The application of life-history and predation allometry to population dynamics to predict the critical density of extinction

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ABSTRACT

Strong Allee effects entail the existence of the Allee threshold A, a population density, below which the population will go extinct, even in absence of environmental stochasticity. To examine Allee effects by observation or experiment is, however, very difficult. This study provides a mechanistic model to quantify Allee effects by breaking down population dynamics into three density-dependent ecological processes: the biomass fluxes due to production, natural death, and predation. The model is calibrated by empirical life-history scalings to species body mass M with a temperature of 20 °C. Calibration reveals three new findings: (i) a single scaling of biomass production at the optimal or steady status, smooth across body mass regardless of reproduction pattern, (ii) a positive response of biomass production to population density, and (iii) allometry regarding predation process. Calculations demonstrate a new A scaling to M with an identical exponent of carrying capacity K scaling. In particular, a constant ratio A/K is of order 0.01, relatively stable to environmental stochasticity. This new protocol could be of wide applicability to invasion biology and conservation biology. The modeling methodology and revealed $A–K$ linearity would be broadly applicable beyond Tuesday Lake, which is used as a reference of carrying capacity in this study. This provides a convenient way to estimate a system-dependent Allee threshold given specific carrying capacity. As a specific example, we show its implication for evaluating ballast water discharge standards in temperate mesotrophic water.

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1. Introduction

The process of population extinction, when the population density is very low, is often associated with Allee effects. An Allee effect can be defined as a positive density dependence of "fitness" (Courchamp et al., 2008). This can be expressed at either the (individual) component level (e.g., mate finding) or the demographic level (i.e., the per capita population growth rate), corresponding to so-called a component Allee effect and a demographic Allee effect, respectively (Courchamp et al., 2008). A demographic Allee effect is a possible consequence of (multiple) component Allee effects (Berec et al., 2007; Courchamp et al., 2008). If the demographic Allee effect is strong enough, we may expect the potential existence of a critical population density (called the Allee threshold A), below which the population would go extinct, even in absence of

environmental stochasticity (Berec et al., 2007; Courchamp et al., 2008). This signifies a strong Allee effect, compared to a weak Allee effect that does not lead to population extinction (Berec et al., 2007; Courchamp et al., 2008). In this study, we focus on strong Allee effects resulting from the component Allee effects associated with three density-dependent processes, i.e., reproduction, natural death, and predation (Berec et al., 2007; Courchamp et al., 2008), which bear great significance to population biology (Amarasekare, 1998; Keitt et al., 2001; Tobin et al., 2011). Unfortunately, to prove the existence of strong Allee effects and to estimate A directly from observation or experiment is very difficult, if not impossible (Gregory et al., 2010; Kramer et al., 2009). Much of the difficulty comes from inflated errors associated with very sparse population. Thus, a reliable A estimate requires long time, large space, and many replicates in natural community (with real interspecific interactions) to overcome erratic fluctuation (Lee et al., 2013). The knowledge gap in A has brought about much confusion in management related to invasion biology and conservation biology (Courchamp et al., 2008; Lee et al., 2013).

Ecological modeling provides an alternative strategy to quantify Allee effects. In particular, the population dynamics of a species can

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List of symbols

A	Allee threshold
A_s	system-dependent Allee threshold
a_x (a_{p°, a_{r^*}, a_θ, etc.)	intercept of an allometric scaling of trait X to body mass
a_k	intercept of the allometric scaling of carrying capacity to body mass
b	a common slope of many allometric scalings to body mass
b_x (b_{p°, b_{r^*}, b_θ, etc.)	slope of an allometric scaling of trait X to body mass
b_k	slope of the allometric scaling of carrying capacity to body mass
C	population concentration (density)
c	normalized population concentration by carrying capacity
C_0	initial population concentration at introduction
C_r	population concentration corresponding to peak growth rate under field condition
E ($E^\wedge$, E°, and E^*)	individual metabolic rate (at the basal, field and optimal statuses)
e ($e^\wedge$, e° and e^*)	mass-specific E ($E^\wedge$, E°, and E^*)
F (F°)	individual rate of biomass loss due to predation (at the field status)
f (f°)	mass-specific F (F°)
i	trophic level
K	carrying capacity
k	Boltzmann's constant
M	species mean body mass
m	predator–prey body mass ratio
P (P° and P^*)	individual biomass production rate (at the field and optimal statuses)
p (p° and p^*)	mass-specific P (P° and P^*)
R (R^*)	individual rate of net biomass growth (at the optimal status)
R_p	individual peak rate of net biomass growth (under the field condition)
r (r^*)	mass-specific R (R^*)
r_m	mass-specific intrinsic net growth rate in the absence of Allee effects
r_p	mass-specific R_p
T	temperature
t	time
V (V° and V^*)	individual ingestion rate (at the field and optimal statuses)
v (v° and v^*)	mass-specific V (V° and V^*)
X	a certain biological (life-history) trait, e.g., biomass production rate
Z (Z° and Z^*)	individual rate of biomass loss due to natural death (at the field and optimal statuses)
z (z° and z^*)	mass-specific Z (Z° and Z^*)
α	Allee coefficient (A/K)
γ	trophic transfer efficiency between consecutive trophic levels
ε	activation energy of metabolism
η	individual maximal-field metabolism ratio (E^*/E°)
θ	semi-abundance for the maximal biomass production
μ	an index indicating density-dependence of natural death ($Z^\circ/Z^* - 1$)
ρ	ingestion-assimilation efficiency at the optimal status (p^*/v^*)
ρ°	ingestion-assimilation efficiency at the field status (p°/v°)
τ	an index indicating density-dependence of biomass production (ρ°/ρ)
φ	handling time
ψ	maximal ingestion-growth efficiency (R^*/V^*)
ω	attack rate

be broken down into three ecological biomass fluxes as (Courchamp et al., 2008):

$$r = \frac{\Delta C}{\Delta t} \times \frac{1}{C} = \frac{P - Z - F}{M} - p - z - f, \tag{1}$$

where r is the net (mass-specific) growth rate; C is population concentration; t is time; M is species mean body mass; P, Z, and F respectively refer to individual rates (mass per time) of production, natural death, and predation while the lower case symbols correspond to the mass-specific rates. Previous modeling studies on Allee effects were often focused on some key biotic interactions, e.g., mating limitation and predator saturation (Bessa-Gomes et al., 2004; Gerritsen, 1980; Jerde et al., 2009; Schreiber, 2003), derived from specific species. Their application is thus limited by a lack of generality to different species, as orders of magnitude variation can exist in a life-history trait across taxa. The established allometry theory provides the feasibility to represent different species (as distinct biological traits) by species body mass.

Allometry, with its simplicity and generality, has been an elegant paradigm in ecology (Brown et al., 2004; Savage et al., 2004a). It has long been known that the magnitude of a life-history trait X (e.g., mortality) of a species tends to scale to its mean body mass M, which can vary over more than ten orders of magnitude, as:

$$X = a_x M^{b_x}, \tag{2}$$

where the intercept a_x and slope b_x tend to be certain constants with respect to trait X at a comparable metabolic level (see below). This allometric relationship has been proposed since the early 20th century and is now well supported by empirical evidence of many different biological characteristics, such as the individual basal metabolic rate $E^\wedge$ (Gillooly et al., 2001), the maximal growth rate R^* (Blueweiss et al., 1978; Hansen et al., 1997; Savage et al., 2004b), the optimal (minimal) mortality Z^*, and the field mortality Z° (McCoy and Gillooly, 2008). Here the superscripts ^, *, and respectively denote the basal, optimal, and field (steady) statuses. Although temperature also plays a role in the allometry theory (Brown et al., 2004; Gillooly et al., 2002), we focused on the role of body mass and kept temperature as 20 °C in this study. Some potential influences of temperature are demonstrated in the Discussion. Each of these scalings is characterized by an indistinguishable exponent $b_x \approx b = 0.75$, explainable by the metabolic theory, which states an allometric relationship between (basal) metabolic rate and body mass, applicable to many other biological characteristics such as growth rate and mortality that are closely related to individual metabolic rate (Brown et al., 2004). For example, maximal growth rate and production rate, as fueled by metabolism, display a similar allometry (Blueweiss et al., 1978; Hansen et al., 1997; Savage et al., 2004b); a similar allometry holds to natural mortality, an inverse to maximal lifespan, assuming an equal amount of energy expenditure lifelong to each individual regardless of taxa (McCoy and Gillooly, 2008). However, it still remains unknown whether or how the process of predation, a biological interaction rather than life-history trait, the remaining component in population dynamics, could be assimilated into allometry. Results of empirical studies on predator–prey body mass ratio m across food webs (Barnes et al., 2010; Brose et al.,