1976) and the probable direct connection between reproductive effort (e.g. egg production) and survival (Roff 1992). When available, we used body mass during the winter to avoid the potentially large fluctuations in mass that occur near the time of egg formation. We used Livezey's (1986, 1991) tribal classification.

We used average annual survival rates for adult females except in cases where reported survival rates did not differ between adult females and other age/sex classes. In several cases, we calculated annual survival rates based on unpublished data and data accessed from the files of the U. S. Fish and Wildlife Service, and the New Zealand Department of Conservation's Banding Office. Unless stated otherwise, the methods of Brownie et al. (1985) were used for recoveries (dead animals) and those of Cormack-Jolly-Seber (Pollock et al. 1990) for recaptures (live animals). When given a choice among models, we chose the most parsimonious model that fit the data adequately. If the chosen model included temporal variation in survival rates, then we used the average survival rate.

In categorizing survival rates by geographic strata, we assigned New Zealand to a separate stratum from Australia because of its disproportionate number of endemic waterfowl species (Marchant and Higgins 1990) and its long geological separation from Australia. To model variation in survival rates among species from various locations, we fitted a linear model to survival-rate estimates. All estimates were obtained using modern banding and capture-recapture models based on Brownie et al (1985) and were maximum likelihood or bias-adjusted maximum likelihood estimates.

Survival-rate estimates were subject to two sources of variation: (1) that arising from the sampling process, and (2) the naturally occurring variation among the true survival rates. Only the second source of variation is of biological interest, but in the modeling process it is important to distinguish between the two sources. Because of this process, standard procedures and software could not be applied. Instead, we used the GAUSS (Aptech 1988) programming language to fit the model described below.

Notation.—The probability that a bird of species j, tribe k, stratum l, survives from the start of year t until the start of year $t + 1$ is $S_{j,k,l}$. For convenience, we use the subscript i ($i = 1, \ldots, n$) to denote a unique combination of the subscripts j, k, and l. $\hat{S}_i$ is an estimate of S_i, and $\hat{Y}_i$ is an estimate of Y_i, where

$$Y_i = \text{logit}(S_i) = \ln\left[\frac{S_i}{1 - S_i}\right]. \quad (1)$$

Model.—The model has two components. The first models the process of obtaining the estimated Y_i and the second the relationship among the Y_i s. Our interest lies in the second component, i.e. the relationship among the Y_i s that contains the information of biological relevance. The first component of the model is required to ensure that the inference process is not corrupted by unmodeled variation arising during the sampling process. The formal model for these two components is as follows.

Conditional on the true value Y_i, the estimated values $\hat{Y}_i$ were modeled as independent normal random

variables with expected value $E[\hat{Y}_i \mid Y_i] = Y_i$, and variance $\text{Var }(\hat{Y}_i \mid Y_i) = \tau_i^2$. From the estimates $\hat{S}_i$ and their standard errors $\text{SE}(\hat{S}_i)$, we obtained estimates of Y_i and τ_i using

$$\hat{Y}_i = \ln\left[\frac{\hat{S}_i}{1 - \hat{S}_i}\right] \qquad (2)$$

and

$$\hat{\tau}_i^2 = \left[\frac{\text{se}(\hat{S}_i)}{\hat{S}_i(1 - \hat{S}_i)}\right]^2. \qquad (3)$$

From maximum-likelihood theory (Mood et al. 1974), equation 2 is the maximum-likelihood estimate of $\hat{Y}_i$ and equation 3 provides a consistent estimate of τ_i^2.

In the most general model, the Y_is were modeled as independent normal random variables with mean μ_i and variance δ_i^2. Various hypotheses were tested using restricted versions of this model created by imposing constraints on the μ_i and δ_i^2.

From equations 2 and 3, and the properties of the normal distribution, it follows unconditionally that the $\hat{Y}_i$ values are independent normal random variables with mean μ_i and variance $\delta_i^2 + \tau_i^2$, and $y = (\hat{Y}_1, \ldots, \hat{Y}_n)'$ is multivariate normal with mean vector $\mu = (\mu_1, \ldots, \mu_n)$ and diagonal variance-covariance matrix Σ with ith diagonal element $\delta_i^2 + \tau_i^2$. All of the models we fitted were linear, hence μ could be expressed in the form $\mu = X\beta$ where X is the model matrix and β is a parameter vector.

Parameter estimation.—So far, all of the models considered include n τ_i^2, and including n μ_i and n δ_i, we have more parameters than data. To reduce the number of parameters we make use of the estimates of τ_i^2 obtained via equation 3 in conjunction with the estimates of Y_i, substituting these $\hat{\tau}_i^2$ for the τ_i^2 in Σ. Thus our analysis is conditional on these $\hat{\tau}_i^2$.

Maximum-likelihood parameter estimates were obtained using a two-stage iterative procedure (Draper and Smith 1981). Conditional on Σ the maximum-likelihood solutions to β are

$$\hat{\beta} = (X'\Sigma^{-1}X)^{-1}(X'\Sigma^{-1}y). \qquad (4)$$

Given a particular value for β, the multivariate likelihood function (5)

$$L(y, \beta, \Sigma) = \frac{-p}{2}\ln(2\pi) - \frac{1}{2}\ln(|\Sigma|)$$
$$- \frac{1}{2}(y - X\beta)'\Sigma^{-1}(y - X\beta) \qquad (5)$$

can then be maximized with respect to δ_i^2 using standard numerical procedures. Note that $|\Sigma|$ denotes the determinant of the matrix Σ, and p is the dimension of the vector β, i.e. the number of parameters comprising the β vector. Once a new value for δ_i^2 has been obtained, and hence a new value for Σ, the procedure can then be repeated until convergence.

Hypothesis testing.—We considered three types of models.

(1) $(G * T * BM * BM^2, \delta^2)$. In this homoscedastic linear regression model, values of μ_i were modeled as linear functions of effects due to geography (G), tribe (T), body mass (BM), and a quadratic function of $\ln(BM^2)$. We investigated the quadratic function because we were interested in whether there was an asymptotic relationship between survival and body mass. All interaction terms except those including $\ln(BM)$ and its square were included in the model. This model included the homoscedastic constraint $\delta_1^2 = \delta_2^2 = \ldots = \delta_n^2$. Within this group of models we fitted reduced versions to test the significance of the different effects.

(2) (μ_i, δ^2). In this model, each unique combination of species, tribe, and stratum had its own mean. The constraint $\delta_1^2 = \delta_2^2 = \ldots = \delta_n^2$ was included as in the previous model. This model treated multiple estimates for species/tribe/stratum combinations as replicates. Usually these replicates were obtained from different geographic locations within the particular stratum. In some cases the replicates were obtained at the same location but from a different time period. These location/time effects were assumed to be random and hence incorporated within the δ^2 term of the model. The inclusion of this model allowed us to test the validity of the linear regression model. The model was fitted to the subset of data for which replicated observations of species/tribe/stratum combination i existed.

(3) (μ_i, δ_i^2). In this model, each unique combination of species, tribe, and stratum had its own mean as in the previous model. In addition, each unique combination of species, tribe, and stratum had its own δ_i^2. Thus, this model relaxed the homoscedastic error assumption. As in the previous model, this model was only fitted to the subset of data for which replicated observations of species/tribe/stratum combination i existed.

Models were compared using the generalized likelihood ratio test (GLRT; Lebreton et al. 1992). To compare $(G * T * BM * BM^2, \delta^2)$ with (μ_i, δ^2) and (μ_i, δ_i^2) using the GLRT, the models needed to be nested. For these comparisons, this was ensured by fitting $(G * T * BM * BM^2, \delta^2)$ to the same subset of data used to fit (μ_i, δ^2) and (μ_i, δ_i^2).

RESULTS

Data from six tribes were collected. Not all tribes were equally represented (e.g. only one species for the Tadornini). The best represented tribe was the Anatini with 14 species from five strata. Annual survival-rate estimates across all species ranged from a low of 0.334 to a high of 0.935 with standard errors of the estimates ranging from 0.010 to 0.294 (Table 1). In all, 107 estimates were collected from five strata. North

TABLE 1. Average annual survival rate ($\times 100$), standard error (in parentheses), and body mass (kg) of adult female waterfowl from around the world.

Species	Survival	Estimator[a]	Reference[b]	Body mass	Reference
Africa					
Anas undulata	72.2 (4.48)	B	1	1.008	Dunning 1993
Australia					
Anas gibberifrons	55.0 (17.0)	B	2	0.474	Marchant & Higgins 1990
Anas superciliosa	63.0 (6.0)	B	2	1.025	Marchant & Higgins 1990
Europe					
Bucephala clangula	77.2 (3.4)	C	3	0.787	Dunning 1993
Somateria mollissima	89.5 (1.46)	C	4	2.142	Dunning 1993
Anas clypeata	58.1 (2.96)	B	5	0.680	Dunning 1993
Aythya ferina	59.2 (2.22)	B	5	0.807	Dunning 1993
Aythya fuligula	70.7 (1.96)	B	5	0.680	Dunning 1993
New Zealand					
Anas platyrhynchos	44.0 (5.0)	B	6	1.123	Marchant & Higgins 1990
	41.0 (4.0)				
	40.0 (5.0)				
	59.0 (6.0)				
Anas superciliosa	55.0 (12.0)	B	7	0.981	Marchant & Higgins 1990
Anas rhynchotis	68.2 (3.56)	B	8	0.614	Marchant & Higgins 1990
Anas gibberifrons	50.1 (11.29)	B	8	0.469	Dunning 1993
Cygnus atratus	84.3 (5.1)	B	8	5.100	Marchant & Higgins 1990
Branta c. maxima	74.0 (1.7)	B	5	4.489	Marchant & Higgins 1990
	77.0 (1.1)	B	5		
Tadorna variegata	79.4 (19.9)	B	8	1.387	Marchant & Higgins 1990
	55.5 (2.4)				
	52.6 (5.7)				
	70.1 (3.93)				
	64.4 (4.45)				
	68.2 (3.56)				
North America					
Cygnus buccinator	80.0 (1.0)	B	9	10.300	Dunning 1993
Cygnus columbianus	92.3 (4.3)	S	6	6.255	Bellrose 1976
	91.9 (4.7)				
	93.5 (6.6)				
Anser albifrons	64.9 (6.9)	B	10	2.456	Dunning 1993
Chen caerulescens	81.6 (1.6)	B	11	2.517	Dunning 1993
Chen canagica	58.6 (4.5)	C	12	2.150	C. Dau & J. Schmutz unpubl.
Branta c. canadensis	66.8 (2.6)	B	13	3.420	Bellrose 1976
	71.9 (1.5)				
	68.2 (1.9)				
B. c. occidentalis	83.6 (4.3)	B	14	3.043	Bellrose 1976
B. c. leucoparia	70.0 (2.0)	C	15	1.940	Dunning 1993
B. c. interior	78.6 (3.1)	S	16	3.514	Bellrose 1976
B. c. maxima	76.4 (5.47)	B	17	4.995	Bellrose 1976
B. c. moffitti	63.6 (1.0)	B	18	4.044	Dunning 1993
B. c. minima	59.9 (1.5)	C	19	1.264	Dunning 1993
Branta bernicla	79.2 (3.64)	B	20	1.230	Bellrose 1976
	83.5 (4.11)	B	21	1.390	Bellrose 1976
Aix sponsa	47.6 (1.66)	B	22	0.635	Dunning 1993
	46.9 (1.85)				
	52.4 (2.15)				
Anas americana	58.2 (3.63)	C	23	0.719	Dunning 1993
	58.9 (6.35)				
	66.7 (6.01)				
	56.0 (6.0)	C	24		
Anas platyrhynchos	56.8 (4.3)	B	25	1.098	Bellrose 1976
	58.1 (12.4)				
	56.0 (4.1)				
	55.0 (2.5)				

TABLE 1. Continued.

Species	Survival	Estimator[a]	Reference[b]	Body mass	Reference
	58.6 (6.9)				
	59.7 (4.8)				
	73.5 (13.7)				
	51.3 (7.5)				
	53.6 (8.8)				
Anas rubripes	45.4 (3.9)	B	26	1.100	Dunning 1993
	48.7 (6.6)				
	57.3 (5.2)				
	39.1 (5.3)				
	36.8 (4.5)				
	52.1 (3.8)				
	50.6 (2.5)				
Anas acuta	69.3 (6.0)	B	27	0.860	Bellrose 1976
	62.0 (7.4)				
	61.4 (4.5)				
	57.3 (5.4)				
	60.3 (6.1)				
	71.2 (4.0)				
	64.7 (2.5)				
	56.7 (4.9)				
	54.2 (5.1)				
	55.1 (4.6)				
	76.9 (9.7)				
	70.8 (5.4)				
	50.0 (4.5)				
	42.1 (21.5)				
	66.8 (10.6)				
	70.1 (5.3)				
	57.1 (9.1)				
	59.8 (4.1)				
Anas discors	52.2 (1.8)	B	28	0.374	Bellrose 1976
	50.0 (2.7)				
	57.3 (3.1)				
	53.1 (9.2)				
	41.0 (6.0)	C	24		
Anas crecca	68.9 (15.1)	B	29	0.318	Dunning 1993
	50.7 (29.4)				
	33.4 (3.22)				
	53.1 (6.01)				
	46.5 (3.04)				
	42.8 (14.98)				
	42.9 (4.75)				
Anas strepera	69.0 (6.51)	B	30	0.828	Bellrose 1976
	56.0 (5.0)	C	24		
Anas fulvigula	46.3 (5.6)	B	31	0.952	P. Gray unpubl.
Anas clypeata	46.0 (5.0)	C	24	0.590	Dunning 1993
Aythya collaris	54.7 (7.7)	B	32	0.680	Dunning 1993
	49.5 (4.3)				
	47.1 (8.0)				
Aythya valisineria	56.2 (5.0)	B	33	1.230	Nichols & Haramis 1981
	56.1 (5.2)				
	69.0 (6.9)				
Melanitta fusca	77.3 (1.76)	B	34	1.467	G. Dobush unpubl.
Somateria mollissima	87.3 (1.56)	B	34	1.521	Bellrose 1976

[a] B = Brownie et al. (1985); C = Cormack-Jolly-Seber (Pollock et al. 1990); S = SURVIV (White 1983).

[b] 1 = Dean and Skead (1989); 2 = Halse et al. (1993); 3 = Dow and Fredga (1984); 4 = Coulson (1984); 5 = J. D. Nichols (unpubl. data); 6 = Nichols et al. (1992); 7 = Caithness et al. (1991); 8 = R. J. Barker (unpubl. data); 9 = Anderson et al. (1986); 10 = Timm and Dau (1979); 11 = Francis et al. (1992); 12 = Petersen (1992); 13 = Hestbeck (1994); 14 = Ratti et al. (1978); 15 = Yparraguirre (1982); 16 = Samuel et al. (1990); 17 = Tacha et al. (1980); 18 = Krohn and Bizeau (1980); 19 = Raveling et al. (1992); 20 = Conroy et al. (1989); 21 = Lensink (1988); 22 = Johnson et al. (1986); 23 = Rienecker (1976); 24 = T. S. Arnold and W. R. Clark (unpubl. data); 25 = Trost (1987); 26 = Krementz et al. (1987); 27 = Hestbeck (1993); 28 = USFWS (unpubl. data); 29 = Chu et al. (1995); 30 = Szymczak and Rexstad (1991); 31 = F. A. Johnson (unpubl. data); 32 = Conroy and Eberhardt (1983); 33 = Nichols and Haramis (1980); 34 = D. G. Krementz (unpubl. data).

TABLE 2. Analysis of deviance for the model Geographic Strata * Tribe * Body Mass * (Body Mass²), δ^2.

	Δ deviance[a]	df	P
Geographic strata	4.93	4	0.295
ln(body mass)	62.64	1	<0.0001
ln(body mass²)	0.37	1	0.545
Tribe	44.87	5	<0.0001
2-way interactions (linear)	27.25	11	0.004
3-way interactions (linear)	8.94	1	0.003
3-way interactions (quadratic)	0.32	1	0.571

[a] χ^2 approximation.

Fig. 1. Relationships between survival rate and body mass in waterfowl tribes. The Tadornini is not included.

America had the greatest number of estimates and Africa the fewest. Tribes were not equally represented across strata; the most tribes were represented by North America and the fewest by Australia and Africa (Table 1).

All variables (geographic strata, tribe, body mass) were important in explaining variation in survival rates (Table 2). Although the main effect of strata was not significant ($\chi^2 = 4.93$, df $= 4$, $P = 0.29$), there were significant interactions between strata and tribe and strata and body mass. Thus, strata influenced both the intercept and the slope of the survival rate/body mass relationship. In particular, Anserini from New Zealand and both Anatini and Aythyini from Europe had relatively high survival rates for their body masses ($P < 0.05$), but the slopes were similar to those of other tribes. In New Zealand, survival rates for Cygnini and Anatini were lower than those of Anserini. Body mass had a noticeably larger effect on survival rates of European Aythyini than on European Anatini or New Zealand Anserini, but the effect of body mass was reduced at higher body masses. That Europe was involved in three interaction terms suggests that the relationship between body mass and survival rate was different than that from the other strata.

Variation in survival rates was affected by tribe ($\chi^2 = 44.87$, df $= 5$, $P < 0.001$; Table 2, Fig. 1). Survival rates were highest for Cygnini, followed by Anserini and Mergini (which were equal), then Anatini and Aythyini (which also were equal). Among tribes represented by more than one species, all except for Cygnini exhibited positive relationships between survival and body mass; this effect was greatest for Mergini (Fig. 1). Survival rates of swans were inversely related to body mass, with *Cygnus buccinator* having relatively low survival for its size. An-
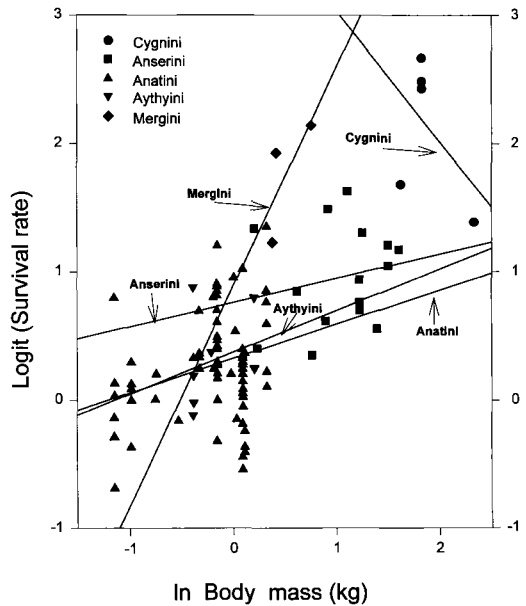
derson et al. (1986) obtained several survival-rate estimates for *Cygnus buccinator*, which varied from 79.6 to 88.2%, and suggested that the true survival rate was "perhaps 90%." We chose to use the lower estimate of 80% because it was derived from the largest data set. Nevertheless, the relationship between body mass and survival for swans remains open to debate.

In testing for a lack of linear fit, we examined only those cases where we had replicate estimates for a species/tribe/strata combination ($n = 15$). In comparing the full regression model with one allowing each of the 15 species/tribe/strata combinations to have its own mean, we found significant evidence of a lack of linear fit ($\chi^2 = 31.48$, df $= 5$, $P < 0.001$). This suggests that additional variation in the data exists that was not accounted for by the main effects and the interaction terms that we modeled. This "unaccounted for" variation does not mean that our results led us to incorrect conclusions. Rather, it suggests that we should be cautious in the strength of our inferences. When we further generalized the model to allow each group to have its own variance (δ_i^2), we found no evidence that the variance changed with the mean μ_i ($\chi^2 = 9.86$, df $= 14$, $P = 0.77$).

We found strong evidence that survival rates depend on body mass ($\chi^2 = 62.64$, df $= 1$, $P <$

0.001; Table 2, Fig. 2), but the significant qua-
dratic term ($\chi^2 = 9.15$, $P < 0.001$) indicates that
the relationship between logit(S_i) and body mass
is nonlinear. Examining the tribe-specific plots
of logit(S_i) and body mass revealed that for spe-
cies with sufficient data (Anserini, Anatini,
Mergini), survival rate was low when body mass
was either low or high, and was high when
body mass was intermediate.

DISCUSSION

Although we examined the effects of geog-
raphy essentially at the level of the continent,
we found evidence that geography was related
to waterfowl life histories (as did Laurila [1988]).
Laurila (1988) based his analyses on distance
from the equator and found that waterfowl
breeding in the arctic: (1) were significantly
heavier than temperate or tropical species; (2)
matured later in life (i.e. live longer); (3) pro-
duced young that matured more rapidly; and
(4) experienced higher rates of nest predation.
We also found that tribes with significant in-
teractions with geography were from strata far-
ther from the equator; Aythyini and Anatini
from Europe, and Anserini from New Zealand,
had higher survival than would be expected for
their body size. We caution that we lacked data
on survival rates of waterfowl residing near the
equator. Thus, the notion of an apparent in-
crease in survival with increasing distance from
the equator may require reassessment if addi-
tional data from southern latitudes becomes
available (see Brawn et al. 1995). Laurila (1988)
also noted that large-sized waterfowl tend to
nest in the arctic, have poorly concealed nests,
and are prone to high levels of nest predation.
He suggested that large body size evolved as a
defense against predators and as a means of
reducing relative heat loss (sensu Bergmann's
rule).

In analyses of the species/tribe/strata com-
binations, we found that the main effects and
interaction terms that we modeled did not ac-
count for the substantial variation in the data.
In an attempt to address Saether's (1987) hy-
pothesis that ecological traits explain much of
the variation in demographic patterns in birds,
Pontier et al. (1990) examined the influence of
seven ecological traits on various demographic
patterns. Their results supported Saether's hy-
pothesis. Furthermore, they determined that the
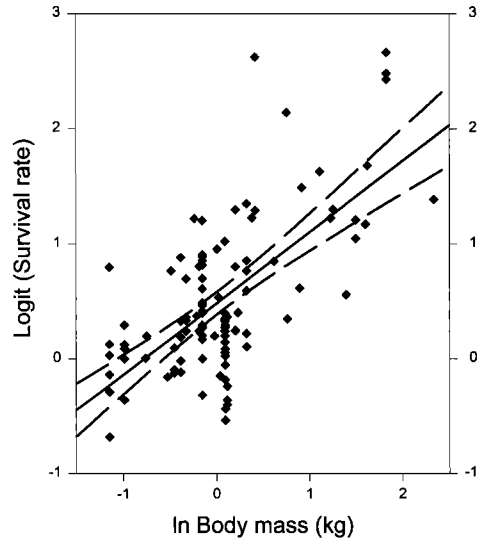Anseriformes was at one end of the slow-fast

Fig. 2. Relationship between survival rate and body
mass in waterfowl. Confidence limits are 95% inter-
vals around the regression line.

continuum among the nine orders examined.
Pontier et al. (1990) found that the anseriforms
were wholly classified as exhibiting character-
istics of very rapid turnover, i.e. low life ex-
pectancy and high reproductive effort. Al-
though we question whether the Cygnini should
be characterized as exhibiting very rapid turn-
over (see Laurila 1988), we concede that eco-
logical traits might help absorb some of the
unexplained variation that we noted.

Unlike Brawn et al. (1995), we and others
(Saether 1987, Dobson 1990, Gaillard et al. 1989)
have found that phylogeny is important in ex-
plaining survival rates. Survival rates varied
among tribes, with the Cygnini having the
highest rates and the Anatini and Aythyini the
lowest. That the Mergini had survival rates
comparable to the Anserini suggests that phy-
logeny does not always coincide with orderly
changes in survival rates. The Mergini is quite
distant phylogenetically from the Anserini
(Livezey 1986) and thus should have had lower
survival rates than we found.

Body mass was important in explaining life-
history parameters (see also Western 1979; Pe-
ters 1983; Stearns 1992; Saether 1985, 1987, 1989;
Gaillard et al. 1989; Pontier et al. 1990; Dobson
1990; Brawn et al. 1995). Our estimate that 44%
of the variation in survival rates was explained
by body mass exceeds the 33% found by Gaillard
et al. (1989). Nonetheless, the similarity of these

estimates is surprising and suggests that the factors responsible for the large amount of explained variation in survival rates are few. Too, our finding that for some tribes, survival rates were low at both low and high body masses is intriguing. We predict that as additional data become available, this same pattern will be demonstrated in the tribes for which we had only small amounts of data. But why does this pattern occur? We agree with Peters (1983) and Gaillard et al. (1989) that the biomechanical constraints of flight constitute a strong selective pressure that probably controls the range of body masses in birds. It appears that waterfowl are being penalized with low survival rates at both ends of the range of body masses. Clearly, body mass plays an important role in determining the life-history characteristics of waterfowl.

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