

Generation time and the maximum growth rate for populations with age-specific fecundities and unknown juvenile survival

Peter W. Dillingham*

Department of Mathematics and Statistics, University of Otago, PO Box 56, Dunedin, New Zealand

ARTICLE INFO

Article history:

Received 22 October 2009

Received in revised form

10 December 2009

Accepted 11 December 2009

Available online 13 January 2010

Keywords:

Age-structured models

Population dynamics

Matrix population models

Population growth rate

Generation time

Demography

Leslie matrix

ABSTRACT

In age-classified population models where all parameters are known, the generation time and growth rate are calculated in a straightforward manner. For many populations, some parameters, such as juvenile survival, are difficult to estimate accurately. In a simplified population model where fecundity and survival are constant from the onset of breeding, it is known that generation time may be calculated given only adult survival, age at first reproduction, and the population growth rate. However, the assumption of constant fecundity from the onset of breeding does not hold for many populations. An extended population model allows calculation of generation time with the additional knowledge of the ratio of age-specific fecundities compared to a maximum fecundity rate. When these relative fecundities are unknown, an ad hoc adjustment to the simplified model performs well.

When the study population is in an ideal environment, the optimal generation time and maximum growth rate are linked, and both may be approximated knowing only adult survival, age at first reproduction, and the relative fecundities. The maximum growth rate has important conservation implications, and calculating it correctly is therefore important. Improper use of the simplified population model to calculate the maximum growth rate, combined with a simple decision rule, leads to an average overharvest of 36%, and >60% for three of six bird species studied, compared to the full population model. By comparison, using the approximation from the extended or adjusted models results in average overharvests of only 8% (extended model) and 5% (adjusted model), and <50% for all six species (either model).

© 2009 Elsevier B.V. All rights reserved.

1. Introduction

Generation time is an important parameter when studying population dynamics, and is particularly useful for understanding the behaviour of matrix models. Age-classified matrix models may be constructed to study a population when age-specific breeding and survival rates are available (Leslie, 1945; Caswell, 2001), and simplified models are often employed when demographic data are incomplete (Oli, 2003; Skalski et al., 2008). One key area of study is the sensitivity of the population growth rate to the different demographic parameters in the model (Caswell, 2001). Generation time is related to the sensitivity of a population to changes in adult survival or fecundity (Lebreton and Clobert, 1993; Gaillard et al., 2005; Lebreton, 2005; Stahl and Oli, 2006). In addition to studying sensitivities, generation time is an important metric in other contexts. For example, the intrinsic maximum growth rate per generation is approximately constant (Fowler, 1988; Niel and Lebreton, 2005), and generation time is also of interest in the study of evolution rates

(Sarich and Wilson, 1973; Martin and Palumbi, 1993; Gillooly et al., 2005). Failure to account for age-specific differences in fecundity may lead to substantial bias in the estimation of generation time.

The relationship between generation time and maximum growth rate may be used to calculate the ability of the population to accommodate additional mortalities, or the *potential biological removal* (PBR) using a simple decision rule (Wade, 1998; Taylor et al., 2000; Niel and Lebreton, 2005; Dillingham and Fletcher, 2008). This rule can be used in a variety of settings (Dillingham and Fletcher, 2008), but is most commonly used in assessing bycatch limits (Moore et al., 2009). A key aspect of this rule is that an overestimate of λ_{\max} leads to an overestimate of the PBR limits, potentially leading to an overharvest of the population. Therefore, calculating generation time correctly has an important management implication.

Various definitions of generation time exist (Leslie, 1966; Caswell, 2001; Niel and Lebreton, 2005). The mean generation time of a population is defined as

$$\bar{T} = \sum_{i=1}^{\infty} i l_i f_i \lambda^{-i} \quad (1)$$

* Tel.: +64 3 4797765.

E-mail address: dillingham@maths.otago.ac.nz.

where $l_i = \prod_{j=1}^i s_j$ is the survival from birth to age i , s_i is the survival from age $i - 1$ to i , f_i is the annual fecundity at age i (mean number of young), and λ is the annual growth rate of the population (Leslie, 1966; Niel and Lebreton, 2005; Gaillard et al., 2005). For a given age class, fecundity is the product of the proportion of animals that are breeding times the mean number of young per breeder; s_1 is the survival rate from birth to age 1. This definition of generation time was chosen as a suitable measure as it is insensitive to senescence (Niel and Lebreton, 2005), which is not accounted for in most population models; ignoring senescence may yield more robust inferences than attempting to estimate its effect (Skalski et al., 2008).

Niel and Lebreton (2005) and Gaillard et al. (2005) presented an estimate of generation time based only on age at first breeding (α), adult survival (s), and population growth rate (λ), assuming fecundity and survival are constant from the onset of breeding (hereafter, the *constant-fecundity model*). That is, in addition to assuming that all individuals within an age class behave similarly, it is assumed that all mature age classes are equivalent. Importantly, juvenile survival, which is often difficult to estimate, does not appear in the calculation of generation time. This is important because survival rates for juveniles are often difficult to estimate (Schwarz and Arnason, 2000), as juvenile age classes may not be present in the study area, and juvenile survival and emigration rates are typically confounded. For this model, generation time is

$$\bar{T} = \alpha + \frac{s}{\lambda - s} \tag{2}$$

When conditions are ideal, allometric relationships lead to a relationship between optimal generation time (\bar{T}_{op}) and maximum growth rate (λ_{max}), via the approximation:

$$\bar{T}_{op} \ln \lambda_{max} \approx a_r a_T \tag{3}$$

where a_r and a_T are allometric coefficients associated with body weight and generation time (Niel and Lebreton, 2005). Hence, under ideal conditions:

$$\lambda_{max} \approx \exp \left[a_r a_T \left(\alpha + \frac{s}{\lambda_{max} - s} \right)^{-1} \right] \tag{4}$$

which can be easily solved using iterative methods. Niel and Lebreton (2005) studied populations of 13 bird species undergoing optimal or near optimal growth, and estimated that, for bird species, $a_r a_T \approx 1$ (asymmetric 95% CI: 0.98–1.15). Maximum growth rates based on allometric relationships were compared to estimates from matrix model methods (Caswell, 2001), and they found that that there was a high level of correlation between the two estimates ($R = 0.88$, excluding two Passerine species).

For many species, fecundity increases over a number of years (Schwarz and Arnason, 2000), in contrast to the assumption in Niel and Lebreton (2005) and Gaillard et al. (2005) that mature age classes have constant fecundity. In fact, for 6 of the 13 species used in Niel and Lebreton (2005), demographic data do not support the constant-fecundity assumption (Table 1). A simple approach

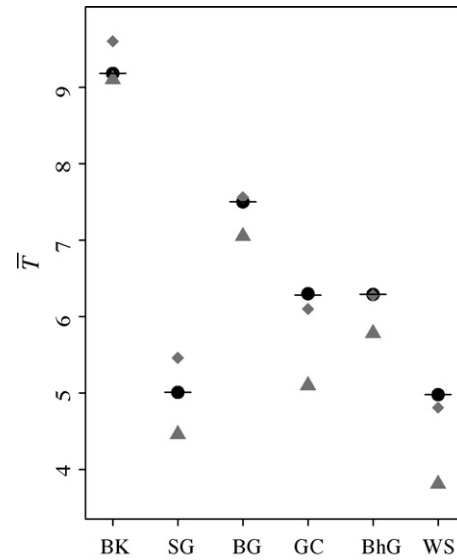


Fig. 1. Mean generation times for black-legged kittiwake (BK), snow goose (SG), barnacle goose (BG), great cormorant (GC), black-headed gull (BhG), and white stork (WS). Values from matrix models (—) are compared to estimates from the naive (▲) and adjusted (◆) constant-fecundity models, and to the varying-fecundity model (●).

to approximating generation time when the constant-fecundity assumption fails to hold is

$$\hat{T} = \hat{\alpha} + \frac{s}{\lambda - s} \tag{5}$$

with $\hat{\alpha} = \beta + \epsilon$, where β is the first age class with non-zero fecundity, and $\epsilon \geq 0$; this is the approach used by Niel and Lebreton (2005).

One cause of varying fecundity for a population could be increased breeding success with experience, while another could be delayed-entry into the breeding population. For species with delayed-entry into breeding, it is unclear what “age at first breeding” means. In the population sense, it could be interpreted as the age at which the first animals begin breeding, or as the “typical” age that they begin breeding, perhaps described by the mean age at first breeding (Schwarz and Arnason, 2000). Using the first interpretation could lead to the use of $\hat{\alpha} = \beta$ in Eq. (5) (the naive estimator). This estimator can result in substantial bias in the estimation of generation time; for the six species with varying fecundity, the magnitude of the bias was greater than 1 year for two of the species (Fig. 1).

A more realistic model – the *varying-fecundity model* – assumes constant survival from the age that the first animals begin breeding (β), but allows fecundity to increase over a number of age classes, becoming constant at some later age (γ). If relative fecundities (the ratio of each age-specific fecundity to fecundity at age γ) are known, Eq. (2) may be modified and an exact calculation of \bar{T} is still possible. As with the formula in Niel and Lebreton (2005) and Gaillard et al. (2005), juvenile survival is not present in the calculation of

Table 1
Demographic parameters and matrix model estimates of the mean generation time (\bar{T}) and annual growth rate (λ) for six bird populations where fecundity increases over several age classes (data from Niel and Lebreton, 2005).

Species		β	γ	s	$k_\beta, \dots, k_{\gamma-1}$	\bar{T}	λ
Black-legged kittiwake	<i>Rissa tridactyla</i>	5	6	0.90	0.90	9.177	1.120
Snow goose	<i>Anser caerulescens</i>	2	4	0.83	0.41,0.91	5.014	1.167
Barnacle goose	<i>Branta leucopsis</i>	3	4	0.95	0.50	7.498	1.184
Great cormorant	<i>Phalacrocorax carbo</i>	2	8	0.90	0.26, 0.47, 0.72, 0.91,0.97,0.99	6.283	1.185
Black-headed gull	<i>Larus ridibundus</i>	2	3	0.90	0.43	6.291	1.138
White stork	<i>Ciconia ciconia</i>	2	4	0.78	0.16,0.40	4.981	1.210

Download English Version:

<https://daneshyari.com/en/article/4377424>

Download Persian Version:

<https://daneshyari.com/article/4377424>

[Daneshyari.com](https://daneshyari.com)