

Temporal shift in density dependence among North American breeding duck populations

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Abstract. Environmental perturbation can have a marked influence on abundance and trend in many animal populations, but information is scant on how numerical change relates to variability in density-dependent and density-independent processes acting on populations. Using breeding population estimates for 10 duck species from a survey area of ~2.2 million km² in central North America (1955–2005), we compared population growth models and related parameters among species and across time. All duck species showed evidence of density-dependent growth, and the best-fit relationship between population growth (r_t) and population size (N_t) was linear or convex for all species. Density dependence and associated population parameters were not related to an index of species life history strategy. Reanalysis of segmented (1955–1979, 1980–2005) r_t time series, where the truncation date coincided with a putative decline in wetland availability on breeding grounds, showed that density-dependent forces were weakened during the latter time segment. Additionally, in later years most populations experienced increased first-order autocorrelation in annual counts, decreased intrinsic growth rate, increased nonlinearity in the relationship between r_t and N_t , increased equilibrium return time, and increased inter-species synchrony in numbers. Such changes were not closely related to species life history strategy or to shifts in mean population size, average trend, and estimated carrying capacity. We speculate that shifts in breeding duck habitat quality altered historical predator–prey dynamics in the system and thereby underlie observed dynamical changes. The paradoxical finding that population abundance and trend do not reveal shifts in population processes highlights the need to go beyond simple numerical assessment when evaluating population responses to environmental perturbation.

Key words: density dependence; ducks; growth rate; population regulation; temporal shifts; time series analysis.

INTRODUCTION

Variability in patterns of animal abundance and population trend are proximally due to changes in demographic attributes of individuals. It follows that changes in population demography ultimately are driven by variation in density-dependent and density-independent processes acting on individuals (Sæther et al. 2002, Lande et al. 2003). Although extensive work has characterized basic population processes and their implications to population dynamics (Sæther and Engen 2002, Sibly et al. 2005), in general, linkages between population processes and numerical variability have not been fully elucidated. This disparity has arisen in part because patterns of population regulation rarely are studied to reveal either their specific nature or the temporal variability underlying such processes (Hassell 1986, Hassell et al. 1989). Furthermore, population processes can vary considerably even among closely related species sharing similar habitats, implying that

species life history or other salient factors can obfuscate underlying patterns (Sæther and Engen 2002, Sæther et al. 2002). This complexity has limited our understanding of mechanisms influencing population variability, which is alarming especially given widespread environmental perturbation across many ecosystems, corresponding numerical declines among many species, and the recognized prevalence of density dependence in shaping population status and viability (Morris and Doak 2002, Lande et al. 2003). Thus, understanding the relationship between population processes and numerical variability should be a priority in animal population ecology and conservation biology.

Patterns of density dependence may be closely related to basic attributes of a given population. For example, weak density dependence at carrying capacity (K) should beget low autocorrelation between consecutive population counts, high numerical variability, rapid growth, and weak population regulation at equilibrium densities (Sæther and Engen 2002). For many species, population growth rates are strongly curtailed by density dependence even at low densities (Sibly et al. 2005), and such populations should exhibit high

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variability, low intrinsic growth rate, and weak regulation at equilibrium (Sæther and Engen 2002, Sæther et al. 2002). However, because the above predictions are integrally linked to life history strategy, it is unclear how local environmental conditions can impose commonality in population processes among sympatric populations. Indeed, to date studies comparing the role of density dependence across taxa have compared populations from disparate geographical areas where site-specific influences cannot be fully discounted (e.g., Sæther and Engen 2002, Sæther et al. 2002, Sibly et al. 2005). Also, comparative studies usually rely on data collected at relatively small numerical and spatial scales, meaning that demographic stochasticity may conceal underlying patterns. It follows that larger-scale analyses, where space and time are held constant across multiple species, are warranted.

Using breeding population survey data (1955–2005) for 10 sympatric duck species from central North America, we examined variability in density dependence across populations and through time. We predicted that patterns of density dependence would correspond with dynamical features such that species with weaker density dependence should have higher variability, higher intrinsic growth rate, and increased return time at equilibrium population densities, compared to species with stronger density dependence. Having first shown that the strength of density dependence failed to follow a clear pattern related to species life history, we then reveal that regulation generally became weaker and most population parameter estimates underwent corresponding changes, with time. Given the prevalence of this phenomenon across duck species, we surmise that recent changes in duck breeding habitat (loss of wetlands, increased predation) elicited widespread shift in duck population dynamics in the central prairies of North America.

METHODS

Breeding waterfowl surveys

Since 1955, duck numbers across the core duck breeding region in central Canada, Alaska, and the north-central United States are estimated yearly through the annual Breeding Waterfowl Population and Habitat Survey (U.S. Fish and Wildlife Service 2005). Surveys are conducted each May using fixed-wing aircraft, with the “traditional” survey area (51 strata in total, numbers 1–18, 20–50, and 75–77) encompassing ~2.2 million km² and constituting the region with highest waterfowl production in North America (U.S. Fish and Wildlife Service 2005). Spatial variation in duck distribution is addressed through systematic stratified sampling with transect density being proportional to duck density; duck detectability is considered (since 1961) via double-sampling involving ground-truthing segments of each transect (U.S. Fish and Wildlife Service and Canadian Wildlife Service 1987, Nichols et al. 1995). Ten duck species [Mallard (*Anas platyrhynchos*), Gadwall (*A.*



PLATE 1. Canvasback with young. Photo credit: Ducks Unlimited Canada.

strepera), American Wigeon (*A. americana*), Green-winged Teal (*A. crecca carolinensis*), Blue-winged Teal (*A. discors*), Northern Shoveler (*A. clypeata*), Northern Pintail (*A. acuta*), Redhead (*Aythya americana*), Canvasback (*A. valisineria*; see Plate 1), and Lesser Scaup (*Aythya affinis*) actively nest on the survey area and are the focus of the present investigation; other duck species were excluded because their core breeding area lies elsewhere. We considered that the survey area constitutes meta-populations of each of the 10 species, with sub-populations inside the area operating largely as a panmictic group on the breeding grounds. Accordingly, we used estimated population size for each species, as well as pooled total numbers, counted annually across the traditional survey area (U.S. Fish and Wildlife Service 2005, Wilkins et al. 2005). This approach permitted evaluation of duck population regulation across constant space and time and at a sufficiently broad scale to discount stochastic forces observed in smaller populations (see also Jamieson and Brooks 2004).

Population dynamics analysis

We characterized population variability using SD, coefficient of variation ($CV = SD/\text{mean}$), and first-order autocorrelation in the untransformed 51-year population abundance (N_t) time series (Sæther et al. 2002). The 50-year time series of log per capita population growth rate (r_t) was $r_t = \ln(N_{t+1}/N_t)$ for each inter-year interval (Royama 1992). First-order autocorrelation in both N_t and r_t was assessed using Ljung-Box white noise tests (Ljung and Box 1978). We assessed the role of evolutionary strategy in duck population trends using a life history index (LHI; Johnson and Grier 1988). The LHI is an average of the stability/predictability of wetlands used by each species and the correlation coefficient between pond and duck densities for each species, and it represents relative opportunism in response to habitat change (Johnson and Grier 1988).

The LHI is corroborated by independent sources supporting the pattern of species ordination (e.g., Patterson 1979, Vickery and Nudds 1984), and is appropriate for our purposes because it was developed for sympatric populations using consistent estimation procedures and over a fixed time. In contrast, demographically based alternatives were not satisfactory due to high vital rate variability (Johnson et al. 1992; D. L. Murray, *unpublished data*).

We assessed density dependence by fitting population growth models to each r_t time series using least squares regression (Sibly et al. 2005). First, we fit a density-independent (exponential) model:

$$r_t = r_{\max} \quad (1)$$

where r_{\max} is the intrinsic rate of increase at N_0 . Second, we fit a linear density-dependent (Ricker) model:

$$r_t = r_{\max} \left[1 - \frac{N_t}{K} \right] \quad (2)$$

where K is the carrying capacity. The third fit was a nonlinear density-dependent (theta-Ricker) model:

$$r_t = r_1 \left[1 - \frac{N_t^\theta - 1}{K^\theta - 1} \right] \quad (3)$$

where r_1 is the observed rate of increase at $N=1$ and θ is the parameter describing the relationship between r_t and N_t (Sæther and Engen 2002). The theta-Ricker reduces to the Ricker equation when θ equals 1, so the latter model characterizes density dependence more parsimoniously. We used the above theta-Ricker model instead of the more common formulation (see Sibly et al. 2005) because of its superior convergence properties and its allowance for nonpositive θ values (Sæther and Engen 2002). To satisfy a reviewer, we fit theta-Ricker models both without restriction and with $\theta > -1$ to respect a parameter space more consistent with first principles associated with the model (Sæther et al. 2008; J. Ross, *unpublished data*); our results were qualitatively similar and we report the latter findings exclusively. Note that inverse density-dependent (Allee effects) models failed to perform well and thus were excluded (see Sæther et al. 2002, Sibly et al. 2005), and we did not fit time-delayed density-dependent models because most species are governed by first-order processes (D. L. Murray, *unpublished data*). Models were ranked using Akaike's information criterion, corrected for small sample size (AIC_c ; Burnham and Anderson 2002). Change in AIC_c between models (Δ_i), and Akaike weights (w_i) were used to guide model selection. We considered that models with $\Delta_i < 2.0$ had comparable support to the best-fit model (Burnham and Anderson 2002).

Spurious detection of density dependence can occur in time series data having strong measurement noise (Shenk et al. 1998, Freckleton et al. 2006). We tested for autocorrelation in residuals for our linear density-dependent models using Ljung-Box white-noise tests

(Ljung and Box 1978); the overall paucity of autocorrelation indicated negligible influence of sampling error (see *Results*; also see Dennis and Otten 2000, Dennis et al. 2006). In addition, we fit both density-dependent models that estimated sampling error and state-space models that explicitly included actual observation standard errors (Appendix A), and conducted simulations assessing the likelihood of falsely detecting density dependence in our data (Appendix B); both exercises supported our basic inference regarding density dependence. Throughout, we emphasize results from fitting the theta-Ricker rather than Gompertz or state-space models because this approach allowed us to explore non-linearity in density dependence and fit models that were minimally phenomenological. Furthermore, simulations across a wide parameter space reveal close correspondence between the theta-Ricker and alternative models except where population time series are short or sampling error is large (A. Brand, *unpublished data*).

The linear density-dependent model was selected as the main equation for comparing population parameters (r_{\max} , K , σ^2) because it provided the best fit for most time series (see *Results*) and allowed us to compare r_{\max} and K while holding constant the relationship between r_t and N_t . We also estimated separately (1) a density-dependence parameter, where $\gamma = ([r_{\max}/K] \times 1000)$ as determined from the stochastic logistic equation (Dennis and Taper 1994), and (2) θ representing the level of nonlinearity in the relationship between r_t and N_t from the theta-Ricker equation (Sæther and Engen 2002). All 95% confidence limits were derived by repeatedly simulating time series from estimated parameters, and then refitting equations to new series over 2000 iterations; confidence limits are the 95% ranked intervals in re-estimated parameters (Dennis and Taper 1994). To evaluate the prediction that variation in density dependence (or θ) would elicit differential regulation at equilibrium, we calculated the inverse equilibrium return time at K : $\lambda = r_1\theta/(1 - K^{-\theta})$ (Sæther and Engen 2002). All population attributes were compared to LHI using Spearman rank correlations (Sokal and Rohlf 1995).

Segmented time series

The above analyses assume fixed K and stationarity across the 51-year survey period; this assumption was relaxed by creating two separate time series, each spanning 25 one-year r_t time steps (1955–1979, 1980–2004; see Appendix C). Duck abundance between segments was compared qualitatively using ln-transformed mean and corresponding 95% CI. We used equivalence testing to compare population trend between segments, with population half-life/doubling time set at 50 years and degrees of freedom estimated from the Kenward-Rogers approximation (Dixon and Pechmann 2005); this analysis provided comparable results to those from alternate methods (see Dennis et al. 1991, Staples et al. 2004; D. L. Murray, *unpublished data*). As

TABLE 1. AIC_c differences (Δ_i) and AIC_c weights (w_i) for three population growth models fit to rate of change (r_t) time series for 10 duck species (1955–2004).

Species	Density independent		Density dependent (linear)		Density dependent (curvilinear)	
	Δ_i	w_i	Δ_i	w_i	Δ_i	w_i
Mallard	3.684	0.103	0.000	0.649	1.928	0.248
Gadwall	0.888	0.316	0.000	0.493	1.897	0.191
American Wigeon	9.472	0.007	0.000	0.759	2.352	0.234
Green-winged Teal	10.114	0.004	1.434	0.327	0.000	0.669
Blue-winged Teal	7.760	0.013	1.229	0.346	0.000	0.640
Northern Shoveler	2.204	0.190	0.000	0.573	1.766	0.237
Northern Pintail	3.836	0.095	0.000	0.643	1.796	0.262
Redhead	6.742	0.022	1.165	0.351	0.000	0.628
Canvasback	14.732	0.000	0.000	0.622	0.999	0.378
Lesser Scaup	6.053	0.033	1.704	0.289	0.000	0.678
Total ducks	5.895	0.038	0.000	0.720	2.180	0.242

with full time series, parametric bootstrap provided a probability distribution for each parameter estimate for density-dependent models fit to segmented time series, and we applied the percentile method on the difference in parameter estimates between segments to assess temporal variability within species (Efron and Tibshirani 1993). Temporal changes in parameter estimates across species were compared using Wilcoxon matched pairs signed-rank tests (Sokal and Rohlf 1995). Interspecific associations between N_t and r_t time series segments were compared via matrices derived from coherence correlative analysis (Redfern et al. 2006).

We consider that temporal changes in some duck population survey techniques (Smith 1995) may account for differential measurement noise and thereby contribute to apparent shifts in density dependence. We evaluated sampling error changes explicitly via restricted maximum likelihood methods (Staples et al. 2004, Dennis et al. 2006) and found that the overall estimated level of sampling error was comparable between time segments (Wilcoxon test: $W^+ = 41$, $W^- = 14$, $P = 0.193$; Appendix A). This led us to infer that any temporal difference in density dependence likely was not due to sampling error variability, although we acknowledge that CV (SE/annual population estimates; see Wilkins et al. 2005, Appendix A) appeared to decline through time for most species and thus could suggest improved survey techniques in recent years (K. Newman, *unpublished data*).

Truncation serves to detect changes in abundance and autocorrelation in time series relative to perturbation (Morris and Doak 2002, Turchin 2003). The particular truncation year (1980) was chosen because it provided (1) similar number of transitions in each segment for density dependence assessment (see Solow and Steele 1990, Brook and Bradshaw 2006) and (2) minimum number of observations (>20) for detecting density dependence from survey data (Woiwod and Hanski 1992). The early 1980s also coincided with intensified wetland loss in central Canada, and one duck species in particular, northern pintail, declined substantially be-

ginning around 1980 (Podruzny et al. 2002; see Appendix C). To confirm that results from segmented time series analysis were not an artifact of the specific truncation year, we subjected total duck counts to the analyses using a floating cutoff date (1975–1985); truncation year failed to provide qualitative differences implying that our results are robust.

RESULTS

Complete time series

Duck numbers were highly variable for most species through the 51-year time series (Appendix C; see also Wilkins et al. [2005:19] for original data). All species had significant, positively autocorrelated N_t time series and nonsignificant negatively autocorrelated r_t time series (Appendix D). Evolutionary strategy was not related to any of the basic population attributes (all Spearman rank $P > 0.07$). All duck species exhibited some degree of density-dependent population growth, with six species and total duck numbers conforming to a linear density-dependent model and all remaining time series being best-fit with the curvilinear model (Table 1, Fig. 1). For American Wigeon and total ducks, linear density dependence provided a superior fit compared to competing models (all $\Delta_i > 2.0$), and linear density dependence had some support for all remaining species (all $\Delta_i < 2.0$). Gadwall was the only species where the density-independent model was supported ($\Delta_i < 2.0$), although the linear density-dependent equation provided a better fit (Table 1). Overall, the weight of support (w_i) for the three population models across the 10 duck species averaged 0.505 ± 0.053 (SE), 0.417 ± 0.066 , and 0.078 ± 0.033 for the linear density-dependent, curvilinear density-dependent, and density-independent models, respectively. Diagnostics on the linear density-dependent model for each time series revealed that for seven species model residuals were not autocorrelated (all $P > 0.22$), whereas for Northern Shoveler ($\chi^2 = 3.402$, $P = 0.065$) and Scaup ($\chi^2 = 3.037$, $P = 0.081$) autocorrelation was marginally significant. Residuals for the Northern Pintail model exhibited significant, nega-

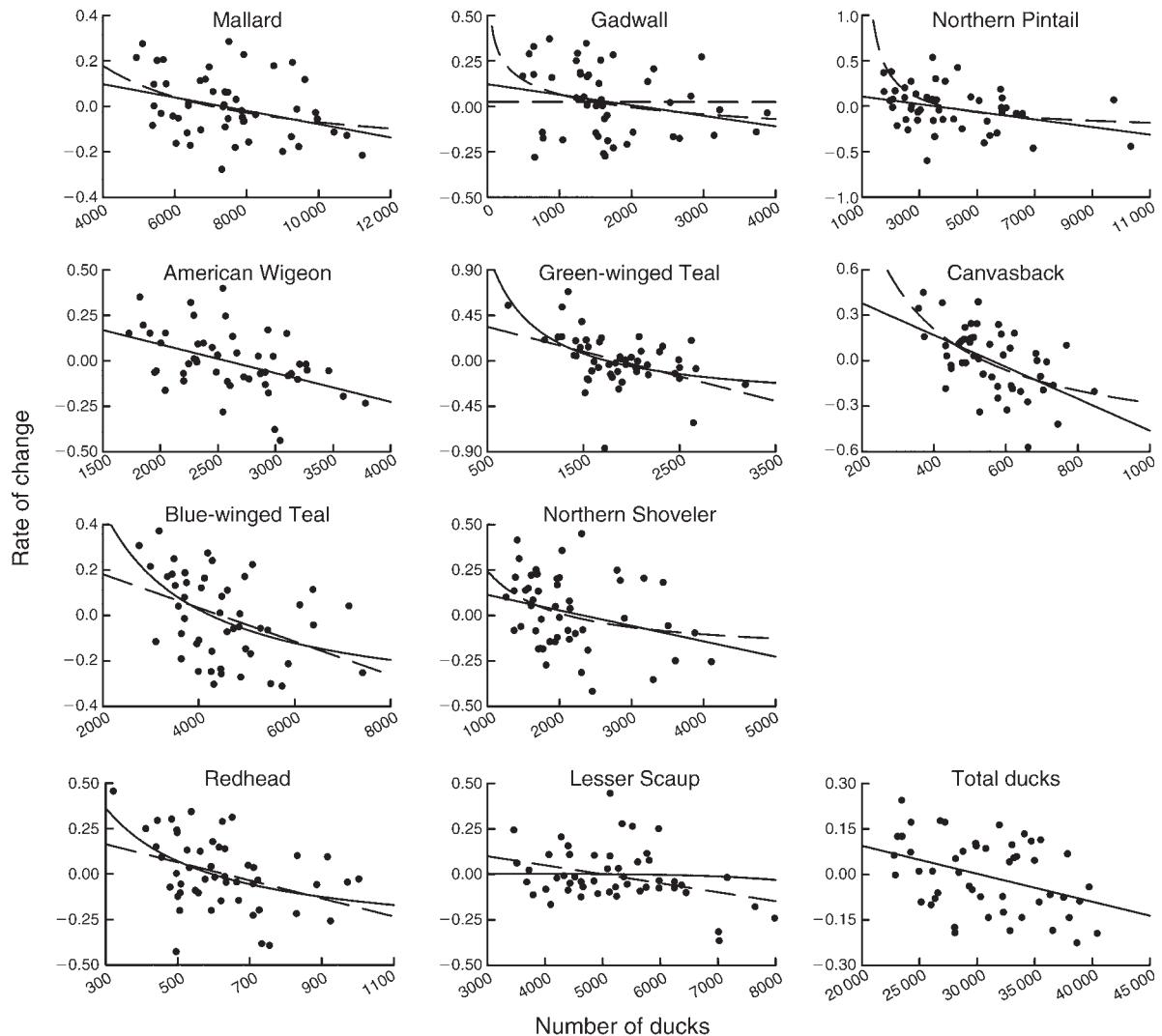


FIG. 1. Relationship between population growth rate [r_t , $\ln(N_{t+1}/N_t)$] and numbers of ducks (in thousands) in central North America (1955–2004). Best-fit relationships are represented with a solid line, and models with substantial support ($\Delta_i < 2.0$) are represented with a dashed line.

tive autocorrelation with a one-year lag ($\chi^2 = 7.114$, $P = 0.008$). Because LHI and AIC_c weight (w_i) for the density-independent model were not correlated ($r = -0.420$, $P = 0.23$), we surmise that life history strategy was not clearly related to the strength of density dependence.

Using the linear density-dependent equation, confidence intervals for the density dependence parameter, γ , excluded 0 for all species, thereby corroborating the finding that density dependence was the dominant population growth pattern for duck time series (Appendix E). The relationship between LHI and parameters for the Ricker model was not significant (all $P > 0.17$). Fitting the theta-Ricker equation to each dataset, only Lesser Scaup had a concave form of density dependence, whereas all other species and total duck numbers had a convex ($\theta < 1.0$) relationship between r_t and N_t

(Appendix E; Fig. 1). However, estimates of θ were not significantly different from 1.0 for any of the species (Appendix E), and LHI was not related to either basic shape of the line fit between r_t and N_t , nor estimates for θ ($r = -0.304$, $P = 0.39$) or λ ($r = 0.012$, $P = 0.97$).

Segmented time series

Over time, numbers of Gadwall, Green-winged Teal, and Northern Shoveler increased, Northern Pintail and Lesser Scaup decreased, and other species remained largely stationary (Table 2, Appendix C). Equivalence testing revealed that for all species population trend was nonsignificant during the first time period, whereas during the second segment only Lesser Scaup experienced significant (negative) trend (Appendix C; Lesser Scaup $t_{5,78} = 7.93$, $P = 0.003$, all other $P > 0.068$). Also, neither SD ($W_+ = 12$, $W_- = 43$, $P = 0.13$) nor CV ($W_+ =$

TABLE 2. Summary statistics for population estimates (in thousands) of 10 duck species surveyed annually in central North America (1955–2005).

Species	1955–1979		1980–2005		ΔCV	ΔN_t	Δr_t
	Mean	95% CI	Mean	95% CI			
Mallard	7912.9	7302.0–8523.9	7094.3	6464.2–7724.4	0.033	0.178	0.159
Gadwall	1219.3	1038.8–1399.7	2147.1	1828.8–2465.3	0.008	0.131	0.141
American Wigeon	2798.5	2602.1–2994.8	2439.1	2258.9–2619.4	0.013	0.020	0.001
Green-winged Teal	1644.5	1478.0–1810.9	2081.4	1906.0–2257.0	−0.036	0.612	0.236
Blue-winged Teal	4392.3	4097.5–4687.2	4605.4	4088.9–5121.8	0.115	0.311	−0.187
Northern Shoveler	1803.3	1658.6–1948.1	2539.0	2212.0–2866.0	0.125	0.385	−0.033
Northern Pintail	5536.0	4814.8–6257.2	2741.7	2477.0–3006.4	−0.077	−0.108	−0.186
Redhead	584.1	534.9–633.3	662.9	595.5–730.2	0.048	0.409	0.357
Canvasback	555.0	514.0–595.9	568.9	520.6–617.1	0.031	0.667	0.513
Lesser Scaup	5698.2	5327.4–6069.0	4690.0	4272.4–5107.7	0.063	0.471	0.300
Total ducks	32 144.0	30 223.1–34 064.9	29 572.0	27 541.2–31 602.7	0.025	0.177	0.048

Notes: ΔCV , ΔN_t , and Δr_t represent the change in coefficient of variation and first-order autocorrelation for the bisected N_t time series ([1981–2005] – [1955–1980]), and autocorrelation for the bisected r_t time series ([1980–2004] – [1955–1979]).

13, $W^- = 42$, $P = 0.16$) varied significantly over time. However, first-order autocorrelation in the N_t time series increased during the second time period for all species except Northern Pintail (mean difference in autocorrelation coefficient: 0.295 ± 0.076 ; $W^+ = 53$, $W^- = 2$, $P = 0.006$; Table 2). Autocorrelation in the r_t time series was consistent between time periods ($W^+ = 42$, $W^- = 13$, $P = 0.16$).

Patterns of duck population density dependence changed fundamentally between the first and second time segments. Overall, linear density dependence was either the best model (16 of 20 time series segments) or substantially supported ($\Delta_i < 2.0$; 4 of 20), whereas curvilinear density dependence was rarely the best (1 of 20) or a strong contender (6 of 20). Remarkably, the density-independent model was more strongly supported during the second period in all species except American Wigeon and Northern Pintail, and for Mallard, Gadwall, and Redhead this shift actually provided a superior fit to competing models (Appendix F). Eight species had substantial support ($AIC_c < 2.0$) for density-independent growth during the second period, compared to only two species during the first period. Overall, support (w_i) for density independence increased by 0.239 ± 0.053 during the second period compared to declines in the two density-dependent model types (Fig. 2). Diagnostic tests revealed that autocorrelation in linear density-dependent model residuals was absent for all time series (all $P > 0.13$).

For the linear density-dependent model, all species except northern pintail experienced at least qualitative reductions in r_{\max} (mean $\Delta r_{\max} = -0.313 \pm 0.084$; $W^+ = 52$, $W^- = 3$, $P = 0.010$, $z = 2.667$, $P = 0.008$; Table 3), although it is notable that two cases of increasing r_{\max} were detected using a state space approach (see Appendix A: Table A4). We determined that r_{\max} declined significantly for Canvasback (median $\Delta r_{\max} = 0.687$ (0.160, 1.150)), and Lesser Scaup (median $\Delta r_{\max} = 0.427$ (0.030, 0.900)). Although parameter K remained comparable between periods ($W^+ = 31$, $W^- = 24$, $P = 0.77$, Table 3), σ^2 for the density-dependent model

tended to decrease with time (mean $\Delta \sigma^2 = -0.012 \pm 0.006$; $W^+ = 46$, $W^- = 9$, $P = 0.064$). Overall, γ also declined with time (mean $\Delta \gamma = -0.284 \pm 0.137$; $W^+ = 49$, $W^- = 6$, $P = 0.027$), although parametric bootstrapping indicated that all species experienced significant density dependence during both time segments (Table 3).

Most duck species experienced declines in θ over time (mean $\Delta \theta = -1.320 \pm 0.571$; $W^+ = 26$, $W^- = 2$, $P = 0.047$), although changes for individual species were not significant (95% CI of $\Delta \theta$ always overlapped 0). Overall, five species (Mallard, Green-winged Teal, Blue-winged Teal, Northern Pintail, and Redhead) had a convex relationship ($\theta < 1.0$) between r_t and N_t that spanned both time segments, Gadwall and Northern Shoveler had a concave ($\theta > 1.0$) relationship during both periods, and American Wigeon, Canvasback, Lesser Scaup, and total duck numbers had a concave relationship that became convex with time (Table 3). The observed change in duck population dynamics was further reflected in an

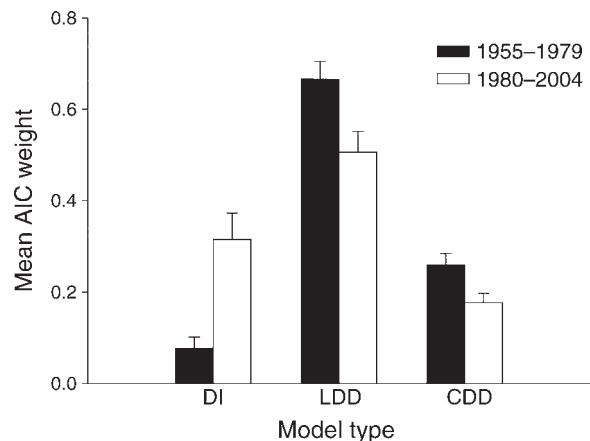


FIG. 2. AIC_c weight (w_i ; mean and SE) for density-independent (DI), linear density-dependent (LDD), and curvilinear density-dependent (CDD) models fit to r_t time series for 10 duck species in central North America. Time series were truncated into two time periods.

TABLE 3. Parameter estimates for population growth models fit to rate of change (r_t) time series for 10 duck species (1955–2004).

Species and time period	r_{\max}		K		γ		θ	
	Mean	95% CI	Mean	95% CI	Mean	95% CI	Mean	95% CI
Mallard								
1	0.332	0.161–0.852	7790.8	6488.8–9109.0	0.043	0.023–0.110	–1.0	–1.0–12.7
2	0.149	0.052–0.726	6865.0	4608.3–9131.4	0.022	0.009–0.102	–1.0	–1.0–18.6
Gadwall								
1	0.259	0.134–0.700	1381.5	928.8–1878.5	0.187	0.089–0.584	5.8	–1.0–37.5
2	0.126	0.058–0.610	2501.7	1358.4–4256.3	0.050	0.014–0.333	2.0	–1.0–30.3
American Wigeon								
1	0.514	0.288–1.049	2822.9	2478.5–3161.5	0.182	0.105–0.364	1.4	–1.0–10.7
2	0.474	0.273–0.856	2352.4	2078.8–2620.8	0.201	0.122–0.354	0.3	–1.0–4.8
Green-winged Teal								
1	0.878	0.552–1.341	1653.9	1454.2–1862.0	0.531	0.337–0.816	0.3	–1.0–4.0
2	0.264	0.131–0.806	2094.6	1630.3–2525.1	0.126	0.065–0.402	–1.0	–1.0–16.5
Blue-winged Teal								
1	0.557	0.310–1.040	4367.1	3896.4–4810.1	0.128	0.074–0.236	–1.0	–1.0–7.8
2	0.269	0.121–0.808	4561.8	3245.8–5934.5	0.059	0.028–0.179	–1.0	–1.0–9.5
Northern Shoveler								
1	0.620	0.370–1.108	1825.3	1628.6–2026.3	0.340	0.198–0.603	6.5	–1.0–23.1
2	0.220	0.100–0.698	2800.2	1834.0–3824.7	0.079	0.036–0.288	7.2	–1.0–45.3
Northern Pintail								
1	0.367	0.184–0.790	5105.2	3858.7–6351.1	0.072	0.041–0.144	–1.0	–1.0–2.6
2	0.503	0.299–0.905	2630.5	2244.1–3024.2	0.191	0.122–0.329	–1.0	–1.0–2.5
Redhead								
1	0.589	0.342–1.087	596.2	517.1–677.7	0.988	0.594–1.824	–0.9	–1.0–6.3
2	0.181	0.072–0.730	636.6	412.5–845.5	0.284	0.131–1.113	–1.0	–1.0–16.1
Canvasback								
1	1.029	0.641–1.455	559.7	517.8–601.0	1.838	1.166–2.613	2.6	–1.0–6.2
2	0.285	0.125–0.770	544.5	428.0–647.5	0.523	0.261–1.356	–1.0	–1.0–12.8
Lesser Scaup								
1	0.622	0.376–1.116	5745.1	5206.7–6353.9	0.108	0.065–0.196	3.0	–1.0–14.2
2	0.168	0.052–0.599	4120.4	2827.6–5382.7	0.041	0.017–0.130	–1.0	–1.0–12.9
Total ducks								
1	0.395	0.202–0.909	31 789.8	28 446.3–35 503.8	0.012	0.007–0.028	10.1	–1.0–31.8
2	0.225	0.088–0.752	28 734.3	23 098.1–34 286.9	0.008	0.003–0.025	–1.0	–1.0–19.2

Notes: Models were fit to 1955–1979 (period 1) and 1980–2004 (period 2) time series separately. Parameter r_{\max} is the intrinsic growth rate (at N_0), K is the carrying capacity, γ is an index of density dependence ($r_{\max}/K \times 1000$), and θ represents the curvature in r_t vs. N_t plots. Parameters r_{\max} and K were calculated from the Ricker, γ from the stochastic logistic, and θ from the theta-Ricker model. Bootstrap 95% CI are given.

overall increase in equilibrium return time during the second time segment ($\Delta\lambda = 0.306 \pm 0.082$; $W_+ = 53$, $W_- = 2$, $P = 0.006$). In most cases change in population parameters were not related to LHI (all $P > 0.11$), except for the larger decline in parameters r_1 ($r = -0.75$, $P = 0.012$) and θ ($r = 0.695$, $P = 0.026$) during the second segment, and thus the tendency for increased concave fit between r_t and N_t , among survival-driven species.

Overall, mean interspecies correlation in the N_t and r_t time series increased during the second period (N_t , $W_+ = 10$, $W_- = 45$, $P = 0.084$; r_t , $W_+ = 1$, $W_- = 54$, $N = 10$, $P = 0.004$; Fig. 3). For the N_t time series, no individual species correlation coefficients varied significantly between segments (all $P > 0.008$, with Bonferroni correction), but for the r_t series, associations between mallard, gadwall, and canvasback vs. each of the nine species increased with time (all $P < 0.004$).

DISCUSSION

Our analysis revealed fundamental temporal change in patterns of duck population regulation, with most species exhibiting weakened density dependence in favor of increased support for density-independent growth. This change was reflected in prevalent decline in intrinsic population growth rate (r_{\max}), the density dependence parameter (γ), and inverse equilibrium return time (λ), decrease in environmental variance σ^2 , and shift in the relationship between r_t and N_t (parameter θ) from concave to convex. Yet, surprisingly autocorrelation in the N_t time series increased with time, and increased interspecies correlation in N_t and r_t added further credence to the apparent ubiquitous shift in duck population dynamics. Because observed changes were not closely associated with either species evolutionary strategy or commensurate responses in duck population abundance or trend, we

infer that starting in the 1980s environmental variation influenced the breeding duck community by altering underlying population processes while allowing most basic numerical attributes to remain unchanged.

The breeding waterfowl survey is arguably the largest and best-designed population survey in the world, involving census of over 2.2 million km² of core waterfowl breeding habitat (Nichols et al. 1995, Smith 1995, Yoccoz et al. 2001). Because abundance estimates and associated variances incorporate correction for spatial variation and duck sightability, the data set should provide a robust basis for assessing temporal shift in population processes. Yet, regression-based methods in density dependence assessment can yield spurious results through autocorrelation (Hassell 1986, Hassell et al. 1989). As well, Type I error (falsely detecting density dependence) is more likely when survey data are subject to high measurement error (Shenk et al. 1998, Freckleton et al. 2006). It follows that if sampling error varies systematically across a given time series, assessment of variability in population processes will be flawed. However, evidence supporting our contention that observed temporal shift in density dependence was biological reality rather than statistical artifact include (1) comparable SD and CV between time segments (although CV on point estimates appeared to decline with time for most species; K. Newman, *unpublished data*), (2) diagnostic tests detecting consistent autocorrelation among model residuals between time periods, and (3) increased inter-species correlation in N_t and r_t (contrasting with predicted reduced correlation if survey methods improved appreciably over time). Thus, the sum of our diagnostic tests allow us to consider duck time series as being comprised of process error only (see Dennis and Otten 2000, Dennis et al. 2006). Perhaps most importantly, our conclusions regarding shifts in density dependence do not change qualitatively when methods that explicitly estimate sampling and process error are used (Appendix A), and simulations parameterized to reflect our data support the position that our tests for density dependence were sufficiently robust (Appendix B).

Density dependence occurs across a range of spatial and temporal scales in North American ducks (Vickery and Nudds 1984, Jamieson and Brooks 2004, Viljugrein et al. 2005, Sæther et al. 2008), so its observed prevalence among our study species was expected. Yet, surprisingly the strength of density dependence did not reflect either basic population attributes or estimated parameters when assessed for complete time series. This finding runs counter to similar investigations on other bird species (Sæther and Engen 2002, Sæther et al. 2002), and may suggest that the broader spatial and temporal scale used in the present analysis captured additional variability that is excluded from more restricted approaches. Consistent with this theme, evolutionary strategy also failed to correlate with density dependence metrics for the 51-year time series, which is similar to patterns

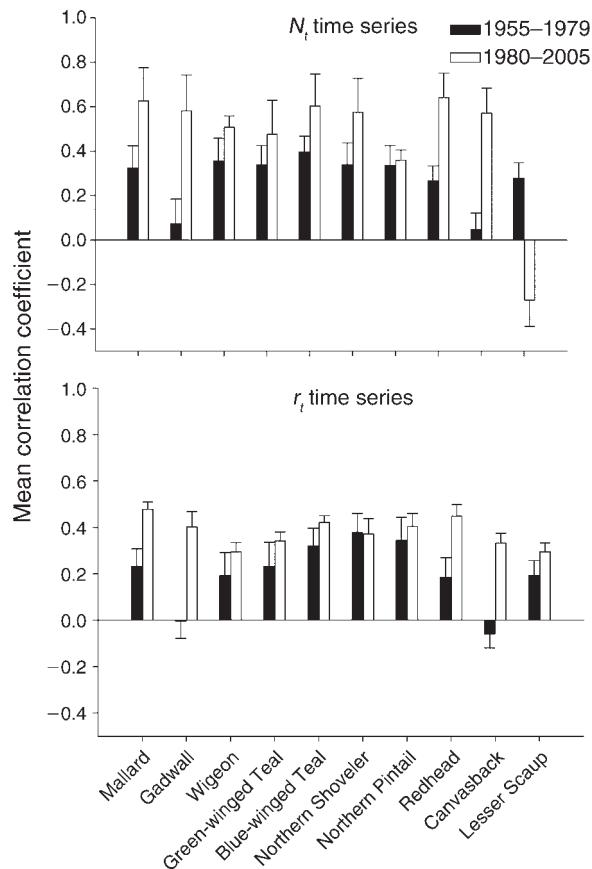


FIG. 3. Mean correlation coefficients for N_t and r_t time series for 10 duck species in central North America (1955–2005). Time series were truncated into two time periods, and correlation coefficients are derived from correlative cohesive analysis (Redfern et al. 2006).

reported for fish (Myers et al. 1999) but contrasts with observed linkages among birds (Sæther and Engen 2002, Sæther et al. 2002). We interpret this disparity as illustrative of the need for studies to place greater emphasis on the potential role of environmental variation when assessing patterns of population growth and regulation. Indeed, in our study it is only through refined analysis that we detected association between duck population processes, population parameters, and to a lesser extent, species life history.

The relationship between strength of density dependence and several population parameters (r_{max} , σ^2 , γ , θ , and λ) is known from other studies (Sæther and Engen 2002, Sæther et al. 2002), but ours is the first to highlight how dynamical changes in parameter estimates can occur over time within a given population. First, this implies that species may be more plastic in their responses to perturbation than previously assumed, and that to the fullest extent possible population analyses from time series data should strive for replicate samples or extended timelines to account for spatial/temporal heterogeneity. For example, mean time series

length was only 16.5 ± 14.2 (mean \pm SD) years (range 5–157 years) in an analysis of growth parameters for 1780 populations (Sibly et al. 2005), which could be preclusive for robust detection of temporal shifts and density dependence (see Woiwod and Hanski 1992, Brook and Bradshaw 2006). Second, because parameter variability occurred in a largely consistent manner across the duck community, the influence of environmental change on species plasticity may mask clear linkages with evolutionary strategy. In light of ongoing environmental perturbation across most global landscapes, this confound may provide additional challenge for effective population monitoring and status assessment. Clearly, the relationship between environmental variability and population parameter change requires additional research emphasis.

Although our study joins others in demonstrating temporal variability in duck population dynamics (see Hoekman et al. 2002, Podruzny et al. 2002, Drever 2006), we quantify such variability in the context of shifting population processes and related parameters. The observed temporal change implies that variation in biological or environmental factors operating at a broad spatial scale elicited widespread variability in duck population dynamics. This tantalizing finding should prompt both further assessment of factors contributing to duck population regulation, as well as quantifying spatial and temporal heterogeneity in such factors across the survey area. For example, in theory temporal decline in r_{\max} should characterize populations subject to reduced primary productivity (Sæther and Engen 2002, Sæther et al. 2002). Because duck time series tend to be governed by simple processes spanning single-year time lags (D. L. Murray, *unpublished data*), it is likely that density dependence acts via short-term feedback. This alone limits the list of candidate factors restricting duck productivity to determinants like intraspecific competition, predation by generalist predators, or resource limitation, rather than more complex processes causing longer time delays (see Royama 1992, Turchin 2003).

Increased generalist predation has gained attention due to marked reductions in nest success and duck survival (e.g., Beauchamp et al. 1996, Sovada et al. 2001). Not only could increased predation reduce productivity and population growth, but if predators exhibit large-scale synchrony in demographic trends, they also could contribute to increased correlation in duck numbers across the prairie landscape (Drever 2006), and stronger autocorrelation between successive counts. Evidence from the study region suggests spatial similarities in relative predator abundance (Sargeant et al. 1993) but a lesser degree of temporal synchrony. Nevertheless, generalist predation is plausibly an important determinant in the observed changes in duck population processes.

Ultimately, the observed shifts in duck population dynamics may reflect recent and marked expansion of agriculture in central North America, which is known to

reduce nesting habitat and thereby lead either directly to lower duck population productivity, or indirectly to increased food/nest site competition or higher nest predation (Bethke and Nudds 1995, Drever et al. 2004). Agricultural expansion also may underlie aforementioned changes in the predator complex in favor of generalist carnivores (Cowardin et al. 1985, Sargeant et al. 1993). Collectively, such changes may promote reduced productivity and increased homogeneity among local populations, which ultimately should weaken population regulation mechanisms operating at larger spatial scales (Rodenhouse et al. 1997, but see Wang et al. 2005).

Regardless of the mechanism involved in observed shifts in duck population dynamics, it remains surprising that fundamental variation in population processes did not elicit corresponding changes in abundance and trend. Although site-specific variation in population numbers and trend are difficult to detect given the geographical extent of our study, some degree of concordance between population parameters and duck numbers is expected. One possibility is that prairie duck numbers are increasingly augmented by immigration from regions outside our survey area, thereby compensating for shifting population processes, and in turn, masking local population declines. This conjecture implies that a productive avenue for further research should involve assessment of population processes acting on duck population dynamics at a variety of spatial scales (e.g., Sæther et al. 2008, see also Freckleton et al. 2006). More generally, the lack of concordance between population attributes and model parameters highlights the need to consider more than just abundance and trend when assessing population responses to perturbation. Indeed, if populations can experience fundamental changes in their dynamics without showing concomitant numerical responses, then population status may only be fully revealed following additional analytical efforts complementing standard monitoring protocols. This condition poses a substantial challenge to future population monitoring if it is to serve tangibly and expeditiously in alerting of variation in population processes.

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APPENDIX A

Methodology and results for state–space modeling of duck time series data (*Ecological Archives* E091-041-A1).

APPENDIX B

Results from simulations assessing statistical power in detection of density dependence (*Ecological Archives* E091-041-A2).

APPENDIX C

Population counts for 10 duck species in central North America (*Ecological Archives* E091-041-A3).

APPENDIX D

Summary statistics for estimates of 10 duck species surveyed annually in central North America (*Ecological Archives* E091-041-A4).

APPENDIX E

Parameter estimates for population growth models fit to time series for 10 duck species (*Ecological Archives* E091-041-A5).

APPENDIX F

AIC_c differences (Δ_i) and AIC_c weights (w_i) for three growth models fit to population time series for 10 duck species (*Ecological Archives* E091-041-A6).