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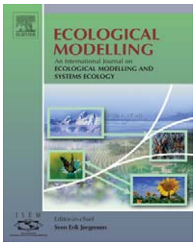

Population momentum across vertebrate life histories

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ABSTRACT

Population abundance is critically important in conservation, management, and demographic theory. Thus, to better understand how perturbations to the life history affect long-term population size, we examined population momentum for four vertebrate classes with different life history strategies. In a series of demographic experiments we show that population momentum generally has a larger effect on long-term population size for organisms with long generation times than for organisms with short generation times. However, patterns between population momentum and generation time varied across taxonomic groups and according to the life history parameter that was changed. Our findings indicate that momentum may be an especially important aspect of population dynamics for long-lived vertebrates, and deserves greater attention in life history studies. Further, we discuss the importance of population momentum in natural resource management, pest control, and conservation arenas.

1. Introduction

Population size and growth rate are central aspects of biology that are commonly estimated with tools that assume stability of population structure (i.e., age, stage, or size structure) through time (e.g., see papers within Heppell et al., 2000; Sibly et al., 2002). Ecologists, however, realize that this assumption may rarely be met in nature (Bierzychudek, 1999; Fox and Gurevitch, 2000; Clutton-Brock and Coulson, 2002; Nichols and Hines, 2002; Hastings, 2004). An unstable population structure can have a strong inertial effect on future population size, which is known as population momentum (Keyfitz, 1971). In human demography, studies of population momentum have influenced international policy (e.g., Bos et al., 1992, 1994; United Nations, 2003); however, the relevant tools are rarely used in population ecology (Koons et al., 2006), and theory describing the behavior of population momentum across species is lacking.

Population momentum occurs in structured populations because there is often a time-lag between a change in the vital rate (i.e., a life history parameter such as survival, fertility, etc.) and the actual observed impact on the population. For example, imagine a population with high per capita fertility rates, where offspring have a high likelihood of surviving to maturity. If fertility suddenly dropped to the stationary level (i.e., $\lambda_1 = 1$, the level of lifetime individual replacement), a population would keep growing because overabundance of young individuals would ensure high net fertility rates long after

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the transition to stationary per capita fertility (sensu Keyfitz, 1971). In structured populations, changes in any vital rate will alter population structure, causing transient dynamics (i.e., unstable short-term dynamics), and ultimately, population momentum (Caswell, 2001). Activities that directly alter population structure, like commercial fishing (Hall, 1999), will do the same. Understanding population momentum and its effect on population dynamics is important to increase our understanding of life history evolution and the efficacy of conservation, natural resource management, and pest control practices.

Recent studies across vertebrates have found that asymptotic population dynamics (e.g., sensitivities and elasticities) are directly related to values of individual vital rates (Heppell, 1998; Heppell et al., 2000b; Sæther and Bakke, 2000), or ratios of vital rates (Oli and Dobson, 2003). To truly understand population dynamics, however, it is necessary to look at the entire life history, not just selected vital rates. Generation time, measured as the mean age of offspring production, is a function of all demographic vital rates. The inverse of generation time measures population turnover, and is expected to provide a reliable measure of a given life history along the "slow-fast" continuum (Gaillard et al., 2005) where slow species are typified by late maturation, high annual survival, and low reproductive rates, whereas fast species have low annual survival, early maturation, and high reproductive rates (sensu Gaillard et al., 1989; Charnov, 1993). Not surprisingly, the rate at which population structure approaches the stable state (e.g., stable age distribution) is related to generation time (Tuljapurkar, 1986). In addition, Koons et al. (2005) have recently shown that transient dynamics of vertebrates with long generation times are more reactive to changes in population structure than they are for vertebrates with short generation times. Thus, population momentum should be related to generation time as well; however, it is possible for large transient increases and decreases in population size to effectively cancel each other out over time and have little effect on long-term population size. Interspecific studies of population momentum have not been conducted to elucidate these possibilities. Here, we use extensions of Keyfitz's formula (1971) and simulation to calculate and examine population momentum across both semelparous and iteroparous vertebrate life history strategies. We predict that the magnitude of population momentum will increase with generation time, and discuss some of the underlying demographic mechanisms that may be responsible for variation in population momentum across life histories.

2. Methods

2.1. Life history data

To reveal how life history and population momentum are related, we explored life histories where reproduction can occur several times within a lifetime (i.e., iteroparous), and where reproduction occurs once and is followed by death (i.e., semelparous). We attained life history data from the peer-reviewed literature for 10 iteroparous species within each of 4 vertebrate classes: Aves, Mammalia, Reptilia, Osteichthyes; and for 5 semelparous Osteichthyes species (all pacific salmon; Table 1). Species within each vertebrate class were selected such that population momentum could be examined across life histories exhibiting a large range in age at maturity (α), a close surrogate to generation time (Cole, 1954; Lewontin, 1965). Because first-year and sub-adult survival are poorly studied for many vertebrate organisms, we had to impose assumptions about these vital rates to generate a complete life cycle for selected species (see Table 1).

We parameterized the life history variables for each species into a partial life-cycle projection matrix using a 1-yr time step (shown below, **A** is an iteroparous and **B** a semelparous life-cycle matrix), which can accommodate reproductive delay (Oli and Zinner, 2001), but do not capture the potential importance of seasonal variation in reproductive effort. We assumed birth-pulse reproduction and used a pre-birth census, where fertility (F) equalled the product of fecundity (m, the number of female offspring produced per female each year) and age-class 1 survival ($F = m \times P_1$) (Caswell, 2001), P_{sa} equalled sub-adult survival, and P_a equalled adult survival:

$$\mathbf{A} = \begin{bmatrix} 0 & \cdots & 0 & F \\ P_{sa} & \cdots & 0 & 0 \\ & \ddots & & \\ 0 & \ddots & 0 & 0 \\ 0 & \cdots & P_{sa} & P_a \end{bmatrix}, \qquad \mathbf{B} = \begin{bmatrix} 0 & \cdots & 0 & F \\ P_{sa} & \cdots & 0 & 0 \\ & \ddots & & \\ 0 & \ddots & 0 & 0 \\ 0 & \cdots & P_{sa} & 0 \end{bmatrix}.$$

Partial life-cycle matrices are amenable to comparative life history studies, and have been shown to accurately portray the dynamics of many age-structured vertebrate populations (Heppell et al., 2000b; Sæther and Bakke, 2000; Oli and Dobson, 2003; Oli, 2003).

To develop our demographic experiments, we created growing ($\lambda_1 = 1.1$) populations by numerically changing fertility, which often causes fast population growth when at high levels in nature. Because quickly declining populations are often caused by suppressed survival probabilities (Ricklefs, 1990), we created declining ($\lambda_1 = 0.9$) populations by numerically changing adult survival for iteroparous species, and subadult survival for semelparous species. For simplicity, we limited our study to these special cases of growing and declining populations, but acknowledge that fertility or survival could cause populations to change in either direction.

2.2. Demographic experiments

Here, we consider scenarios where populations are growing so rapidly that they could cause environmental damage and where populations are declining at a rate that could yield extinction (i.e., the growing and declining populations defined above). Our objective was to examine population size following changes in vital rates designed to halt the growth or decline. Although vital rates are expected to vary over time in most environments, we purposefully ignored such stochastic variation to isolate and study the effects of historical age structure on long-term population size following isolated changes in a vital rate (i.e., population momentum). Furthermore, large, temporally isolated changes in environmental conditions do occur in nature and are of interest in ecology and evolution (e.g., hurricanes, large floods, petroleum catastrophes, etc.).

In the demographic experiments, we first started with a growing population ($\lambda_1 = 1.1$) in its stable population structure

Table 1 – The fertility rate (F), modal age at maturity (α), sub-adult survival probability (P_{sa}), adult survival probability (P_a), and generation time (μ_1) of the vertebrate species used in our demographic experiments (see Section 2 for calculation of fertility and generation time)

Common name	Species, Aves	F	α	P_{sa}	P_a	μ_1	Source
Sooty Albatross	*Phoebetria fusca*	0.10	12	[a]	0.95	31.00	Russell (1999)
Wandering Albatross	*Diomedea exulans*	0.21	10	0.86	0.93	23.71	Weimerskirch (1992), Weimerskirch et al. (1997) and Sæther and Bakke (2000)
Northern Fulmar	*Fulmarus glacialis*	0.16	8	[a]	0.94	23.67	Sæther and Bakke (2000)
King Penguin	*Aptenodytes patagonica*	0.05	6	[a]	0.94	20.38	Russell (1999) and Sæther and Bakke (2000)
Parasitic Jaeger	*Stercorarius parasiticus*	0.44	4	[a]	0.80	8.00	Sæther and Bakke (2000)
Northern Spotted Owl	*Strix occidentalis*	0.08	3	[a]	0.84	8.25	Sæther and Bakke (2000)
Lesser Snow Goose	*Chen caerulescens*	0.32	2	0.83	0.83	6.92	Cooch et al. (2001)
Lesser Kestrel	*Falco naumanni*	0.32	2	[a]	0.71	4.45	Sæther and Bakke (2000)
American Coot	*Fulica Americana*	0.88	1.5	–	0.43	2.06	Kiel (1955), Burton (1959) and Crawford (1980)
Blue Tit	*Parus caeruleus*	0.68	1	–	0.40	1.67	Sæther and Bakke (2000)

Common name	Species, Mammalia	F	α	P_{sa}	P_a	μ_1	Source
African Elephant	*Loxodonta africana*	0.07	14	0.98	0.94	29.67	Heppell et al. (2000b)
Chimpanzee	*Pan troglodytes*	0.08	14	0.92	0.95	33.00	Heppell et al. (2000b)
Hippopotamus	*Hippopotamus amphibius*	0.09	10	0.95	0.94	25.67	Heppell et al. (2000b)
Gorilla	*Gorilla gorilla*	0.09	8	0.98	0.95	27.00	Heppell et al. (2000b)
Black Bear	*Ursus americanus*	0.24	5	0.87	0.86	11.14	Heppell et al. (2000b)
Manatee	*Trichechus manatus*	0.15	4	0.90	0.91	14.11	Heppell et al. (2000b)
Northern Fur Seal	*Calorhinus ursinus*	0.18	3	0.75	0.90	12.00	Heppell et al. (2000b)
Reindeer	*Rangifer tarandus*	0.23	2	0.96	0.79	5.76	Heppell et al. (2000b)
Coypu	*Myocastor coypus*	1.09	2	0.44	0.52	3.08	Heppell et al. (2000b)
Snowshoe Hare	*Lepus americanus*	0.95	1	–	0.20	1.25	Heppell et al. (2000b)

Common name	Species, Reptilia	F	α	P_{sa}	P_a	μ_1	Source
Loggerhead Sea Turtle	*Caretta caretta*	51.64	22	0.72	0.81	40.75	Wilbur and Morin (1994) and Heppell (1998)
Snapping Turtle	*Chelydra sperpentina*	1.04	19	0.75	0.97	47.41	Wilbur and Morin (1994) and Heppell (1998)
Desert Tortoise	*Gopherus agassizi*	1.88	14	0.81	0.94	29.95	Wilbur and Morin (1994) and Heppell (1998)
Painted Turtle	*Chrysemys picta*	0.40	8	0.77	0.96	32.00	Wilbur and Morin (1994) and Heppell (1998)
Slider Turtle	*Trachemys scripta*	0.13	7	0.76	0.81	10.38	Heppell (1998)
Common Mud Turtle	*Kinosternum subrubrum*	0.25	4	0.67	0.88	11.06	Wilbur and Morin (1994) and Heppell (1998)
Broad-Banded Copperhead	*Agkistrodon contortrix*	0.61[b]	3	[a]	0.70	5.33	Dunham and Miles (1985) and Shine and Charnov (1992)
Common Gartersnake	*Thamnophis sirtalis*	1.00[b]	2	[a]	0.50	3.00	Dunham and Miles (1985) and Shine and Charnov (1992)
Viviparous Lizard	*Lacerta vivipara*	1.33[b]	1.5	–	0.20	1.42	Dunham and Miles (1985) and Shine and Charnov (1992)
Japanese Grass Lizard	*Takydromus takydromoides*	0.76[b]	1	–	0.24	1.32	Dunham and Miles (1985) and Shine and Charnov (1992)

Table 1 (*Continued*)

Common name	Species, *Osteichthyes* (Iteroparous)	F	α	P_{sa}	P_a	μ_1	Source
Dogfish	*Squalas acanthias*	0.62[b]	23	[a]	0.91	33.62	Gunderson (1997) and King and McFarlane (2003)
Rougheye Rockfish	*Sebastes aleutianus*	0.08[b]	20	[a]	0.96	44.50	Gunderson (1997) and King and McFarlane (2003)
Long Rough Dab	*Hippoglossoides platessoides*	2.98[b]	15	[a]	0.82	19.52	Roff (1984) and Frisk et al. (2001)
Pacific Halibut	*Hippoglossus stenolepis*	1.40[b]	12	[a]	0.83	16.78	Gunderson (1997) and King and McFarlane (2003)
Pacific Ocean Perch	*Sebastes alutus*	0.08[b]	11	[a]	0.95	30.50	Gunderson (1997) and King and McFarlane (2003)
Yellowtail Rockfish	*Sebastes flavidus*	0.46[b]	10	[a]	0.87	16.65	Gunderson (1997) and King and McFarlane (2003)
Haddock	*Melanogrammus aegelfinus*	0.49[b]	6	[a]	0.82	10.52	Gunderson (1997) and Frisk et al. (2001)
Pacific Cod	*Gadus macrocephalus*	1.36[b]	5	[a]	0.69	7.23	Gunderson (1997) and King and McFarlane (2003)
Striped Bass	*Morone saxatilis*	3.81[b]	4	[a]	0.60	5.50	Cohen et al. (1983) and Heppell et al. (1999)
Sand Lance	*Ammodytes hexapterus*	4.67[b]	3	[a]	0.37	3.58	Gunderson (1997) and King and McFarlane (2003)

Common name	Species, *Osteichthyes* (Semelparous)	F	α	P_{sa}	P_a	μ_1	Source
Chinook Salmon	*Oncorhynchus tshawytscha*	15.84	5	0.48	–	5.00	Wilson (2003)
Sockeye Salmon	*Oncorhynchus nerka*	38.37	5	0.60	–	5.00	Groot and Margolis (1991) and Quinn (2005)
Chum Salmon	*Oncorhynchus keta*	85.37	4	0.31	–	4.00	Groot and Margolis (1991) and Quinn (2005)
Coho Salmon	*Oncorhynchus kisutch*	25.90	3	0.32	–	3.00	Groot and Margolis (1991) and Quinn (2005)
Pink Salmon	*Oncorhynchus gorbuscha*	22.67	2	0.12	–	2.00	Groot and Margolis (1991) and Quinn (2005)

In most cases, life history parameters were attained directly, or calculated from data provided within interspecific studies of vertebrate life history (for original source of data please see the cited references). Here, life history parameters are rounded to the second decimal.

[a] Because first-year and sub-adult survival are poorly studied for many vertebrate organisms, we assumed sub-adult survival to be equal to adult survival if sub-adult survival estimates were not available for the noted species.

[b] According to Heppell (1998) and Heppell et al. (2000b), if estimates of first-year survival were not available for noted species, we numerically calculated the value that gives $\lambda_1 = 1$. Estimated values of first-year survival were $\ll$adult survival, which agrees with life history theory (Stearns, 1992). Simulation has shown that our results are robust to assumptions *a* and *b* (Koons, 2005).

as the initial condition and then instantaneously decremented fertility by the necessary amount to attain stationary growth ($\lambda_1 = 1$) (i.e., an instantaneous transition; sensu Keyfitz, 1971). A gradual transition in fertility to the replacement level can substantially increase population momentum (Schoen and Kim, 1998; Li and Tuljapurkar, 1999). Yet, unlike in human populations where it can take decades for fertility rates to approach the replacement level (Li and Tuljapurkar, 1999), wild vertebrate populations can experience relatively rapid changes in environmental conditions and vital rates, either naturally (Young, 1993) or via anthropogenic factors (e.g., Piatt and Lensink, 1989). Furthermore, management and conservation objectives are often centered on near-term outcomes (Fox and Gurevitch, 2000). Accordingly, we conducted a second set of experiments where we decremented fertility in a monotonic fashion over 5 years by the amounts necessary to eventually attain stationary growth (i.e., we reduced fertility linearly from the initial level to the final level over 5 years).

In the second group of experiments, we started with a declining population ($\lambda_1 = 0.9$) in its stable population structure as the initial condition and then instantaneously augmented adult survival (sub-adult survival for semelparous species) by the amount necessary to attain stationary growth. We then conducted a similar experiment, but augmented adult survival (sub-adult survival for semelparous species) in a monotonic fashion over 5 years by the amounts necessary to eventually attain stationary growth.

2.2.1. *Calculation of population momentum*

Population momentum (M) is always calculated according to Keyfitz (1971):

$$M = \lim_{t\to\infty} \frac{||\mathbf{n}_t||_1}{||\mathbf{n}_0||_1} \qquad (1)$$

where $||\mathbf{n}||_1 = \sum_i |n_i|$ is the 1-norm, which gives total population size. This is simply the ratio of the ultimate population size following a transition to the stationary level, to the size immediately before the transition. For discrete-time models, Eq. (1) can be approximated with

$$M_{\text{inst}} = \frac{\mathbf{e}^T(\mathbf{v}_1^{(\text{new})} \times \mathbf{w}_1^{(\text{initial})})\mathbf{w}_1^{(\text{new})}}{\mathbf{e}^{\mathrm{T}} \times \mathbf{w}_1^{(\text{initial})}} \qquad (2)$$

when changes in vital rates are instantaneous, denoted by the subscript$_{\text{inst}}$ on M (Caswell, 2001:104). Here, $\mathbf{e}$ is a vector of ones, $\mathbf{w}_1$ is the dominant right eigenvector of the projection matrix ($\mathbf{A}$ or $\mathbf{B}$) that describes the stable population structure (scaled such that $||\mathbf{w}_1||_2 = 1$), $\mathbf{v}_1$is the dominant left eigenvector of the projection matrix that describes reproductive value, 'initial' refers to the projection matrix for the initial conditions (growing or declining population), and 'new' refers to the projection matrix following change in fertility or survival probability. The left and right eigenvectors of a projection matrix satisfy $\langle \mathbf{v}_i, \mathbf{w}_i \rangle = 1$ and $\langle \mathbf{v}_i, \mathbf{w}_j \rangle = 0$ for $i \neq j$ where $\langle\ \rangle$ is the scalar product.

Because iteroparous organisms can reproduce in successive time steps, projection matrices for iteroparous life histories are primitive, meaning that there exists one dominant eigenvalue and the asymptotic dynamics approach a stable point. However, semelparous organisms have positive fertility in only one age class; therefore, projection matrices for semelparous life histories are imprimitive and have co-dominant eigenvalues. Thus, unless the population structure begins in the stable state, the asymptotic population size and (st)age distribution of semelparous organisms are cyclic with a period equal to the number of eigenvalues that share the largest magnitude (d) (Caswell, 2001). Still, a running average of the (st)age distribution over d converges to $\mathbf{w}_1$ and grows at the rate λ_1 (Cull and Vogt, 1973). For semelparous life histories, we always measured population momentum with the limit of these running average values.

2.2.2. *Measuring the impacts of gradual change in a vital rate on population momentum*

To compute population momentum for gradual changes in vital rates, we calculated the numerator of Eq. (1) with a Markov chain of gradually changing vital rates (in the following equations, $\mathbf{A}$ can also be replaced with $\mathbf{B}$):

$$\mathbf{n}_t = \mathbf{A}_{t-1}\mathbf{A}_{t-2}\cdots\mathbf{A}_1\mathbf{A}_0\mathbf{n}_0. \qquad (3)$$

Thus, a numerical calculation of population momentum for gradual change in any vital rate to the stationary level can be written as

$$M_{\text{grad}} = \lim_{t\to\infty} \frac{||\mathbf{A}_{t-1}\mathbf{A}_{t-2}\cdots\mathbf{A}_1\mathbf{A}_0\mathbf{n}_0||_1}{||\mathbf{n}_0||_1} \qquad (4)$$

where $\mathbf{A}_t$ represents the time-specific projection matrix of vital rates (e.g., Schoen and Kim, 1998; Li and Tuljapurkar, 1999, 2000; Goldstein, 2002). All measures of population momentum are centered on 1. Values of momentum above 1 indicate that the population will grow to a larger ultimate size following change in a vital rate to the stationary level, and values below 1 indicate that the population will decline to a smaller ultimate size.

When a vital rate gradually changes to the stationary level, two factors cause population momentum. First, gradually changing vital rates will contribute to population growth or decline regardless of population structure. Second, the actual population structure that acts on each new set of vital rates is not stable, which produces inertia in population size (Tuljapurkar and Lee, 1997; Schoen and Jonsson, 2003). This measurement of net population growth following gradual change in a vital rate is not directly comparable to that following an instantaneous change, in which only the second factor causes momentum (Keyfitz, 1971). To explicitly understand the two components contributing to population momentum following gradual change in a vital rate to the stationary level, we projected a hypothetical stable population (SP) for the set of changing vital rates using another Markov chain:

$$\text{SP} = ||(\mathbf{A}_{t-1}\mathbf{u}_{t-1}||\mathbf{A}_{t-2}\mathbf{u}_{t-2}||_1\cdots||\mathbf{A}_1\mathbf{u}_1||_1||\mathbf{A}_0\mathbf{u}_0||_1)||_1 \qquad (5)$$

where $\mathbf{u}_t = \mathbf{w}_{1,\,t}/||\mathbf{w}_{1,\,t}||_1$ is the stable (st)age distribution at time t. Eq. (5) can be written as

$$\text{SP} = \lambda_{1,t-1}\lambda_{1,t-2}\cdots\lambda_{1,1}\lambda_{1,0} \qquad (6)$$

where $\lambda_{1,t}$ is the dominant real eigenvalue of $\mathbf{A}_t$. Placed on the same number scale as population momentum (see above), SP simply describes the ultimate population size that would be expected if population structure were ignored or somehow remained stable throughout time. Although the latter will rarely be true, one can compare M_{grad} to SP in order to better understand how historical population structure contributes to M_{grad}. If $M_{grad} = SP$, then population structure has no effect on the ultimate population size. However, if $M_{grad} < SP$, this implies that population structure limits the population from becoming as large as it could, given the vital rates. Conversely, if $M_{grad} > SP$, this implies that population structure causes a larger ultimate population size than would be expected from the vital rates alone. Demographic experiments and calculations were conducted in MATLAB (The MathWorks, 2005).

2.3. *Statistical analysis*

To test our prediction that the magnitude of population momentum would increase with generation time, we used Proc REG (SAS Institute, Inc. 2000) to examine null, linear, and quadratic models of the relationship between population momentum and generation time. Generation time (μ_1) was measured from the stationary populations as the mean age at which members of a cohort (of newborns) produce offspring (Coale, 1972; Caswell, 2001). Although consideration of body size and phylogenetic relatedness would be of interest in an evolutionary analysis, statistically controlling for these variables in the models would only obscure the current demographic relationship between population momentum and life history (Price, 1997; Kelly and Price, 2004), which is the focus here.

We used Schwarz's Information Criterion (SIC; Schwarz, 1978) to evaluate the amount of support in our data for each model in our candidate list (see above) because it has been shown to more accurately estimate the order of the underlying model than Akaike's Information Criterion (Akaike, 1973; Stone, 1979; Hooten, 1995). We considered the best approximating model to be that with the lowest SIC value. If the difference (ΔSIC) between information criteria values of competing models is $\leq$2, then the models are statistically indistinguishable (Sakamoto et al., 1986). Thus, models with generation time as a predictor variable had to beat the null model by >2 SIC units to provide support for a relationship between population momentum and generation time.

3. Results

Our results allow for interspecific comparisons of population momentum for iteroparous and semelparous vertebrates. For initially increasing and decreasing populations, population momentum following instantaneous (M_{inst}) and gradual (M_{grad}) change in a vital rate exhibited similar patterns across generation time within taxa. However, the relationship between population momentum and generation time differed somewhat among the four vertebrate classes that we examined.

Following instantaneous decrements of fertility, population momentum caused the historically increasing population ($\lambda_1 = 1.1$) to actually decrease in abundance before reaching the stationary level ($M_{inst} < 1$; Fig. 1, solid circles; see Table 1 for generation times of specific species). Furthermore, population momentum declined linearly with generation time ($\Delta SIC \geq 3.04$ units better than null model) among the iteroparous Aves ($R^2 = 0.59$; Fig. 1a), Mammalia ($R^2 = 0.41$; Fig. 1b), and Reptilia ($R^2 = 0.98$; Fig. 1c) species and for the semelparous pacific salmon ($R^2 = 0.81$; Fig. 1e). Among the iteroparous Osteichthyes, population momentum decreased until a generation time of approximately 30 years but then levelled out (quadratic model 3.09 SIC units better than null model; $R^2 = 0.54$; Fig. 1d). Thus, the magnitude of population momentum $|M - 1|$ increased with generation time, lending support to our hypothesis (Fig. 1, solid circles).

Population momentum following gradual changes in fertility (i.e., 5-year transitions) declined with generation time as well. However, population momentum following gradual change was generally >1, indicating that momentum usually caused net population growth (Fig. 1, open circles). Yet, in all cases the actual population structure that experienced the 5-year transition in fertility restricted populations from growing as large as they could have given the surplus levels of fertility ($M_{grad} < SP$), especially amongst vertebrates with long generation times (Fig. 1, comparison of open circles to plus signs). In fact, the effect of population structure was so strong in Reptilia and Osteichthyes species with long generation times that it actually caused a net population decline ($M_{grad} < 1$; Fig. 1c and d).

After instantaneously augmenting adult survival probability (sub-adult survival for semelparous species) in the declining population experiments ($\lambda_1 = 0.9$), the magnitude of population momentum was small, causing slight decline in abundance before ultimately reaching stationary growth for most vertebrates that we studied ($M_{inst} < 1$; Fig. 2, solid circles). However, population structure of the declining loggerhead sea turtle (*Caretta caretta*), snapping turtle (*Chelydra sperpentina*), dogfish (*Squalas acanthias*), long rough dab (*Hippoglossoides platessoides*), and pacific halibut (*Hippoglossus stenolepis*) populations actually reversed the direction of population growth before eventually reaching the stationary level ($M_{inst} > 1$; Fig. 2c–d, solid circles; see Table 1 for generation times of specific species). Population momentum declined linearly with generation time ($\Delta SIC \geq 2.70$ units better than null model) among the iteroparous Aves species ($R^2 = 0.41$; Fig. 2a), increased slightly across semelparous pacific salmon species ($R^2 = 0.58$; Fig. 2e), but was not related to generation time in the other vertebrate classes (no model > 2 SIC units better than null model).

Population momentum following gradual changes in survival displayed similar patterns as that following instantaneous change. However, with the exception of loggerhead sea turtle, gradual changes in survival resulted in substantial declines in abundance before reaching the stationary level ($M_{grad} \ll 1$; Fig. 2, open circles). Nevertheless, most of this momentum was caused by the deficient survival probabilities rather than population structure (M_{grad} similar to SP). Thus, population structure generally had a smaller effect on population momentum following both instantaneous and gradual changes in survival probabilities when compared to changes in fertility.

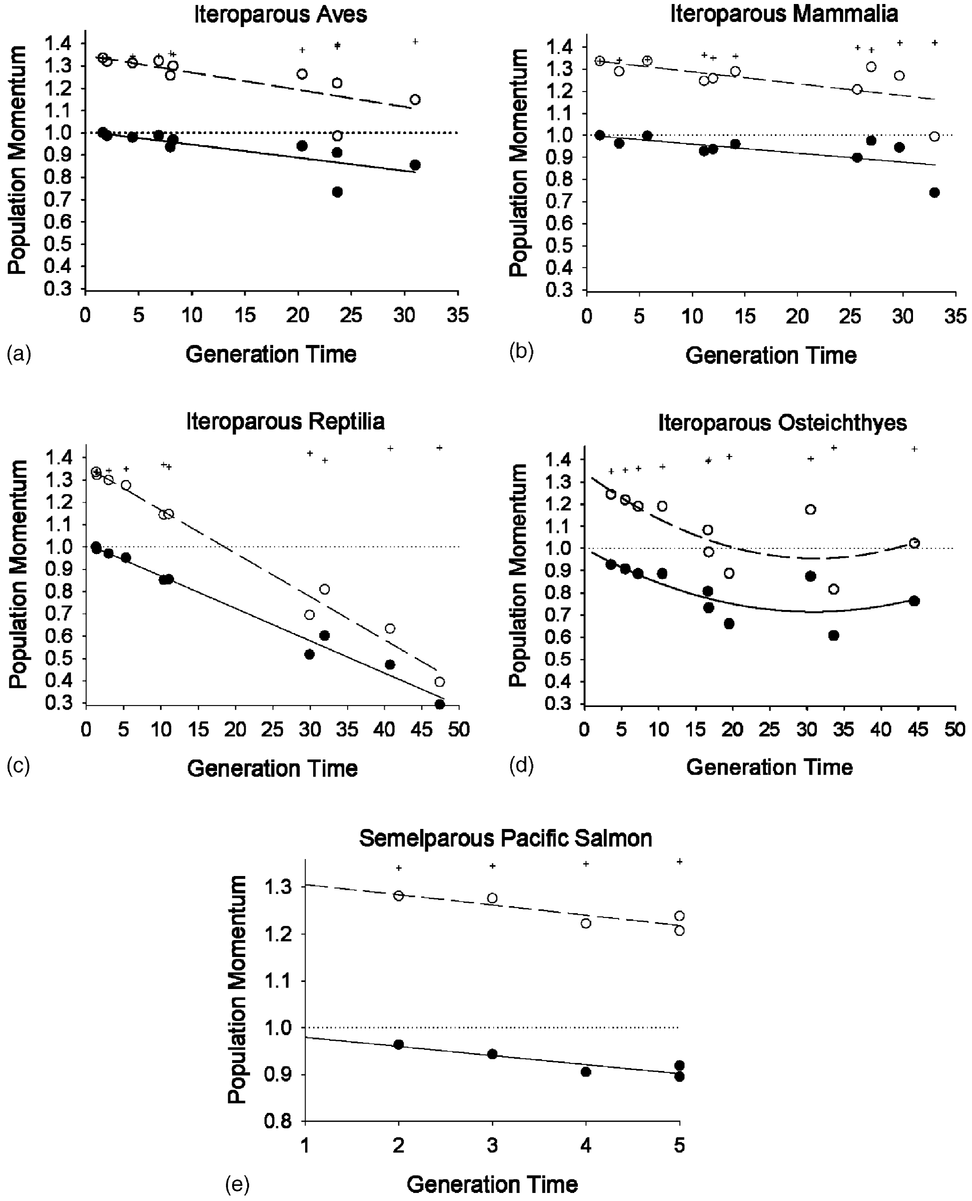

Fig. 1 – Plots of population momentum for the growing population experiments ($\lambda_1 = 1.1$) where fertility was decremented instantaneously (solid circles and solid lines) or gradually (open circles and dashed lines) to the stationary level across life history generation time of the iteroparous (a) Aves, (b) Mammalia, (c) Reptilia, and (d) Osteichthyes vertebrate classes as well as the semelparous (e) pacific salmon (Class Osteichthyes). The light dotted line is a reference line for population momentum = 1. For comparison with population momentum following a gradual transition in fertility, the + symbols represent the hypothetical stable populations (SP) for each life history, which simply describe the ultimate population size that would be expected if population structure were ignored or somehow remained stable throughout the gradual transition. See Table 1 for generation times of specific species.

Because the stable population structure created by the increasing population's vital rates ($\lambda_1 = 1.1$) is not immediately stable to the experimentally introduced stationary level of fertility ($\lambda_1 = 1$), it takes some time to reach the new stable population structure. For example, the stable population structure of growing populations had a surplus of young immature individuals, and a deficit of mature adults relative to the stable population structure associated with stationary levels of fertility (see Fig. 3, solid circles; 'ratio of adults' in the stable population vector of the growing populations relative to that for the stationary populations is <1). The decrease in fertility also shifted some of the reproductive value away from adults and toward younger age classes, especially amongst life histories with long generation times (see Fig. 3, open circles; the 'ratio of adult reproductive value' for the increasing populations relative to that in the stationary populations is >1, indicating that adult reproductive value was higher, and immature reproductive value lower, before the transition to stationary levels of

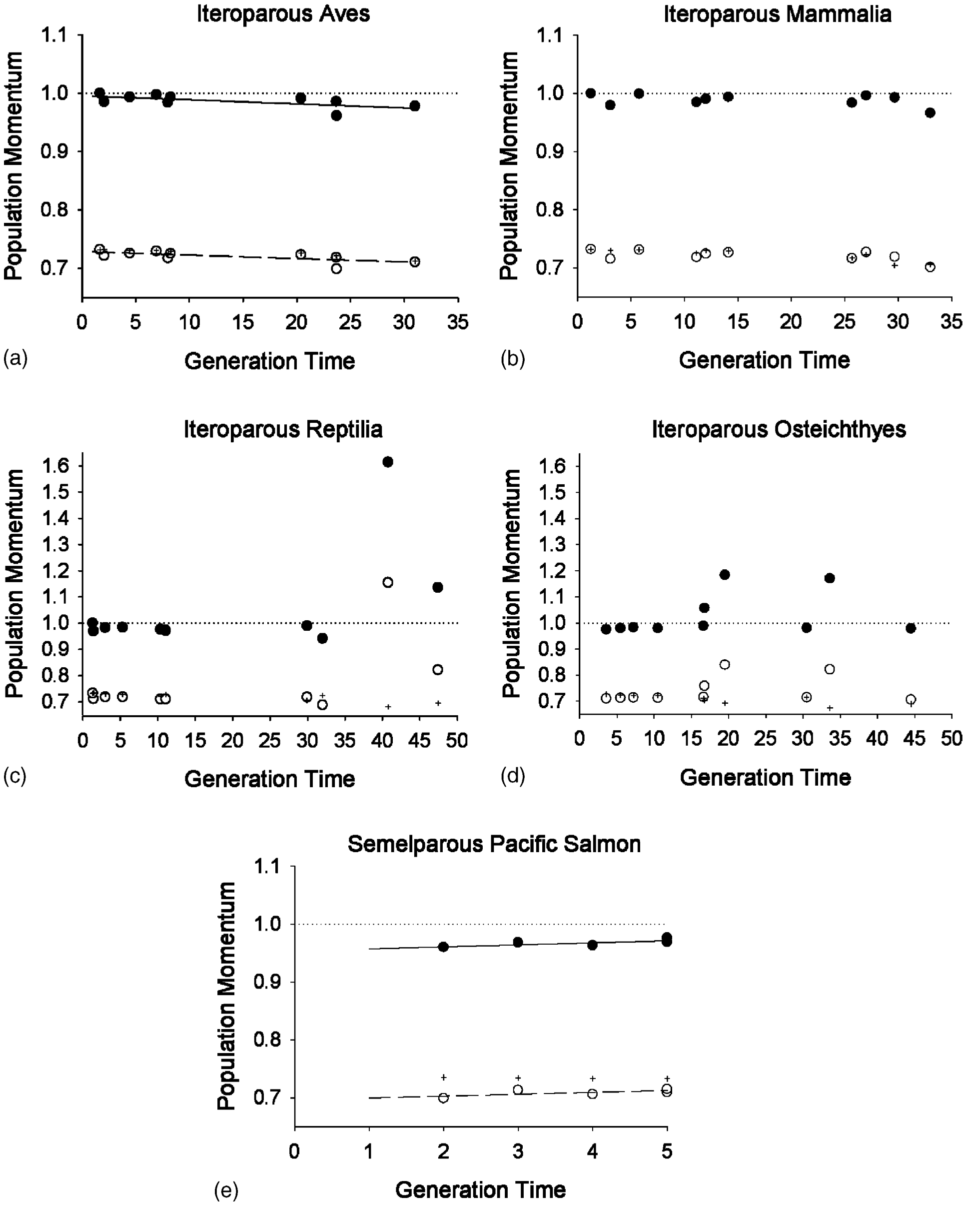

Fig. 2 – Plots of population momentum for the declining population experiments ($\lambda_1 = 0.9$) where adult survival (sub-adult survival for pacific salmon) was augmented instantaneously (solid circles and solid lines) or gradually (open circles and dashed lines) to the stationary level across life history generation time of the iteroparous (a) Aves, (b) Mammalia, (c) Reptilia, and (d) Osteichthyes vertebrate classes as well as the semelparous (e) pacific salmon (Class Osteichthyes). Lack of a prediction line indicates lack of evidence for a relationship between population momentum and generation time based on SIC model values (see Section 2). The light dotted line is a reference line for population momentum = 1. For comparison with population momentum following a gradual transition in survival, the + symbols represent the hypothetical stable populations (SP) for each life history, which simply describe the ultimate population size that would be expected if population structure were ignored or somehow remained stable throughout the gradual transition. See Table 1 for generation times of specific species.

fertility). The combined differences in population structure and reproductive value before and after the experiment led to transient population dynamics with greater net mortality and lesser net reproduction than would have occurred under asymptotic conditions for each life history. This caused the reversal in direction of population growth following instantaneous change in fertility ($M_{\text{inst}} < 1$), limited population growth during gradual changes ($M_{\text{grad}} < \text{SP}$), and caused the strong relationships between population momentum and life history generation time (Fig. 1).

Although less pronounced than in the aforementioned experiment, population structures of declining populations

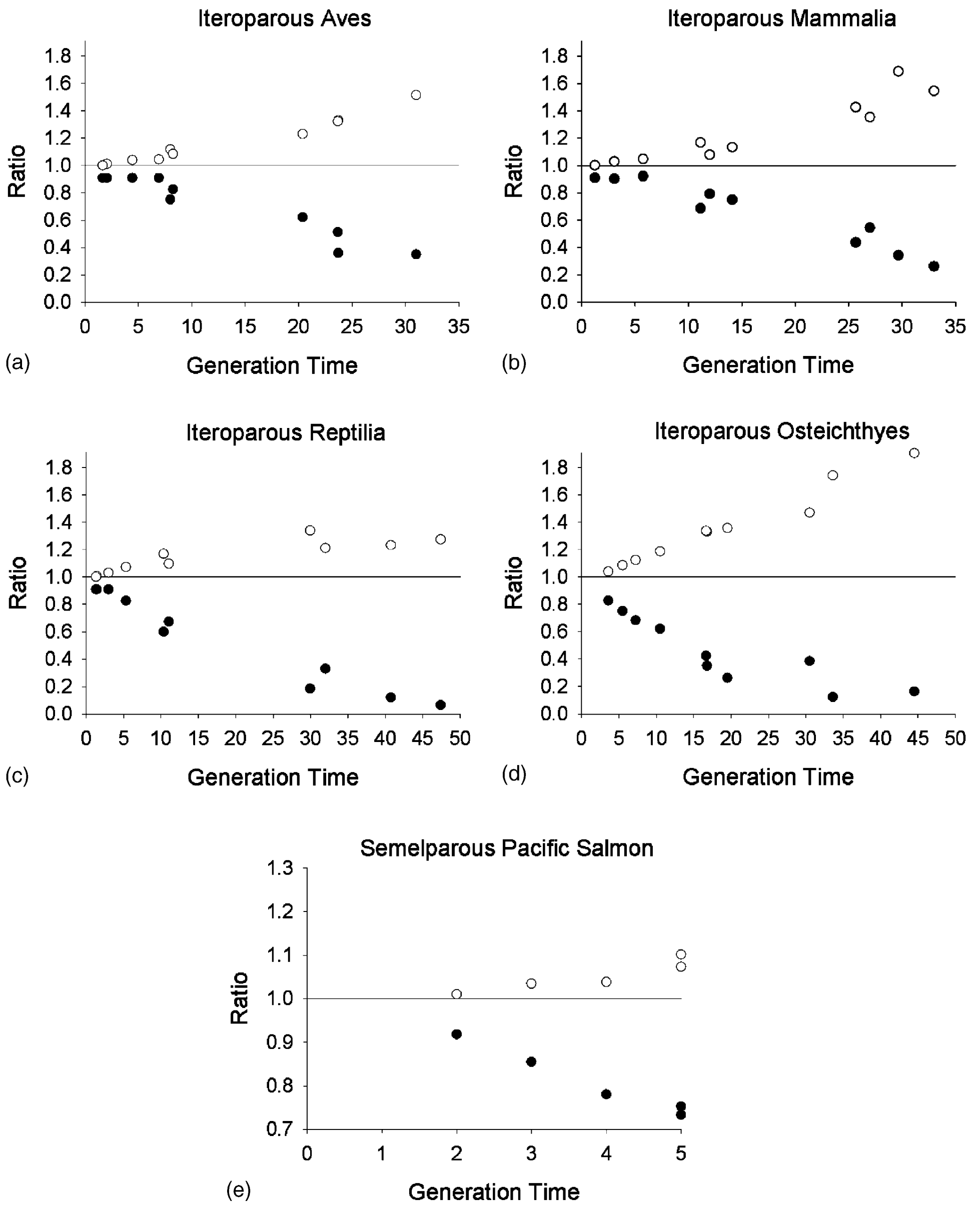

Fig. 3 – The ratio between number of adults in the stable population structure of initially increasing populations relative to number of adults in the eventually stable populations with stationary levels of fertility (solid circles; values < 1 indicate a deficit of mature adults, and implicitly, a surplus of immature individuals in the former relative to the latter, while the converse would be true for values > 1), and the ratio between adult reproductive value in increasing populations relative to that when fertility is at the stationary level (open circles; values > 1 indicate that when the initially increasing population undergoes a transition to stationary levels of fertility, the adult reproductive value decreases, and implicitly, net reproductive value of immature individuals increases; the converse is true for values < 1) across life history generation time of the iteroparous (a) Aves, (b) Mammalia, (c) Reptilia, and (d) Osteichthyes vertebrate classes as well as the semelparous (e) pacific salmon (Class Osteichthyes). (See Table 1 for generation times of specific species.)

($\lambda_1 = 0.9$) also had a deficit of mature adults relative to the stable population structure associated with stationary ($\lambda_1 = 1$) survival probabilities (Fig. 4, solid circles). However, unlike results following experimental change in fertility, the increase in survival shifted reproductive value towards adults (Fig. 4, open circles; see pacific salmon for exception), which usually resulted in population momentum in the same direction as historical population growth (Fig. 2). Furthermore, experimental changes in survival produced smaller and more variable differences between historical (declining population) and ultimate (stationary population) stable population structure and reproductive value across the life histories when compared to experimental changes in fertility (Figs. 3 and 4), which is why population momentum was not related to generation time in the declining population experiments for several vertebrate classes.

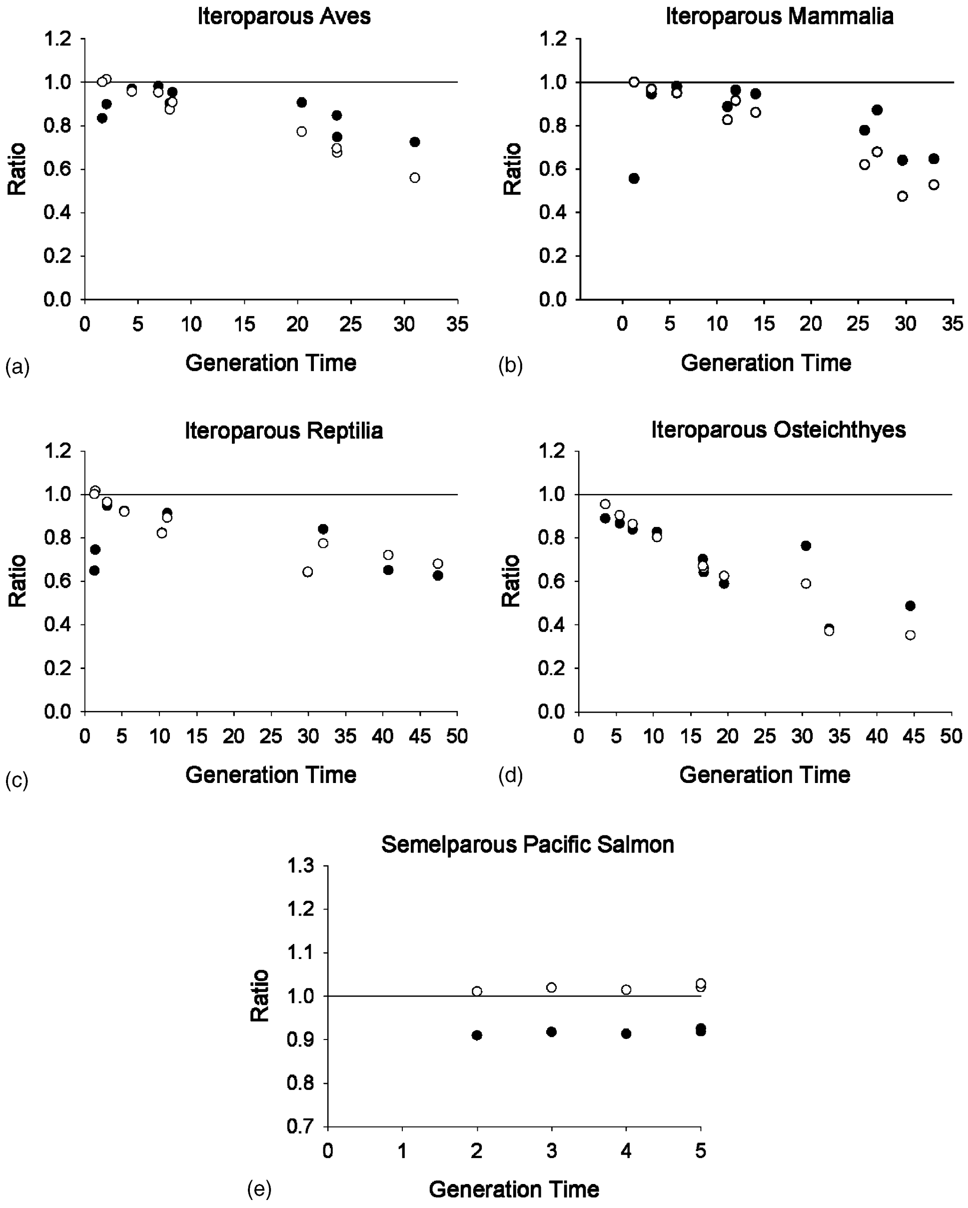

Fig. 4 – The ratio between number of adults in the stable population structure of declining populations relative to number of adults in the eventually stable populations with stationary-growth levels of adult survival (sub-adult survival for pacific salmon) (solid circles; values < 1 indicate a deficit of mature adults, and implicitly, a surplus of immature individuals in the former relative to the latter, while the converse would be true for values > 1), and the ratio between adult reproductive value in declining populations relative to that when survival probabilities are at the stationary level (open circles; values < 1 indicate that when the initially decreasing population undergoes a transition to stationary levels of survival, the adult reproductive value increases, and implicitly, net reproductive value of immature individuals decreases; the converse is true for values > 1) across life history generation time of the iteroparous (a) Aves, (b) Mammalia, (c) Reptilia, and (d) Osteichthyes vertebrate classes as well as the semelparous (e) pacific salmon (Class Osteichthyes). (See Table 1 for generation times of specific species.)

4. Discussion

Our understanding of population momentum is limited because it has not been examined for most animals. Recently, Koons et al. (2006) examined three animal life histories and found that population momentum varied according to the specific vital rate that was changed, the magnitude of that change, and overall life history strategy. We used life histories representative of a wide variety of vertebrate species to examine this latter finding in greater depth, and discovered interesting relationships between life history and population momentum.

Li and Tuljapurkar (1999) discovered that population momentum increased exponentially with the time over which a gradual transition in fertility to the stationary level occurred, and was generally much larger than that following instantaneous change. Yet, momentum following gradual change in a vital rate is caused by historical population structure as well as gradually changing, non-stationary vital rates, whereas momentum following instantaneous change in a vital rate is only caused by historical population structure (Bongaarts and Bulatao, 1999; Schoen and Jonsson, 2003). By comparing population momentum following gradual changes in a vital rate (M_{grad}) to the size of a hypothetical stable population (SP), we found that population structure actually had the same effect on momentum following both gradual (M_{grad}) and instantaneous (M_{inst}) change in a vital rate. Hence, population momentum following gradual change in a vital rate displayed the same pattern across life history generation time as population momentum following instantaneous change. The differences between M_{grad} and M_{inst} were primarily caused by the set of non-stationary vital rates that populations experienced during gradual, monotonic change to the stationary level. It remains to be seen whether this finding holds for transitions taking a longer time to complete and in stochastic environments.

Notwithstanding, population momentum following changes in fertility always declined with generation time, and following instantaneous changes, caused historically increasing populations to decrease in size. As a result of instantaneous changes in fertility, the magnitude of momentum $|M-1|$ increased with generation time, which lends support to our original hypothesis. This relationship was most pronounced in the Reptilia and Osteichthyes classes (Fig. 1c and d, solid circles). However, because the effect of population structure was to reduce population size, the magnitude of momentum decreased with generation time across Aves, Mammalia, and pacific salmon species following gradual changes to the stationary level. In fact, the effect of population structure was so strong in Reptilia and Osteichthyes species with long generation times that it actually caused a reduction in abundance, despite the surplus levels of fertility during the gradual change ($M_{\text{grad}} < 1$; Fig. 1c and d).

Demographically, these patterns can be explained by population structure and reproductive value, which directly affect population momentum (e.g., see Eq. (2)). Because the functional contributions of fertility and survival to λ_1 (measured with elasticities) vary with life history (Heppell et al., 2000b; Sæther and Bakke, 2000; Oli and Dobson, 2003), larger change in a vital rate was generally required to achieve the stationary level for species with long generation times than for species with short generation times. Larger changes in a vital rate can cause larger changes in stable population structure and cause larger shifts in reproductive value (e.g., Figs. 3 and 4). As a result, a historical population structure that acts on the newly changed vital rates will effectively have either a large surplus or deficit of breeding adults. This produces transient population dynamics with greater or lesser net reproduction, recruitment to adulthood, or both, than would occur under asymptotic conditions. Following our experimental reductions in fertility, adult reproductive value was changed in such a way that the population structure of the increasing populations ($\lambda_1 = 1.1$) was not favorable to reproduction and produced transient dynamics that led to a reduction in long-term population size (Fig. 1, M_{inst}) or limited populations from becoming as large as they could have (Fig. 1, comparison of M_{grad} to SP).

Experimental augmentations of survival probability did not affect reproductive value and asymptotic population structure as much as reductions in fertility did. Furthermore, change in survival had an opposite effect on the reproductive value of adults when compared to reductions in fertility (Figs. 3 and 4, open circles), which seemed to diminish the effects of historical population structure and transient dynamics on population momentum for most vertebrates that we examined (M_{inst} similar to 1, M_{grad} similar to SP; Fig. 2). Still, a few Reptilia and Osteichthyes species with long generation times did not fit this generalization, indicating an imperfect relationship between generation time and population momentum.

Furthermore, patterns between population momentum and generation time differed amongst the vertebrate classes because stable population structures and the allocation of reproductive value across age classes are inherently different among the vertebrate classes. For example, the stable population structure of fish species is heavily skewed towards young and the distribution of reproductive value is heavily skewed toward adults. This may be why the relationship between population momentum and generation time was more complex across iteroparous Osteichthyes species than in the other vertebrate classes where these distributions are less skewed. Yet, to better understand the demographic connection between population momentum and population structure, reproductive value, and life history parameters, a method for measuring the sensitivity of population momentum to equal unit or proportional changes in life history parameters will be needed. These tools are currently being developed.

Population size is important in ecology, conservation, pest control, and harvest management. Thus, ecologists and resource managers should consider population momentum in population projections that are used to make management decisions or when quantifying the ecological causes of historical population dynamics (Caswell, 2001). Our results indicated that population momentum will generally have the strongest effect on population size of vertebrates with long generation times, especially amongst Reptilia and Osteichthyes species, the latter of which are often harvested for commercial or sport purposes. Recently, C. Hauser, E.G. Cooch, and J.-D. Lebreton found that population momentum could limit the ability of managers to regulate populations with harvest techniques (unpublished data). Thus, we highly recommend implementation of population momentum into harvest-management models to better assess the effects of harvest on population dynamics.

The direction of population momentum (>1 or <1) will be critically important to consider in pest control and conservation. Human demographers have always found population momentum to follow the direction of historical population growth (e.g., Fischer and Heilig, 1997). Yet, population momentum for a stage-structured population of *Calathea ovandensis* was in the opposite direction of historical growth (Caswell, 2001:106), and Koons et al. (2006) found similar results for pseudo age-structured animal populations. In Physics, momentum of an object that changes direction is known as an ‘impulse’ (Buckwalter and Riban, 1987). Similar to the aforementioned studies, impulses occurred in our study, causing momentum in the opposite direction of historical population growth following instantaneous decrements in fertility for all species, and following augmentations of survival in populations of several long-lived Reptilia and Osteichthyes species. On the other hand, population momentum following instantaneous augmentation of survival in most other vertebrate species was small and in the same direction as historical population growth. Thus, the vital rate that is changed, and the time scale over which it is changed (e.g., instantaneous versus gradual), will dictate the direction of momentum, which will determine whether population momentum is beneficial or detrimental for pest control and conservation purposes. Our results should provide guidance to population ecologists and resource managers that will have to carefully assess how population momentum could affect population size of the animals they monitor.

To conclude, future studies should build on our findings by studying population momentum in stochastic, periodic, and seasonal environments. From our findings it is evident that population momentum varies across life histories in predictable ways. We recommend that studies of population viability (sensu Gilpin and Soulé, 1986), and other subject matter of conservation and evolutionary concern, consider the contribution of population momentum to projected dynamics. Lastly, population momentum will play a critically important role in the population dynamics of long-lived, late maturing organisms that are exposed to large changes in environmental conditions that are caused naturally or via anthropogenic actions.

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