Tests of density dependence using indices of relative abundance in a deer population

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A major question in animal ecology is explaining the causes of population fluctuations. Consensus about the most reliable method to detect density dependence (DD) or environmental effects from time-series data, however, has not yet been achieved. Times series analyses have been used with indices of relative abundance in numerous studies, although these indices are rarely validated. Here, we used three different time series of relative abundance (number of deer seen per hunter per day, hunting success and proportion of males in the harvest) to explore direct and delayed DD in a white-tailed deer *Odocoileus virginianus* population on Anticosti Island, Québec, Canada. Three mathematical approaches were tested: linear models, autoregressive (AR) models, and total DD in life history. Tests of DD using different indices of abundance on the same population should lead to similar results if all indices exhibit similar behaviour. Indices of relative abundance correlated with each other, although sometimes weakly, such that we obtained similar DD estimates with each index using detrended non-stationary series. In most time series, linear regression of N_{t-1} and N_t and AR models did not detect DD, while we obtained strong evidence for DD from the life-history approach. This meant that contrasting conclusions about the role of density dependence within this population were reached depending on which method was used. We conclude that the method that incorporates most biological realism, the life-history approach, provided a different result than classical interpretation of autoregressive coefficients. Only the life-history interpretation supported our a priori belief that density dependence operating through competition for food regulates the Anticosti deer population. Phenomenological analysis aiming to investigate changes in abundance should be carefully conducted as the use of inappropriate indices or methods could lead to inappropriate conclusions or management strategies. Preferably, the method used should match the time scale of the population sampling regime and species life history.

Explaining changes in population size is a fundamental objective of population ecology (Nicholson 1933, Andrewartha and Birch 1954, White 2001). Time-series analysis or phenomenological analysis has been the approach most widely used to investigate changes in abundance (Forchhammer et al. 1998, Kendall et al. 1999, Post 2005). This approach predominantly works with estimates of population size to provide a quantitative description of patterns in population fluctuations and to estimate the shape of the relationship between population size and growth rate (Moe et al. 2002, Turchin 2003). Times series analysis can be used to identify direct density dependence (DD) since the negative relationship between per capita population growth rate (λ) and population density should produce a discernible signature in the data (Royama 1992, Bjørnstad and Grenfell 2001). Bjørnstad and Grenfell (2001) reported that the first analyses of DD signatures had numerous pitfalls and generated spurious results, but that recent tests were more robust and unbiased, including

autoregressive (AR) models (Royama 1992, Bjørnstad et al. 1995). Models now consider the effects of time lags in response to density dependence (i.e. order of DD) that may have been induced by trophic interactions (Stenseth et al. 1998), age structure effects (Lande et al. 2002), and asynchrony in demographic responses among sexes (Forchhammer et al. 1998). However, different methods used to investigate DD or delayed DD (DDD) frequently led to contrasting results when applied to the same time series (Holyoak 1993, Wolda and Dennis 1993, Forchhammer et al. 1998). DD tests have been criticized, including AR models, because their inferences refer to statistical DD, which may be hard to interpret in the context of population ecology (Wolda and Dennis 1993, Lande et al. 2002, Turchin 2003). Nevertheless, AR models are still widely used to investigate the dynamic of animal populations (Bjørnstad et al. 2008, Vik et al. 2008, Ziebarth et al. 2010). Lande et al. (2002) proposed an alternative interpretation of autoregressive parameters, where instead of considering annual

changes in population growth rate, DD is scaled by generation time by incorporating life-history parameters into estimates of the strength of DD.

Issues arising from the use of phenomenological analysis are not only statistical, but often relate to the time series itself as the quality and suitability of the data are the first critical steps for reliable DD estimates (Carrete et al. 2008). Estimates of population size are limited by three main factors: 1) the spatial scale at which density fluctuations are measured is generally hard to define (Freckleton et al. 2006, Carrete et al. 2008), 2) census errors in population estimates are common but generally ignored (Solow 2001, Freckleton et al. 2006), and 3) relative indices of population abundance may be artefactual as they include uncontrolled biases (Mysterud et al. 2007, Ranta et al. 2008). Unfortunately, reliable census methods to estimate population size, such as capture–mark–recapture, are limited by visibility, behavioural and/or other logistic constraints. The only possible alternative is generally to use relative indices of abundance assumed to track inter-annual variation in population size, including counts of footprints (Beaudoin et al. 2004), den sites (Wilson and Delahay 2001), feces (Ellis and Bernard 2005), browsing indices (Morellet et al. 2001), or hunting statistics (Mysterud et al. 2007). Indices of abundance are therefore commonly used to estimate population growth rate (Kilpatrick et al. 2005), and to test the influence of density and environmental factors on population size (Mysterud et al. 2000, Post 2005), as well as in population management (Morellet et al. 2001, Kilpatrick et al. 2005). In the majority of times series from natural populations, a temporal trend (non-stationarity) often complicates the analysis (Wu et al. 2007). Detrending data is thus a necessary step prior to conducting most time-series analyses (Box et al. 1994), including autoregressive models (Royama 1992), although in some cases trends are an interesting feature of the data in their own right (Wu et al. 2007). Unfortunately, our understanding of the consequences of detrending on the interpretation of the strength of DD estimates is still limited (Jonzén et al. 2002, Wu et al. 2007).

Ecosystem impacts associated with high density of ungulate populations are frequent and occur on a global scale (Côté et al. 2004). Yet obtaining accurate estimates of abundance in such populations is often problematic due to uncertainty in censuses and the long time required to study the entire life history of ungulates (Månsson et al. 2007). The abundant white-tailed deer *Odocoileus virginianus* population on Anticosti Island (Québec, Canada) is a good example where knowledge of population size is imprecise despite the strong interest to implement specific deer management objectives. The use of capture–mark–recapture is logistically unfeasible and aerial survey estimates are expensive, often inaccurate and achieved irregularly (Potvin and Breton 2005). Hunting statistics are the only long-term indices available to estimate variation in population abundance (Grøtan et al. 2005, Mysterud et al. 2007). In moose *Alces alces*; Solberg et al. 2004, and red deer *Cervus elaphus*; Mysterud et al. 2007, hunting statistics were related to variation in population abundance. However, it is unclear whether hunting statistics are useful indices to estimate the strength of DD in ungulate populations. Based on results from other ungulate populations, DD should dominate when predators are absent (Sæther et al. 1996, McCullough 1999), such as on Anticosti Island. We expected particularly strong DD because a century of heavy chronic browsing on Anticosti Island should have increased competition for forage (Simard et al. 2008). In addition, density was already identified to negatively influence survival and lactation rates of female deer on the island (Simard et al. 2010). Finally, lag effect of DD should be considered because three-year lags in growth and recruitment rates were previously documented in white-tailed deer (Fryxell et al. 1991).

Hunting statistics have been collected on Anticosti Island for > 25 years, and provide a great opportunity to explore the presence of DD in the deer population using different indices of relative abundance: deer seen per hunter per day, hunting success and the percentage of males in the harvest. Considering that these three indices track variation in deer abundance within the same population, we expected similar DD estimates for all indices. Estimates of DD using each index were calculated with three contrasting approaches: a linear model of direct DD, linear AR models that included estimates of DDD, and the approach of Lande et al. (2002) that estimates DD across the life history. Our aim was to verify if DD inference varied across these methods. Given previous results from this population (Simard et al. 2010), we expected to find strong DD annually – both direct and delayed – and at the generation level using the Lande et al. (2002) approach. We hypothesised that choosing one method or one type of index over another should not lead to divergent conclusions, assuming that they provide similar descriptions of the population's dynamics. Here, we innovate by using multiple indices and multiple methods from the same population, which has never been done. In addition, our study is of a wild population, meeting calls for tests of DD to come from the field – where population size can be hard to measure – rather than from the laboratory (Bjørnstad and Grenfell 2001).

Methods

Study area

Anticosti Island (49°N, 62°W; 7943 km²) is located in the Gulf of St. Lawrence, Québec, Canada. The climate is maritime sub-boreal with cool summers, relatively mild but long winters, and a mean annual rainfall of 63 cm and snowfall of 406 cm (Simard et al. 2010). The vegetation of the eastern balsam fir–white birch bioclimatic forest region is dominated by balsam fir *Abies balsamea*, white spruce *Picea glauca*, and black spruce *P. mariana*. As a consequence of severe deer browsing in recent decades, most deciduous shrubs and trees are only present sporadically, including white birch *Betula papyrifera*, or have almost been extirpated (Tremblay et al. 2005). Following a reduction in browse availability, deer now rely mainly on litter fall of arboreal lichens and balsam fir twigs, as well as fallen trees in winter (Tremblay et al. 2005). This food source, independent of deer browsing, may have helped maintain high densities despite the scarcity of winter browse (Tremblay et al. 2005).

The island is divided into 20 hunting zones that service approximately 5000 hunters each year (Gingras 2002).

The number of harvested deer km^{-2} has remained relatively stable over the last 25 years, ranging from 1 to 1.4 deer km^{-2}, giving an annual harvest rate of about 5–8% of the total population size, of which 65% are males due to hunter selectivity (Simard et al. 2008). Hunter selectivity for trophy versus meat varies depending on nationality (Mysterud et al. 2006): foreign hunters (mostly American) harvest 75% males compared to 57% for Québec hunters ($t = 6.5$; $p < 0.001$; Ministère des Ressources naturelles et de la Faune, unpubl.).

Density estimates

Estimates of deer population density on Anticosti Island were conducted using the double count technique (see Potvin and Breton 2005 for more details) from helicopter surveys of the entire island in 1996 (Rochette and Gingras 2001), 2001 (Rochette et al. 2003) and 2006 (Rochette and Gingras 2007), as well as on restricted portions of the island in 2003 and 2005. Aerial surveys have been divided into four sectors of the island: west, central–north, central–south, and east (around 1200, 960, 800 and 1400 km^2, respectively). This method was found to provide estimates of between 64–83% of actual population size (Potvin and Breton 2005). Given the low frequency of aerial surveys, we used time series from hunting statistics available from 1975 to 2006 to investigate DD. Indices included hunting success (deer havested/hunter), as well as the proportion of males in the harvest (male/total harvest), the latter having the advantage of accounting for an increase in male selectivity as harvest becomes easier. Since 1983, the number of deer seen per hunter per day (deer seen/hunter/day) was also available, an index that was not influenced by hunting quotas or hunters selectivity. Annual hunting statistics were provided by the Québec government and included all deer hunters legally registered on Anticosti Island.

Statistical analyses

We used regression models (lm in R 2.10.1) to assess relationships between each of the four density estimates, i.e. aerial surveys, deer seen/hunter/day, male/total harvest, and deer harvested/hunter (all data were logged prior to analysis). Although all indices may include certain inaccuracy or bias, those errors are likely to be specific to each index, such that strong correlations among indices are still a good indication of similitude in their expression of change in population size. We assessed goodness of fit and checked for heteroscedasticity by plotting residuals. We verified that outliers remained inside Cook's distance, so that they did not have a disproportionate influence in models (Crawley 2007).

We verified the stationarity of hunting statistic time-series using the KPSS Test for level stationarity ($p < 0.05$ = non-stationary) and the Phillips-Perron Unit root test ($p < 0.05$ = stationary), which both suggested that male/total harvest (respectively $p = 0.02$ and 0.11; Fig. 1C), but not deer seen/hunter/day ($p = 0.1$ and 0.01; Fig. 1A) or deer harvested/hunter ($p = 0.1$ and 0.01; Fig. 1B), exhibited a significant temporal trend. The non-stationary time series male/total harvest was detrended using two different methods. First, we fitted a polynomial regression to the data

and analysed the residuals. Second, we fitted a loess function, which produced a smooth regression curve using a regression function, and again we analysed the residuals (Venables and Ripley 2002; Fig. 1D). The appropriate span of the loess function was selected based on Akaike's information criterion ($AIC = -2ln[max\ likelihood] + 2[number\ of\ parameters]$), to which we applied a correction for finite sample sizes (AICc; Burnham and Anderson 2002). We presented the results of each detrending method but showed only the graphical representation of Loess residuals. Density-dependent tests were conducted on the logged trended data and detrended logged data.

We used three different methods to test for DD. The first two methods, linear and AR models, are widely used for biological inference using time series data (Bjørnstad et al. 2008, Saitoh et al. 2008, Vik et al. 2008), while the third one, the Lande et al. (2002) approach, has seldom been used (Sæther et al. 2005). The Lande method, although derived from AR models, has the particularity of including life history parameters into DD estimates. Although all three methods diverge in regard to their inference to DD, they are all related, which facilitates their comparison. Next, we describe each method in detail.

We first estimated the strength of direct DD with a simple linear model for unstructured populations (i.e. not accounting for age or group age), and without considering potential DDD. DD is defined as the slope, β_1 of the regression line, between the natural log of population size N at time t (N_t) and the log of population size at year t−1.

$$lnN_t = \beta_0 + \beta_1\ ln(N_{t-1}) + \varepsilon_t \qquad (1)$$

We used this linear model to test for the presence of DD with the three indices of relative abundance. We plotted direct log-transformed density indices at time t−1 (N_{t-1}) against density at time t (N_t) and tested the significance of β_1, a negative slope indicating direct DD. Turchin (2003) suggested that plotting N_{t-1} against N_t sometimes results in obscuring DD, and suggested using per capita rate $r = ln(N_t/N_{t-1})$ against N_{t-1} instead. We consequently followed Turchin's (2003) recommendation. Examination of residuals of both N_{t-1} against N_t and N_{t-1} against r_t allowed us to determine evidence for non-linear effects of density. Simple linear models are still commonly used to investigate direct DD in animal populations (Saitoh et al. 2008, Wang et al. 2009).

Second, we used linear autoregressive models to estimate DDD, after accounting for DD effects, which a widespread method in population ecology (Ziebarth et al. 2010). The linear autoregressive model using the Yule–Walker equation (R 2.10.1) refers to (Bjørnstad et al. 1995, Royama 1992):

$$lnN_t = \beta_0 + \beta_1\ ln(N_{t-1}) + \beta_2\ ln(N_{t-2})$$
$$+ \beta_3\ ln(N_{t-3})....+ \beta_k\ ln(N_{t-k}) + \varepsilon_t \qquad (2)$$

where ε_t (environmental stochasticity) is assumed to be independently and identically distributed (Bjørnstad et al. 1995). The influence of population size at time t−1, t−2, t−3 … t−k on current population size (N_t) is explained by autoregressive coefficients ($\beta_{1\ to\ k}$). From an ecological point
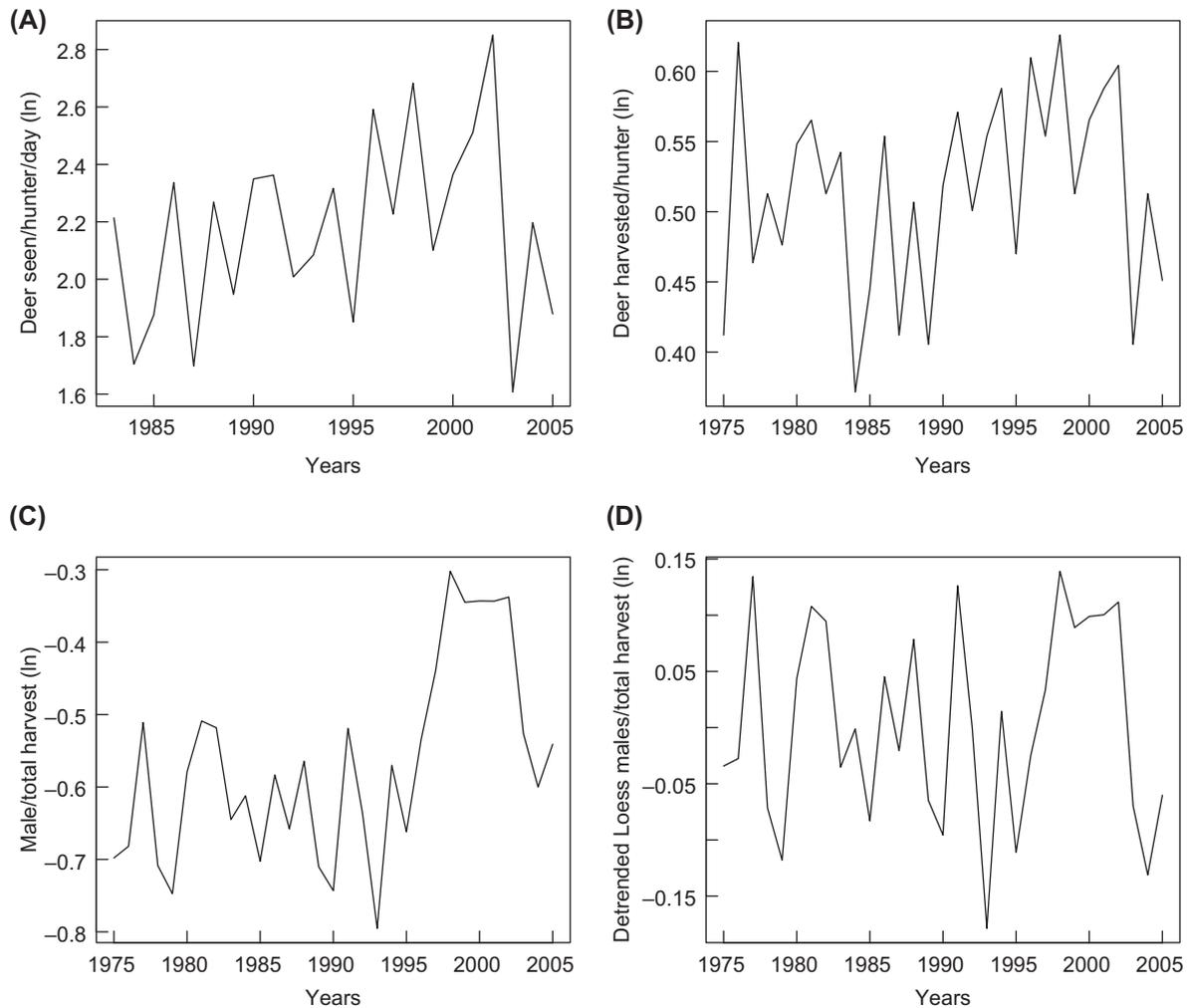
Figure 1. Time series of different indices of relative abundance (natural log-transformed) of white-tailed deer on Anticosti Island (Québec, Canada) based on hunting statistics: (A) the number of deer seen per hunter per day (1983–2006), (B) the number of deer harvested per hunter (1975–2006), (C) the proportion of males per total harvest (1975–2006), and (D) the detrended proportion of males per hunter using loess regression.

of view, β_1 indicates the strength of direct DD while β_2 through β_k estimate the strength of DDD for different time lags k (Royama 1992). We report significant coefficients from the AR model with the most support based on AICc (Bjørnstad et al. 1995). We plot AR coefficients and partial correlation coefficients ($\beta_{1\,to\,k}$; Crawley 2007). We only interpreted coefficients for which $\Delta AICc < 2$ (difference in AIC with the best model). By providing auto correlation function (ACF) graphs, we verified similarity between observations as a function of the time separation between them.

Finally, we used the approach of Lande et al. (2002) to estimate DD across the life history of an age-structured population, expressed here as DD_{LH}. Although both DD and DD_{LH} are based on AR coefficients, they differ in the fact that DD_{LH} provides a per generation estimate of the strength of density dependence in contrast to the annual estimates of its strength. The strength of DD is defined as the slope between the log of the per generation population growth rate (λ^T) and the log of population size:

$$DD_{LH} = \frac{(\partial \ln \lambda^T)}{(\partial \ln N_t)} \qquad (3)$$

Generation time T is defined as the mean age of mothers in an age-structured population assuming a stable age distribution (details in Lande et al. 2002, 2003). The formula to estimate DD_{LH} is based on the linear autoregressive structure of a time series of population size in relation to age at first reproduction α and adult (i.e. >2-year-old in white-tailed deer) mortality rate μ (Lande et al. 2003). It results in:

$$DD_{LH} = \frac{1 - \sum_{k=1}^{\alpha} \beta_k}{\mu} \qquad (4)$$

where if $\alpha = 3$ then $\Sigma\beta_k = \beta_1 + \beta_2 + \beta_3$. Autoregressive coefficients β_k (Eq. 1) from 1 to α are summed in the formula disregarding their significance, in contrast to the AR model where only the term with the lowest AIC is kept. The resulting DD_{LH} corresponds to the slope of the return rate to equilibrium per generation time. A null DD_{LH} indicates an absence of DD and as DD_{LH} increases, DD effects also increase. This approach has the advantage of facilitating DD comparisons between different species (Sæther et al. 2005), but it assumes that deviations of population size from

equilibrium are of a small to moderate amplitude (Lande et al. 2003, Sæther et al. 2005). DD_{LH} has not been widely used, but was suggested as a possible alternative to purely statistical time series models (Wang et al. 2006). To the best of our knowledge, we are the first to compare results from the Lande et al. (2002) method with insights gained from traditional interpretation of AR estimates.

DD_{LH} of Lande et al. (2002) was calculated using autoregressive coefficients from the previous autoregressive models (Table 1). Considering that fewer than 50% of females reproduce before 3 years of age on Anticosti (Simard et al. 2008, 2010), we used $\alpha = 3$ and summed β_1, β_2 and β_3 in the equation. Overall adult female survival on Anticosti Island was estimated at 0.77 ± 0.04 using the age structure of females collected through hunting from 1982 to 2006 (Simard et al. 2010), consequently we used $\mu = 0.23$ to calculate DD_{LH} with Eq. 4.

Results

Correlation of density indices

Density estimates from aerial surveys had the highest correlation with deer seen/day (log-transformed; $R^2 = 0.52$, $F_{1,19} = 20.8$, $p < 0.001$; Fig. 2A), a relation that showed no heteroscedasticity. The regression between aerial surveys and deer harvested/hunter estimates was weak, but significant ($R^2 = 0.15$, $F_{1,19} = 4.6$, $p = 0.05$) and we observed strong heteroscedasticity. The model underestimated density at both low and high values of deer harvested/hunter, but overestimated density at average deer harvested/hunter, suggesting non-linearity (Fig. 2B). The log-linear positive relationship between male/total harvest and aerial survey densities was also significant ($R^2 = 0.33$, $F_{1,19} = 9.6$, $p < 0.01$; Fig. 2C), but depicted a non-linear relationship. We observed weak heteroscedasticity, which suggested an underestimation of aerial survey densities at high values of male/total harvest. The index of deer seen/hunter/day was highly correlated with deer harvested/hunter, as shown by their strong log-linear relation ($R^2 = 0.86$, $F_{1,21} = 127.4$, $p < 0.001$; Fig. 2D). Other indices were correlated, but not as strongly, including deer seen/hunter/day and male/total harvest ($R^2 = 0.27$, $F_{1,21} = 7.7$, $p = 0.01$; Fig. 2E), and deer harvested/hunter and male/total harvest ($R^2 = 0.19$, $F_{1,29} = 6.9$, $p = 0.01$; Fig. 2F). Consequently, an increase in the number of deer seen/hunter/day positively affected hunting success, but also the selectivity for males.

Density dependence estimates

The regression of deer seen/hunter/day at time $t-1$ against time t did not reveal direct DD ($N_t = 2.57 \pm 0.50 - 0.18 \pm 0.22 \times \ln N_{t-1}$, $R^2 = 0.03$, $F_{1,20} = 0.7$, $p = 0.4$; Fig. 3A). However, deer seen/hunter/day at time $t-1$ against r_t suggested strong DD ($r_t = 2.57 \pm 0.50 - 1.18 \pm 0.22 \times \ln N_{t-1}$, $R^2 = 0.58$, $F_{1,20} = 27.7$, $p < 0.001$; Fig. 4A). The autoregressive model for the time series deer seen/hunter/day (Fig. 1A) was best at order 0 (delta $AIC_c = 0$; predicted variance, $\sigma^2 = 0.090$; Table 1A). The model with order 1 had a delta $AIC_c = 2.0$ and was statistically equivalent, but less

Table 1. Estimates of density dependence (DD) for different time series of hunting statistics as indices of relative abundance (natural log-transformed) of white-tailed deer on Anticosti Island (Québec, Canada), i.e. number of deer seen per hunter per day (1983–2006), the number of deer harvested per hunter (1975–2006), the proportion of males harvested per hunter (1975–2006) and the detrended male per total harvest using polynomial equation and loess equation. Estimates of DD were provided by: (A) regression coefficients β at order t + k (±SE), AICc and ΔAICc for autoregressive models (AR; Eq. 2), and (B) density dependence in life-history ($DD_{LH} \pm SE$; Eq. 4) using the approach of Lande et al. (2002).

|	ln (deer seen/hunter/day)				ln (deer harvested/hunter)				ln (male/total harvest)				Detrended polynomial (male/total harvest)				Detrended loess (male/total harvest)			
	βk	SE	AICc	ΔAICc	βk	SE	AICc	ΔAICc	βk	SE	AICc	ΔAICc	βk	SE	AICc	ΔAICc	βk	SE	AICc	ΔAICc
(A) AR																				
Lag k																				
0			17	0			−73.5	0			−33.2	11.3			−60.6	0			−58.5	0
1	−0.14	0.21	19.0	2.0	−0.09	0.18	−71.3	2.2	0.47	0.18	−44.5	0	0.03	0.18	−58.3	2.3	0.13	0.18	−56.8	1.6
2	0.19	0.23	20.7	3.7	0.24	0.19	−70.7	2.9	0.05	0.20	−42.1	2.4	−0.22	0.18	−56.6	4.0	−0.17	0.18	−55.0	3.5
3	−0.01	0.25	24.0	7.0	0.04	0.21	−67.9	5.6	0.27	0.21	−40.1	4.4	−0.05	0.18	−53.8	6.8	0.01	0.19	−52.1	6.3
4	0.15	0.27	27.4	10.4	0.07	0.20	−64.9	8.7	0.03	0.21	−37.3	7.2	−0.15	0.19	−51.3	9.3	−0.09	0.19	−49.4	9.1
5	0.01	0.31	31.6	14.6	0.13	0.20	−62.0	11.6	−0.19	0.21	−35.4	9.1	−0.22	0.19	−49.2	11.4	−0.21	0.19	−47.3	11.1
6	−0.01	0.30	36.5	19.5	−0.11	0.20	−58.6	14.9	−0.13	0.2	−32.1	12.4	−0.12	0.20	−45.9	14.7	−0.16	0.19	−44.3	14.2
(B) D_{LH}	4.1	1.9			3.5	1.6			0.9	1.5			5.4	1.7			4.5	1.6		
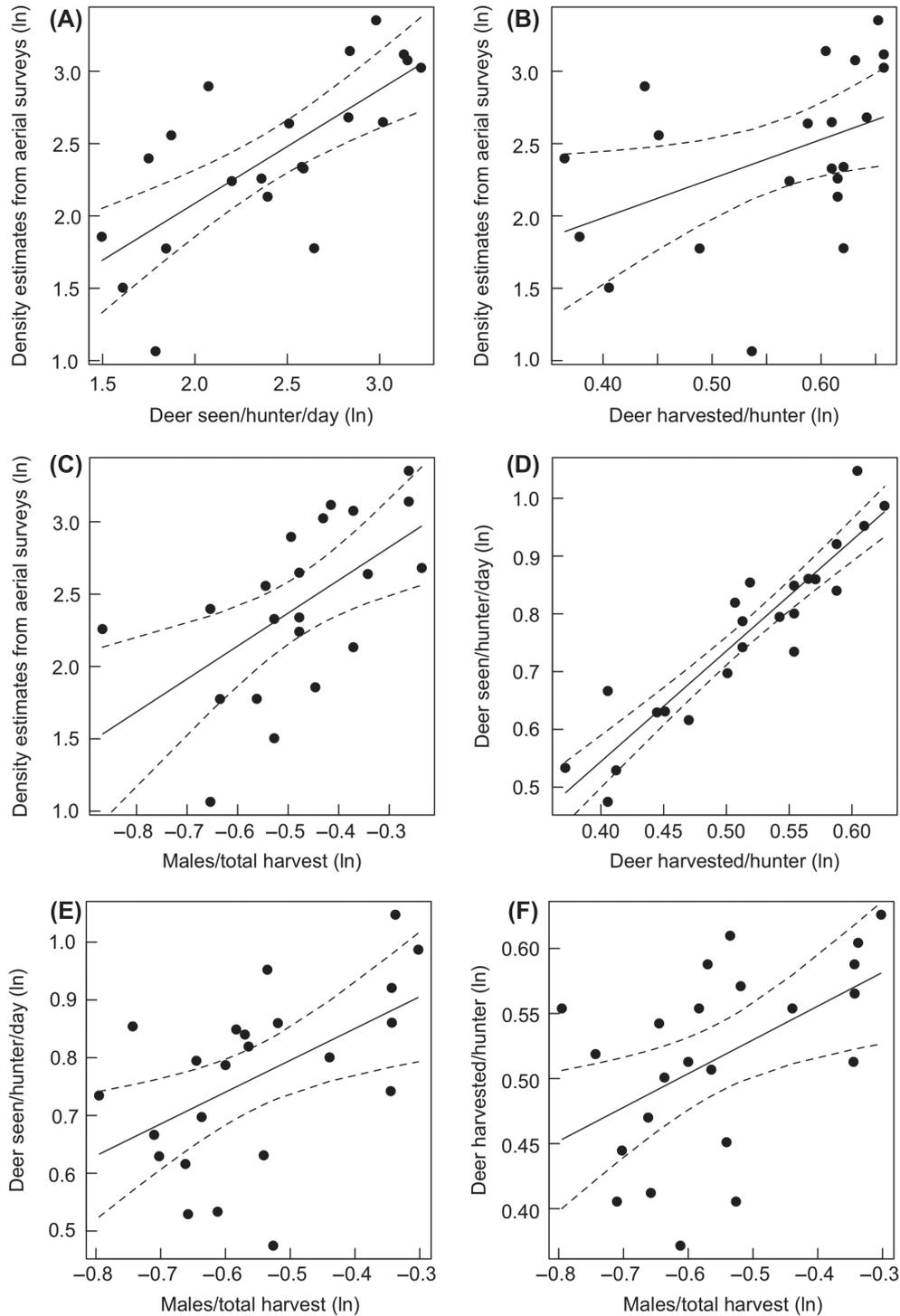
Figure 2. Regressions between white-tailed deer density estimated from aerial surveys (deer km^{-2}; in differents years and sectors between 1996 to 2006) and hunting statistics on Anticosti Island (Québec, Canada), i.e. with (A) the number of deer seen per hunter per day, (B) the number of deer harvested per hunter, and (C) the proportion of males per total harvest. Regression (1983–2006) between the number of deer seen per hunter per day and (D) the number of deer per hunter, (E) the proportion of males per hunter as well as (F) between these last two indices. All indices are natural log-transformed.

parsimonious. No DDD processes were detected (ACF plot, Fig. 5A). In contrast, the approach of Lande et al. (2002) revealed evidence of DD in life history, obtaining a high estimate of $DD_{LH} = 4.1 \pm 1.9$ for deer seen/hunter/day (Table 1B).

The linear model of deer harvested/hunter at time $t-1$ versus time t showed no evidence of DD ($N_t = 0.57 \pm 0.10 - 0.10 \pm 0.18 \times lnN_{t-1}$, $R^2 = 0.01$, $F_{1,28} = 0.3$, $p = 0.6$; Fig. 3B). In contrast, deer harvested/hunter at time $t-1$ against r_t suggested strong DD ($r_t = 0.57 \pm 0.10 - 1.09 \pm$
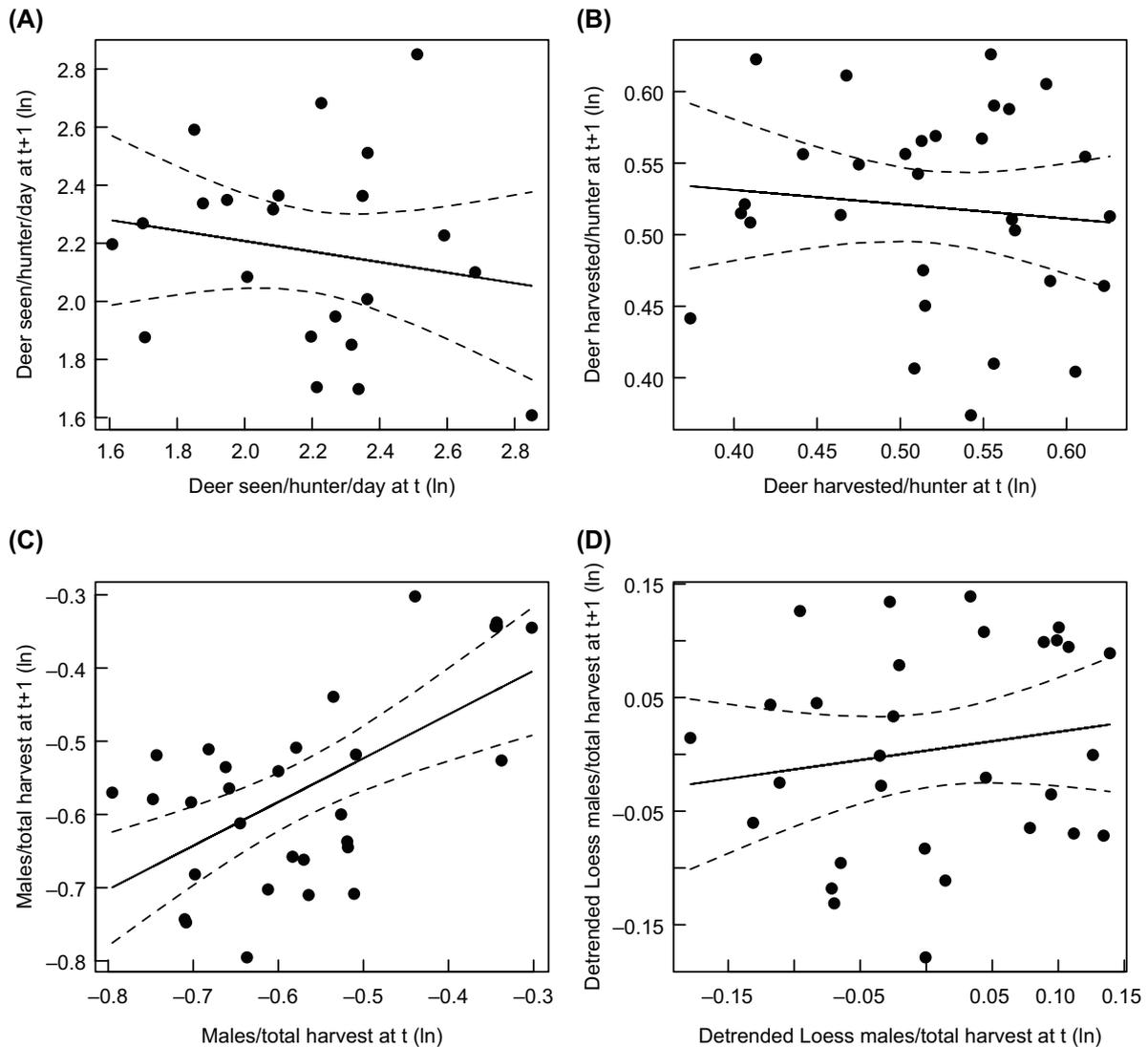
Figure 3. The relation between indices of relative abundance (natural log-transformed) of white-tailed deer on Anticosti Island (Québec, Canada) at time t and t + 1 (time in year) based on hunting statistics: (A) the number of deer seen per hunter per day (1983–2006), (B) the number of deer harvested per hunter (1975–2006), (C) the proportion of males per total harvest (1975–2006), and (D) the detrended proportion of males per hunter using loess regression.

$0.18 \times \ln N_{t-1}$, $R^2 = 0.56$, $F_{1,28} = 35.2$, $p < 0.001$; Fig. 4B). The autoregressive model applied on the time series deer harvested/hunter (Fig. 1B) selected order 0 ($\sigma^2 = 0.004$; Table 1A), thus an absence of DD or DDD (ACF plot, Fig. 5B). The approach of Lande et al. (2002), however, resulted in DD in life history, although $DD_{LH} = 3.5 \pm 1.6$ was lower than for the deer seen/hunter/day time series (Table 1B).

The linear regression between male/total harvest (not detrended) at time $t-1$ and time t showed a positive relationship ($N_t = -0.22 \pm 0.09 + 0.60 \pm 0.15 \times \ln N_{t-1}$, $R^2 = 0.37$, $F_{1,20} = 16.3$, $p < 0.001$; Fig. 3C), i.e. that when male/total harvest was low (or high) at time $t-1$, it tended to remain respectively low (or high) at time $t + 1$. This was in contrast to the negative feedback expected with DD. Surprisingly, a linear regression between male/total harvest (not detrended) at time $t-1$ and r_t did not suggest positive DD but rather weak negative DD ($r_t = -0.22 \pm 0.09 -$

$0.04 \pm 0.15 \times \ln N_{t-1}$, $R^2 = 0.21$, $F_{1,20} = 7.4$, $p = 0.01$; Fig. 4C). Similarly to the pattern observed from the regression of N_{t-1} and N_t, the autoregressive model of the time series male/total harvest (Fig. 1C) selected order 1 with a positive β_1 estimate ($\sigma^2 = 0.010$; Table 1A), but positive DDD feedback was also visible (ACF plot, Fig. 5C). The Lande et al. (2002) approach on male/total harvest did not suggest DD, as $DD_{LH} = 0.9 \pm 1.5$ was the lowest of all estimates (Table 1B).

The higher polynomial model fitted male/total harvest data and successfully removed the trend (parameter estimates $\pm$ SE: ln(male/total harvest) = $-244.9 \pm 84.5 + (0.13 \pm 0.04)$ t + (0.018 ± 0.005) t^2 + (0.0009 ± 0.0003) t^3 + $(-0.000015 \pm -0.000004)$ t^4, $R^2 = 0.52$, $F_{4,26} = 9.2$, $p < 0.001$). The regression between polynomial detrended male/total harvest at time $t-1$ and time t did not reveal direct DD ($N_t = 0.00 \pm 0.02 + 0.07 \pm 0.19 \times \ln N_{t-1}$, $R^2 = 0.01$, $F_{1,28} = 0.15$, $p = 0.7$), but the regression
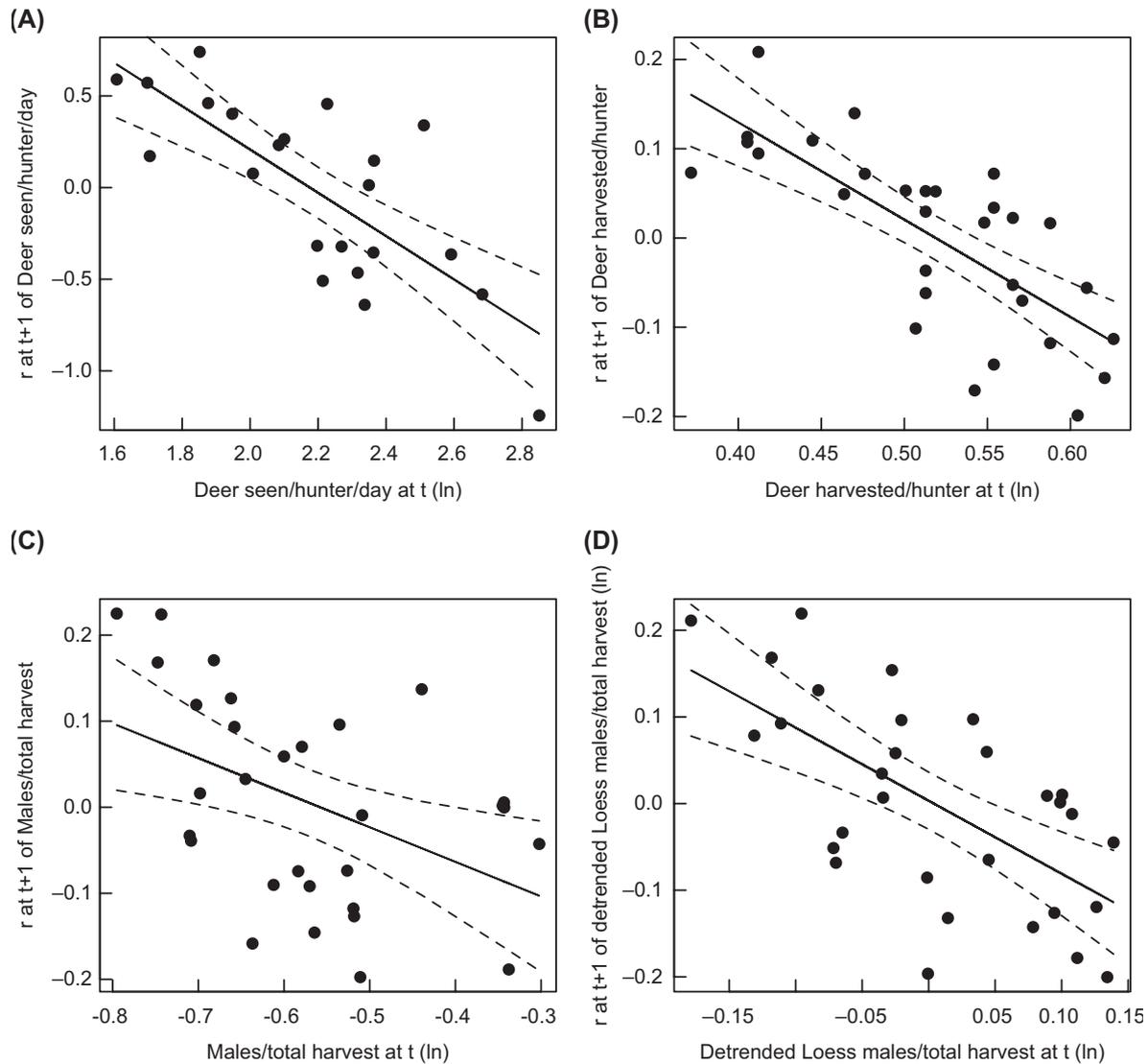
Figure 4. The relation between indices of relative abundance (natural log-transformed) of white-tailed deer on Anticosti Island (Québec, Canada) at time t (time in year) and r t + 1 ($\log(N_{t+1}/N_t)$) based on hunting statistics: (A) the number of deer seen per hunter per day (1983–2006), (B) the number of deer harvested per hunter (1975–2006), (C) the proportion of males per total harvest (1975–2006), and (D) the detrended proportion of males per hunter using loess regression.

between detrended male/total harvest at time t−1 and r_t did ($r_t = 0.00 \pm 0.02 - 0.95 \pm 0.19 \times \ln N_{t−1}$, $R^2 = 0.46$, $F_{1,20} = 23.9$, p < 0.001). The autoregressive model of the time series polynomial detrended male/total harvest did not suggest DD nor DDD and provides the best fit at order 0 (delta $AIC_c = 0$; $\sigma^2 = 0.006$; Table 1A). We obtained contrasting results using the method of Lande et al. (2002) as we obtained a strong $DD_{LH} = 5.4 \pm 1.6$ for detrended male/total harvest (Table 1B).

The male/total harvest data were also successfully detrended using the residuals of a loess model with a span of 0.5 (residual standard error of 0.09643; Fig. 1D). Again, the regression between loess detrended male/total harvest at time t−1 and time t was not significant ($N_t = 0.00 \pm 0.02 + 0.17 \pm 0.19 \times \ln N_{t−1}$, $R^2 = 0.03$, $F_{1,28} = 0.77$, p = 0.4; Fig. 3D), but the regression between loess detrended male/total harvest at time t−1 and r_t suggested direct DD ($r_t = 0.00 \pm 0.02 - 0.84 \pm 0.19 \times \ln N_{t−1}$, $R^2 = 0.41$, $F_{1,28} = 19.6$, p < 0.001; Fig. 4D). The autoregressive model of

the time series loess detrended male/total harvest did not select for DD nor DDD and was best at order 0 (delta $AIC_c = 0$; $\sigma^2 = 0.007$; Table 1A; ACF plot, Fig. 5D). The Lande et al. (2002) approach on male/total harvest did suggest DD with $DD_{LH} = 4.5 \pm 1.6$ (Table 1B). Results using the raw data and the detrended data differed using either AR and the DD_{LH} approaches, but were similar for both polynomial or loess detrending methods.

Discussion

The use of appropriate time series to study the dynamics of animal populations is crucial to make accurate ecological inference (Freckleton et al. 2006). Unfortunately, precise unbiased estimates of population size are challenging to obtain because most estimates of population size include unidentified biases generally impossible to accommodate (Gaillard et al. 2003). We used different indices of population
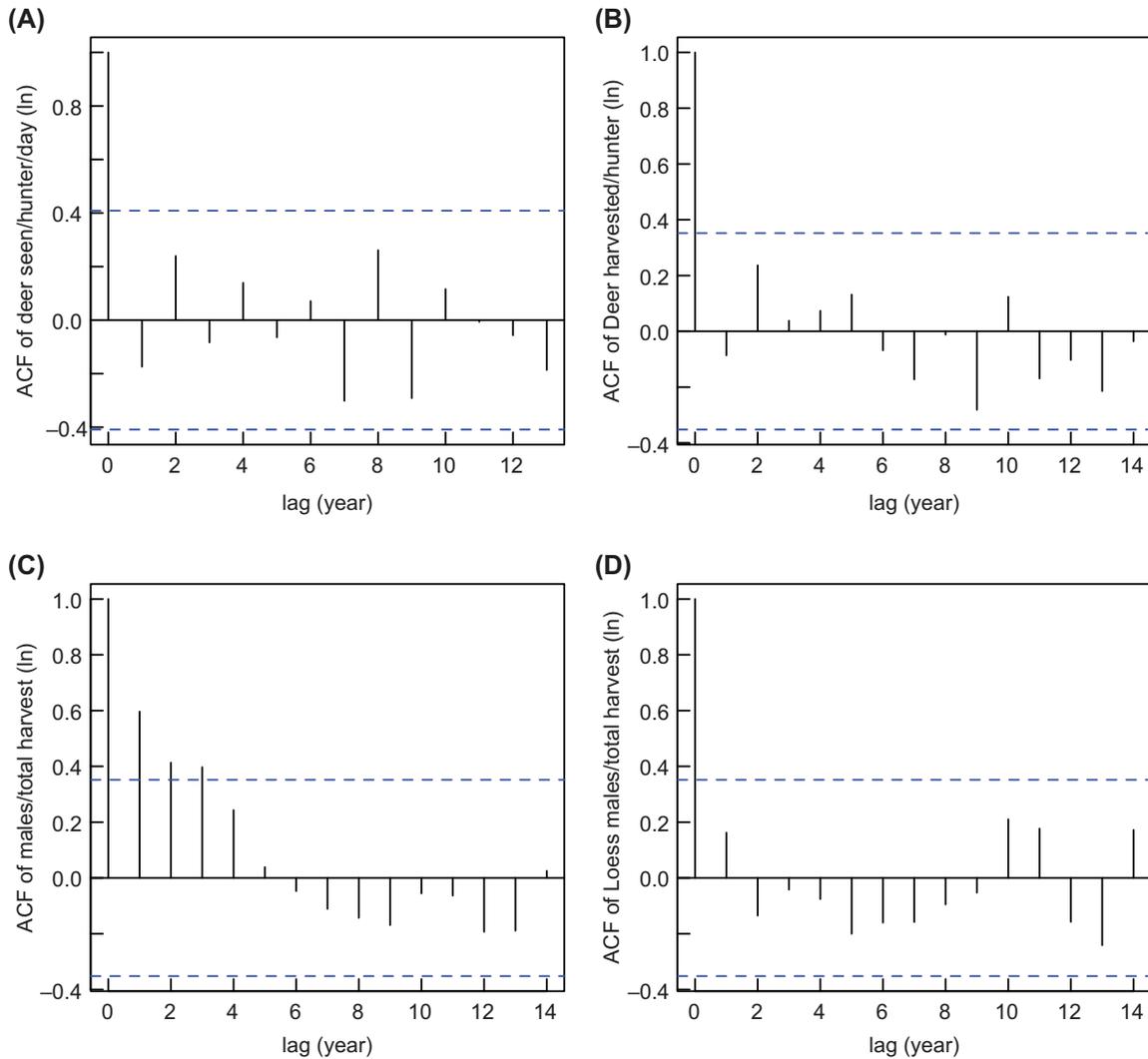
Figure 5. Autocorrelation function (ACF) of different time series representing indices of relative abundance (natural log-transformed) of white-tailed deer population on Anticosti Island (Québec, Canada): (A) the number of deer seen per hunter per day (1983–2006), (B) the number of deer harvested per hunter (1975–2006), (C) the proportion of males per total harvest (1975–2006), and (D) the detrended proportion of males per hunter using loess regression. Significant time lags should be observed outside the dotted lines.

size, which we expected to be correlated because they were from the same population. Accordingly, aerial surveys correlated with all indices, but the correlation was best with deer seen/hunter/day (see also Pettorelli et al. 2007). All indices also correlated with each other, the strongest relationship being between deer seen/hunter/day and deer harvested/hunter. Such correlations suggest that these different indices of relative abundance captured variation in the deer population size in a similar manner. Unfortunately, correlations among indices do not provide the assurance that they accurately describe changes in population size, as external factors may still have affected all indices similarly (Seber 1992, Ranta et al. 2008).

Although all density indices correlated with each other, cross correlation between certain indices was sometimes weak. It is therefore difficult to make clear recommendations about which type of index is most appropriate, because bias or inaccuracy, even if they are not necessarily obvious, can still be present such that without real data on population size it cannot be validated. Differences among hunting

statistics might be related to hunter selectivity, motivation and effort (Bhandari et al. 2006). Hunting selectivity could depend on deer density non-linearly (Holsworth 1973), as a function of hunter origin (Solberg et al. 2000, Mysterud et al. 2006) or the facility to reach hunting quotas (Mysterud et al. 2007). Correlations (this study, Pettorelli et al. 2007) and the literature (Solberg et al. 1999, Sylvén 2000, Mysterud et al. 2007) indicated that deer seen/hunter/day might be a more appropriate index of density that other hunting statistics, likely because it is less susceptible to selectivity bias than other hunting statistics (Solberg et al. 2004, Kilpatrick et al. 2005). Nevertheless, possible biases remain as deer seen/hunter/day may depend on other factors such as habitat visibility, environmental conditions (Hansen et al. 1986), size of the area hunted (Sylvén 2000), hunter density (Foster et al. 1997), prey behaviour (Eros et al. 2005, Mysterud et al. 2007), hunting methods, hunters' age and condition (Bhandari et al. 2006), and the reporting accuracy of statistics by hunters (Kilpatrick et al. 2005). Biases in estimates of population size can compromise the accuracy of

DD estimates, even with the ideal statistical method (Seber 1992, Dennis et al. 2006). When data on real population size are not available, authors should be very clear to stress that they are working with indices and always consider potential biases. Based on our results, we think that male/hunter, that clearly underlined an unexplained trend in the data, is likely less adequate than deer seen/hunter/day and deer harvested/hunter, but it was rather encouraging to find that the last two indices led to similar conclusions. The level up to which a density index has to be accurate in order to justify its use is not only difficult to verify but also to establish: opinions vary as a function of management applications and type of studies (Hone 2008).

Several studies have used indices of population size in DD tests (Stenseth et al. 1998, Hansen et al. 1999, Post 2005), but it is uncommon to test different indices on the same population. Although all hunting statistic indices correlated with each other, in some cases estimates of DD strength differed among indices. Similar results were obtained for indices that were most closely correlated, for example deer seen/hunter/day and deer harvested/hunter showed no direct DD with linear regression of N_{t-1} and N_t or AR models, but direct DD with linear regression of N_{t-1} and r_t and high DD_{LH} with the approach of Lande et al. (2002). In contrast, male/total harvest (not detrended) showed a positive feedback of density with linear and AR models, but an absence of DD_{LH}. Nevertheless, detrended male/total harvest, both using polynomial or loess regression, provided results very similar to the two other indices. This seems to suggest that all indices exhibited the same DD pattern as long as trend was removed.

Other studies previously documented contradictory results between detrended and original time series (Forchhammer et al. 1998, Aanes et al. 2000). Assumptions of autoregressive models stipulate that a time series should be detrended prior to its use if non-stationarity is noticeable, and that it should not affect its autocorrelative structure or biological inference (Box et al. 1994). Although statistical inference of detrended times series should be used over non-detrended data (Royama 1992, Turchin 2003), some authors still have concerns about the difficulty to assess whether detrending affects the reliability of the results (Wu et al. 2007) and about the biological interpretation of detrended data (Jonzén et al. 2002, Wu et al. 2007). Studies investigating long-term population fluctuations associated with environmental changes would not be adequately interpreting data if trends were removed, as they could suppress the influence of external factors such as global warming or human activity (Jonzén et al. 2002, Wu et al. 2007).

Although the biological interpretation of a time series using different mathematical approaches should be similar, statistical interpretations among tests often diverge (Wolda and Dennis 1993). DD tests are based on different assumptions and each test has a specific sensitivity to temporal variation in the data (Royama 1992, Dennis and Taper 1994, Lande et al. 2002). Several studies found that different models frequently led to contradictory outcomes (Holyoak 1993, Forchhammer et al. 1998), even if sometimes they fit the data equally well (Morris 1990). Here, we found that the linear regression between N_{t-1} and N_t and AR models,

in which DD was not detected, were contrary to the negative regression between N_{t-1} and r_t and the strong DD_{LH} we documented in most times series. Similarly, Forchhammer et al. (1998), who used five different tests of DD, found consistent results in only 1 population out of 5. Given such differences among models, choosing which one is appropriate – rather than just a personal preference – becomes a justified concern (Berryman 1992, Coulson et al. 2008).

The contrasted results we obtained when comparing the regression of N_{t-1} with N_t and N_{t-1} with r_t seemed to agree with Turchin (2003) findings that plotting r_t against N_{t-1} allowed a better visual signal of DD than with N_t. Nevertheless, challenged by these divergent results, we repeated the same exercise, i.e. plotting N_{t-1} both with N_t and with r_t, but using random time series of n = 100 having the same maximum and minimum than the index of deer seen/hunter/day. After replicating this randomisation process 100 times, we found that the average slope of N_{t-1} and N_t was 0.08 (minimum and maximum of -0.2 and 0.2), not supporting DD, while the average slope between N_{t-1} and r_t was -1.0, revealing strong DD (minimum and maximum of -1.2 and -0.8). We suggest that because r_t is by definition not independent of N_{t-1}, a regression between these variables will be expected to result in overestimating the strength of DD, as demonstrated using random data sets. Therefore, we considered that the linear regression between N_{t-1} and N_t was more appropriate to investigate DD.

The structure of the linear regression of N_{t-1} and N_t is similar to AR models, as both investigate direct DD or β_1 using N_t. Thus, it was not surprising to obtain converging results with both approaches, especially as DDD appeared uncommon. A possible explanation for not detecting DD using these approaches, however, could be associated with the high variability in density indices. Turchin (2003) suggested that the linear regression of N_{t-1} and r_t limited such problems, but we demonstrated it induced other issues. Yet, we found strong DD_{LH} in most indices, although the Lande et al. (2002) approach is also based on AR coefficients. The first distinction between AR and DD_{LH} is that the AR equation selects only the β_k with the lowest AIC, while DD_{LH} sums β_1 to β_α independently of their significance (Eq. 5), possibly including coefficients with large confidence interval. This explains why we obtained large sampling errors for DD_{LH} estimates. Despite their use of AIC (Bjørnstad et al. 1995), AR models have been criticized because of the difficulty in confirming whether they selected the most appropriate time delay or β_k for density regulation (Berryman and Turchin 2001). We found that different time lags obtain equivalent AIC with AR models (Table 1A) and it became challenging to select the appropriate β_k. Although our results cannot indicate whether it is best to select β_k with AIC in AR models or to include β_1 to β_α in DD_{LH}, we demonstrated that the two approaches can be contradictory.

Another difference between AR models and the approach of Lande et al. (2002) is that they do not investigate DD at the same temporal scale. DD_{LH} operates with a time-lag up to age at maturity $= \alpha$ and mortality rate is integrated in the calculations, which scales DD at generation time (Lande et al. 2003). Conversely, linear and AR models estimate the strength of DD at the annual scale providing estimates of statistical DD without necessarily identifying

mechanisms generating DD (Wolda and Dennis 1993), so they are not always well suited to biological systems (Berryman and Turchin 2001). Bearing in mind that changes in biological populations are precisely induced by individuals that reproduce, die and move (Berryman 2002), this might justify the approach considering life-history parameters when interpreting AR models, as emphasised by Lande et al. (2002, 2003), Sæther et al. (2005), and Wang et al. (2006). While the pros and cons of AR models have been largely documented (Royama 1992, Wolda and Dennis 1993, Berryman and Turchin 2001), few reviews or comments exist relative to the approach of Lande et al. (2002), which has still not been used widely (Sæther et al. 2005). Lande et al. (2003) found DD_{LH} in 4 out of 6 time series of different bird species, and had lower estimates (i.e. from 0.4–2.7) than documented in our study (i.e. from 0.9–5.4). An estimate of $DD_{LH} = 4$ implies that a given increase in adult population density produces an approximately four time proportional decrease in λ^τ. On Anticosti, DD_{LH} might have been amplified by a non-linear relationship between hunting statistics and population size, but this is again difficult to verify. Further studies using the approach of Lande et al. (2002) with other populations would certainly improve our comparisons and interpretation of DD_{LH}.

We caution against the unilateral acceptance of conclusions obtained from phenomenological time series models, and suggest that pros and cons of methods and indices that are used should be conscientiously evaluated. Here, it appears difficult to statistically or objectively decide which method works best as AR and D_{LH} appear incommensurable, both being based on different time units. Nevertheless, we tend to favor D_{LH} because it can accommodate the mismatch between the time scale of population sampling and the life history of the studied organism. Moreover, results obtained with DD_{LH} are in accordance with other studies on the Anticosti deer population that demonstrated a strong relationship between population density (i.e. deer seen/hunter/day) and either survival, reproductive rates (Simard et al. 2010) or deer body condition (Simard 2010). In addition to density, weather in spring also affected deer reproduction and survival (Simard et al. 2010).

Conclusion

Direct and delayed density dependence are complex phenomena that may involve several ecological mechanisms and confounding parameters (Zeng et al. 1998). Not surprisingly, time series are consequently often insufficient for biological inferences in complex systems, such as with herbivore populations (Månsson and Lundberg 2006). Studies attempting to make predictive use of times series analyses should not use times series of uncertain accuracy, and if they are uncertain, they should instead be used to generate testable hypotheses (Berryman and Turchin 2001, Carrete et al. 2008). Relative indices of abundance may incorporate unknown biases that cast doubt on their predictions (Freckleton et al. 2006). We found that different indices of relative abundance, trend versus detrended data, and different approaches gave different insights about DD in the Anticosti deer population. Our results suggest that studies

using only one type of DD test, or one index of abundance, could yield inappropriate conclusions. Although other studies have revealed divergences in the interpretation of different DD methods (Forchhammer et al. 1998, Holyoak 1993), there are no cases where different methods have been applied to multiple indices from the same population. When dealing with populations for which management policies are crucial but where only relative indices of abundance are available, notably the deer population on Anticosti Island, measuring changes in reproduction or body condition might be a more appropriate or complementary approach (Cederlund et al. 1998, Morellet et al. 2007). We support Berryman and Turchin (2001) who emphasised that time-series analysis should be used with caution, being not an end in itself, but rather a starting point.

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