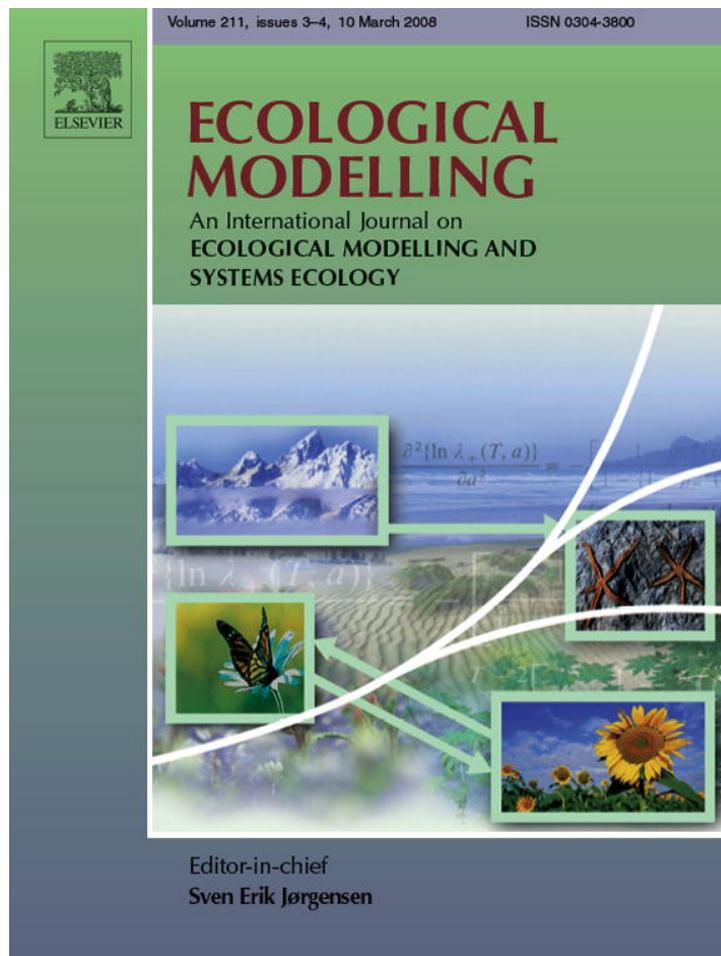


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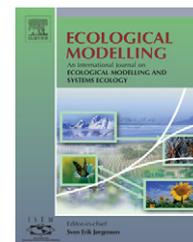
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Evaluating intercepts from demographic models to understand resource limitation and resource thresholds

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ABSTRACT

Understanding resource limitation is critical to effective management and conservation of wild populations, however resource limitation is difficult to quantify partly because resource limitation is a dynamic process. Specifically, a resource that is limiting at one time may become non-limiting at another time, depending upon changes in its availability and changes in the availability of other resources. Methods for understanding resource limitation, therefore, must consider the dynamic effects of resources on demography. We present approaches for interpreting results of demographic modeling beyond analyzing model rankings, model weights, slope estimates, and model averaging. We demonstrate how interpretation of y-intercepts, odds ratios, and rates of change can yield insights into resource limitation as a dynamic process, assuming logistic regression is used to link estimates of resources with estimates of demography. In addition, we show how x-intercepts can be evaluated with respect to odds ratios to understand resource thresholds.

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1. Introduction

Recent focus in demographic modeling has shifted from understanding not only how vital rates change through time, but also why. Modeling tools like program MARK (White and Burnham, 1999) and program POPAN-4 (Arnason et al., 1995) are increasingly used by wildlife scientists to link estimates of demographic parameters (e.g., survival, recruitment, and population growth rate) with explanatory variables such as climate (Franklin et al., 2000; Jones et al., 2002), forest fragmentation (Doherty and Grubb, 2002), poison (Grand et al., 1998; Armstrong et al., 2001), and edge proximity (Moorman et al., 2002). A similar approach could be used to improve our understanding of resource limitation.

A resource is limiting if changes in its availability affect the population equilibrium level (Williams et al., 2002), which is a function of individual survival and reproduction. Esti-

mates of demography, therefore, can be linked with estimates of resource availability, as they change through time, to yield insights into resource limitation (Reynolds-Hogland et al., in press). Subsequently, results can be interpreted by evaluating model ranking, model weights, slope estimates of model variables, and model averaging. Model ranking, which is based on model selection criterion (e.g., AIC; Akaike, 1973), is used to determine which models are most likely to be selected from a suite of models that represent *a priori* hypotheses. Model weights provide strength of evidence for model selection and slope estimates of model variables reveal whether a relationship between a model variable and the demographic parameter is positive or negative. In addition, slope estimates can be evaluated to determine relative effects of model variables on a demographic parameter. Relative importance of model variables can be determined by model averaging (Burnham and Anderson, 2002).

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The above analyses are useful for understanding which resources most likely affect demographic parameters over a study period, but they provide little insight into resource limitation as a dynamic process. Resource limitation usually occurs when a resource is in short supply (Ricklefs, 1993) and a resource is likely to remain limiting through only a narrow range of changes (Leopold, 1933). Therefore, a resource that is limiting at one time may become non-limiting at another, depending upon changes in its availability and changes in the availability of other resources (Ricklefs, 1993).

Understanding the dynamic process of resource limitation would be a powerful tool for wildlife management, particularly in situations where only one or a few resources can be managed due to logistical or financial constraints. For example, several resources may affect survival rate positively for a population, but the effects of each resource on survival may change as availability of each resource changes. Management strategies to increase survival, therefore, can be optimized by shifting efforts from increasing one resource to increasing another resource as resource availabilities change.

Equally important to effective management of wild populations is knowing threshold levels of limiting resources. A threshold is the level at which a stimulus is just strong enough to be perceived or to produce a response (Agnes, 1999). We propose current methods for interpreting results of demographic analyses (i.e., evaluating model ranking, model weights, slope estimates, and model averaging) can be expanded to determine thresholds of limiting resources.

We present approaches for interpreting results of demographic modeling beyond analyzing model rankings, model weights, slope estimates, and model averaging. In our first example, we demonstrate how analyzing odds ratios, *y*-intercepts, and rates of change can be used to understand resource limitation as a dynamic process. In our second example, we present methods for analyzing *x*-intercepts with respect to odds ratios to estimate threshold levels of limiting resources.

2. Example A: odds ratios, *y*-intercepts, and rates of change

Consider a hypothetical population for which we estimated survival probability. Assume we used capture-recapture data collected over 10 years to model two demographic parameters of adult females: annual survival probability and recapture probability. Further assume we *a priori* identified four

resources, or state variables, that may be important to the population and we were able to measure annual availability of all four resources as they changed during the study period. We considered each resource a possible covariate to survival probability. Prior to analyses, we standardized all covariates by subtracting the mean from each observation and then dividing by the standard deviation so comparisons among resource effects would be relative. For simplicity, we did not model interaction effects among four resources. We linked estimates of survival probability with annual estimates of resources via logistic regression in program MARK (White and Burnham, 1999). Program MARK uses a maximum likelihood approach to estimate demographic parameters and the effects of state variables (e.g., resources) on demographic parameters (see Cooch and White, 2002 for complete list of equations used in program MARK). Although survival probability was the parameter of interest for our hypothetical example, estimates of recapture probability were included to increase the precision of survival probability estimates. We used AIC (Akaike, 1973) to rank models and report results in Table 1, which includes four models with resource covariates and one null model with no covariates. Generally, model fit can be tested for logistic regression models using the receiver operator characteristic (ROC) statistic, which evaluates how well each model fits the data (Hosmer and Lemeshow, 2000). In program MARK, bootstrap goodness of fit is often used for model calibration and validation.

Based on results of our analyses (Table 1), we conclude Resources C and D had relatively little effect on survival because both had relatively high Δ AIC values and low model weights. In addition, we conclude Resources A and B did affect survival, but their relative effects were indistinguishable because both had low Δ AIC values and high model weights. In fact, slope estimates for Resource A and Resource B were identical. Current approaches for interpreting results of demographic modeling stop here. Further evaluation of our results in terms of odds ratios, *y*-intercepts, and rates of change, however, will show the effect of Resource A on the probability of survival was not identical to the effect of Resource B.

2.1. Odds ratios and *y*-intercepts

Evaluating odds ratios involves understanding the relationship between an explanatory variable and the odds of two mutually exclusive categories that are binomially distributed, in this case successful versus unsuccessful outcomes. Analysis of odds ratios is used in several fields, including actuarial

Table 1 – Ranking of models of survival, each with a different resource covariate, for a hypothetical population

Model	Δ AIC	AIC weight	Model likelihood	Slope	Slope		
					SE	LCL	UCL
Resource B	0.00	0.45	1.00	5.63	2.21	2.82	14.09
Resource A	0.00	0.45	1.00	5.63	2.21	2.82	14.09
Resource D	4.70	0.05	0.10	0.50	0.44	–0.02	0.97
Null	5.34	0.03	0.07	NA	NA	NA	NA
Resource C	5.39	0.03	0.07	0.40	0.57	–0.11	1.97

Only Resource B and Resource A ranked high and had relatively high model weights.

science (Al-Ghamdi, 2002), economics (Craig and Sandow, 2004), engineering (Ramirez et al., 1994; Del Prete and Grigg, 1999), epidemiology (Slavin, 2002), medicine (Fujiwara et al., 2003), and sociology (Lebel et al., 2002), but it has yet to be applied to demographic modeling to understand the dynamic effects of resource availability on demography.

Logistic regression fits the natural log of the odds of two categories (the logit) using a linear function of the explanatory variables, the forcing function. For example, if we look at the number of times two mutually exclusive categories, such as survival and death, occurred given an explanatory variable X , the probability (π) of survival, given the covariate X_i , can be modeled using logistic regression as follows:

$$\ln \left(\frac{s/(s+d)}{d/(s+d)} \right) = \ln \left(\frac{\pi_s}{\pi_d} \right) = \ln \left(\frac{\pi_s}{1-\pi_s} \right) = \beta_0 + \beta_i X_i \quad (1)$$

$$\pi_s = \frac{e^{\beta_0 + \beta_i X_i}}{1 + e^{\beta_0 + \beta_i X_i}} \quad (2)$$

where s is the number of individuals that survived, d the number of individuals that died, π_s the probability of survival, π_d the probability of death, B_0 the y-intercept, B_i the slope, and X_i is the standardized value of resource i . The probability of survival is sigmoidally related to X , however, the logit ($\ln(\pi_s/(1-\pi_s))$) is linearly related to $X(\beta_0 + \beta_i X)$.

According to Eq. (1), if $B_0 = 0$ and $X_i = 0$, the odds of surviving are 50/50:

$$\ln \frac{\pi_s}{1-\pi_s} = 0, \quad \pi_s = e^0(1-\pi_s), \quad \pi_s = 0.50 \text{ or } 50\%$$

$$\text{odds} = \frac{\pi_s}{1-\pi_s} = \frac{50\%}{50\%}$$

Because we standardized all covariates by subtracting the mean and then dividing by the standard deviation, the value 0 for standardized X_i corresponds to the mean value of resource i available throughout the study period. Therefore, if $B_0 = 0$ and $X_i = 0$, the probability of surviving is equal to the probability of dying when resource i equals mean availability of resource i . By changing the value of only the y-intercept, the probability of survival also changes. For example, if $B_0 = 1$ and $X_i = 0$, the odds of surviving versus dying are 73/27, which is greater than the odds of dying versus surviving (27/73) when resource i equals mean availability of resource i . Alternatively, if $B_0 = -1$ and $X_i = 0$, the odds of surviving versus dying are 27/73 and the odds of dying versus surviving are 73/27.

To show the utility of evaluating y-intercepts, we graphed y-intercepts from the top two models of survival from our hypothetical example (Fig. 1). We used y-intercept values (Table 2) and slope values (Table 1) to plot the linear relationships between Resource A and the logit (i.e., $\ln\{\pi_s/1-\pi_s\}$) and

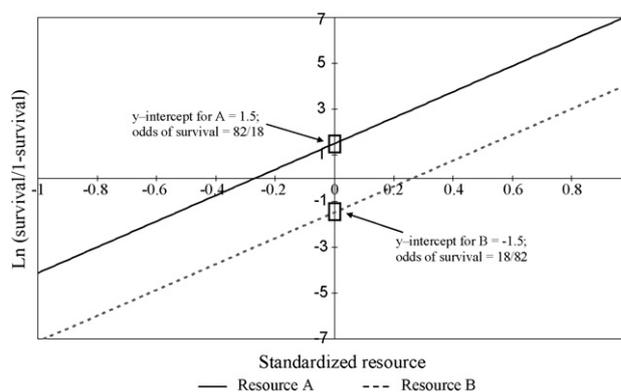


Fig. 1 – Linear relationships between the logit (i.e., \ln odds of survival vs. dying) and standardized availability of Resource A and the logit and standardized availability of Resource B and comparison of y-intercepts. y-Intercept for Resource A = 1.5, which corresponds to odds of survival = 82/18 when Resource A is at its mean value. y-Intercept for Resource B = -1.5, which corresponds to odd of survival = 18/82 when Resource B is at its mean value.

Resource B and the logit (Fig. 1). Although both Resource A and B affected survival positively and slope estimates were identical (Table 1), y-intercepts differed (Table 2), which influenced the way each resource affected the probability of survival (Fig. 1).

For example, when Resource A was at its mean level (i.e., standardized $X_i = 0$ in Fig. 1), the probability of surviving (0.82) was much higher than was the probability of dying (0.18). Alternatively, when Resource B was at its mean level, the probability of surviving (0.18) was much lower than was the probability of dying (0.82). The linear relationship between Resource B and the logit was “shifted” far below the linear relationship between Resource A and the logit (Fig. 1). Therefore, mean availability of Resource B had a smaller effect on the odds of survival versus death compared to mean availability of Resource A.

2.2. Rates of change

Resource limitation is a dynamic process that changes as availability of resources change. At some level of Resource A, Resource B might become more limiting and vice versa. To examine these relationships, we graphed the probability of survival against availability of standardized values of Resources A and B (Fig. 2). Although the relationship between the logit and resource availability was linear (Eq. (1), Fig. 1), the relationship between probability of survival and resource availability was sigmoidal (Fig. 2). Therefore, we can evaluate rates of change in the probability of survival in relation to increases in standardized values of Resource A and Resource B.

When mean availability of each resource was present, probability of survival was 0.82 and 0.18 for Resource A and Resource B, respectively (points A_1 and B_1 ; Fig. 2). By increasing both resources by 0.5 standardized units (points A_2 and B_2), probability of survival increased from 0.82 to 0.99 (17%

Table 2 – Estimates of y-intercepts for the top two models of survival for a hypothetical population

Model	y-Intercept	SE	LCL	UCL
Resource B	-1.50	0.73	-3.88	-0.36
Resource A	1.50	0.73	0.36	3.88

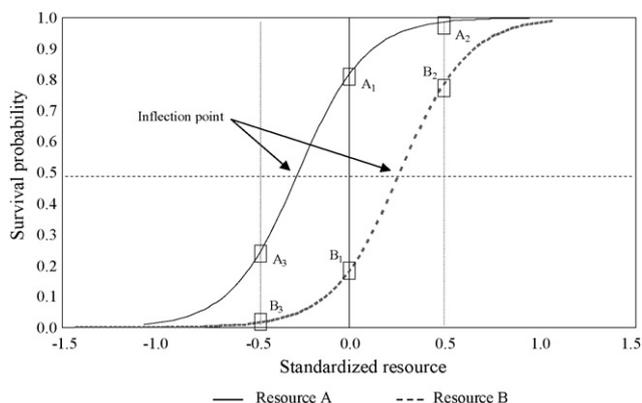


Fig. 2 – Sigmoidal relationships between probability of survival and Resource A (standardized) and probability of survival and Resource B (standardized). A_1 , A_2 , and A_3 correspond to survival probabilities when mean Resource A was available, when mean Resource A was increased by 0.5 standardized units, and when mean Resource A was decreased by 0.5 standardized units, respectively. Similarly, B_1 , B_2 , and B_3 correspond to survival probabilities when mean Resource B was available, when mean Resource B was increased by 0.5 standardized units, and when mean Resource B was decreased by 0.5 standardized units, respectively. The inflection point on the sigmoidal curve occurs when probability of survival = 0.50.

increase) for Resource A and from 0.18 to 0.79 (61% increase) for Resource B. Equal increases in standardized amounts of Resources A and B led to unequal increases in probability of survival; an increase in mean Resource B had a relatively large effect on survival. This occurred because the rate of change in survival, as Resource A increased above its mean, was lower than the rate of change in survival, as resource B increased above its mean.

The same relationships can be evaluated to understand how a decrease in each resource affects probability of survival. By decreasing mean availability of Resource A and Resource B (points A_1 and B_1 ; Fig. 2) by 0.5 standardized units (points A_3 and B_3 ; Fig. 2), the probability of survival fell from 0.83 to 0.21 (61% decrease) for Resource A and from 0.18 to 0.01 (17% decrease) for Resource B. Equal decreases in standardized amounts of Resources A and B yielded unequal decreases in probability of survival. Therefore, the effects of Resources A and B on probability of survival were not equal even though their linear logit slope estimates, from Table 1, were identical.

When modeling the logit of survival versus death, slope estimates from Eq. (1) (which are represented in Table 1 and Fig. 1) represent the relative effect of explanatory variables on the logit. The larger the slope estimate, the larger the effect of an explanatory variable. If resources are modeled as explanatory variables of the logit, the resource with the largest slope will have the largest effect on probability of survival (assuming the model with this resource ranked high and had high model weight). Such a resource, if its slope is positive, should be relatively limiting to the probability of survival. The same rationale can be used to examine slope estimates in Fig. 2. The difference is that slope estimates in Eq. (1) are static, whereas

slope estimates in Fig. 2 change as availability of resources change. Depending upon resource availability, Resource A may be more limiting than Resource B and vice versa.

2.3. Y-intercept values

The relationships in Figs. 1 and 2 can be evaluated to understand what y-intercept values from Eq. (1) mean. The y-intercept from Eq. (1) for each resource i (standardized $X_i = 0$ in Fig. 1) corresponds to the position of mean availability of resource i on the sigmoidal curve (Fig. 2). The inflection point on the sigmoidal curve occurs when the probability of survival = 0.50. If mean availability of resource i is positioned above the inflection point on the sigmoidal curve (which occurs when y-intercept > 0; e.g., point A_1 Fig. 2), an increase in mean availability of resource i results in a convex increase in probability of survival (Resource A; Fig. 2). Alternatively, if mean availability of resource i is positioned below the inflection point on the sigmoidal curve (which occurs when y-intercept < 0; e.g., point B_1 Fig. 2), an increase in mean availability of resource i results in a relatively concave increase in probability of survival (Resource B; Fig. 2). At both extreme ends of the sigmoidal curve (e.g., when y-intercept values are either $\ll 0$ or $\gg 0$) rates of change in survival probability are very small.

2.4. Management implications

Aldo Leopold described a limiting factor as “the one which has to be moved first, usually the one to which the application of a given amount of effort will pay the greatest returns, under conditions as they stand” (1933). If only current methods were used to analyze our hypothetical example (i.e., model ranking, model weights, and evaluation of slope estimates from Eq. (3)), results would show Resource A and Resource B had equal effects on survival (Table 1), suggesting managers should maintain or increase both Resources A and B to maintain or increase population survival. Evaluating odds ratios, y-intercepts (Fig. 1) and rates of change in survival probability (Fig. 2) provides a more comprehensive understanding of resource limitation as conditions change, which is useful for optimizing management strategies.

For example, when Resource A and Resource B were both available in their mean amounts, the effect of Resource A on odds of survival was larger than the effect of Resource B (Fig. 1). Moreover, a decrease in mean availability of Resource A resulted in an exponential decrease in survival probability whereas a similar decrease in mean availability of Resource B did not (Fig. 2). Therefore, if the management goal is to maintain population survival probability, managers should focus efforts on maintaining mean levels of Resource A before investing efforts to maintain mean levels of Resource B. Alternatively, if mean levels of both Resource A and B are already available on a landscape, an increase in Resource B will result in an exponential increase in the probability of survival, whereas a similar increase in Resource A will not (Fig. 2). In this situation, managers should focus efforts on increasing Resource B before investing efforts to increase Resource A.

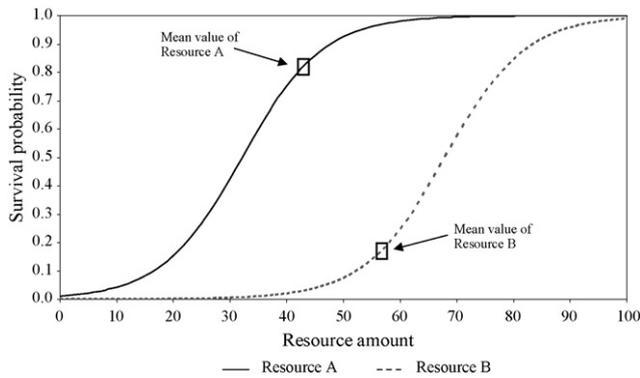


Fig. 3 – Sigmoidal relationships between probability of survival and real values of Resource A and probability of survival and real values of Resource B.

2.5. Real values of resource availability

It may be useful to back transform the resource data and graph its relationship with probability of survival (Fig. 3), which provides a more tangible tool for management. Moreover, back transformation can yield non-intuitive insights into resource limitation. For a resource to limit survival, positive changes in its availability must affect survival positively (Williams et al., 2002), which usually happens when a resource is in short supply (Ricklefs, 1993). In Fig. 3, mean availability of Resource B (57 units) was large relative to mean availability of Resource A (42 units), but a 0.5 unit increase in mean Resource B had a larger effect on survival compared to the effect of a similar increase in mean Resource A (Fig. 2). Therefore, at some levels of resource availability, a resource may be limiting (i.e., in short supply) even when its availability is relatively large.

3. Example B: resource thresholds

Knowing the level at which a resource must be maintained to sustain population growth rate would be useful information to wildlife managers. To calculate population growth rate (λ), managers and researchers often estimate the number of individuals present at two mutually exclusive time periods, t1 and t2, and divide the number of individuals occurring at t2 by the number of individuals at t1. Values >1 reflect a population that is growing between these two time periods, where as values <1 reflect a population that is declining. Similar to our example regarding survival probability, logistic regression can be used to link estimates of λ with estimates of resource availabilities as follows:

$$\lambda = \frac{N_{t2}}{N_{t1}} = \text{odds},$$

$$\ln(\lambda) = \ln\left(\frac{N_{t2}}{N_{t1}}\right) = \ln\left(\frac{N_{t2}/(N_{t2} + N_{t1})}{N_{t1}/(N_{t2} + N_{t1})}\right)$$

$$= \ln\left(\frac{\pi_{N_{t2}}}{\pi_{N_{t1}}}\right) = \ln\left(\frac{\pi_{N_{t2}}}{1 - \pi_{N_{t2}}}\right) = \beta_0 + \beta_i X_i \quad (3)$$

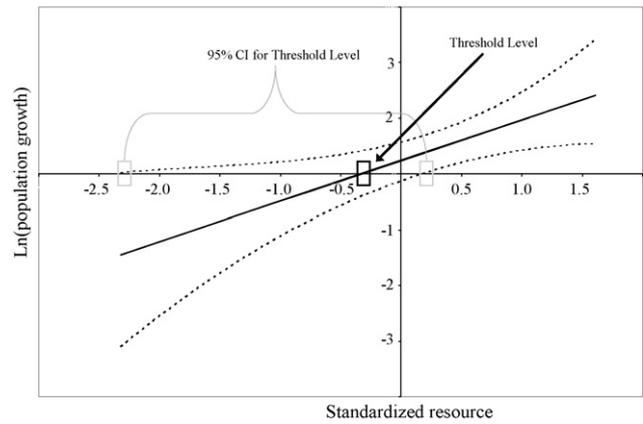


Fig. 4 – Linear relationship between Resource R and $\ln \lambda$ and its 95% confidence interval for a hypothetical scenario. The threshold point of Resource R occurs where the function crosses the x-axis (dark rectangle). Gray rectangles represent the 95% CI, or the range of variation associated with the threshold point.

$$\pi_{N_{t2}} = \frac{e^{\beta_0 + \beta_i X_i}}{1 + e^{\beta_0 + \beta_i X_i}} \quad (4)$$

where N_{t2} is the number of individuals occurring in time period 2, N_{t1} the number of individuals occurring in time period 1, $\pi_{N_{t2}}$ the probability that an individual was present in time period 2, $\pi_{N_{t1}}$ the probability that an individual was present in time period 1, B_0 the y-intercept, B_i the slope, and X_i is the standardized value of resource i .

We explored the relationship between λ and resource availabilities using a 22-year dataset for a hypothetical female population. Assume we a priori identified resources that may be important to the population and we were able to measure annual availability of resources as they changed during the study period. We considered each resource a possible covariate to annual λ and we linked estimates of $\ln(\lambda)$ with annual measures of resource availabilities via logistic regression. Based on model ranking, slope estimates, and model averaging, we found only one resource (Resource R) explained λ .

To evaluate biological threshold levels of Resource R with respect to λ , we graphed the linear relationship between $\ln \lambda$ and standardized availability of Resource R (Fig. 4) based on data from Table 3. One biological resource threshold should be the level at which the odds of the population growing is equal to the odds of the population dying. Based on Eq. (3), the odds of population growth are 50/50 when $y=0$. When $y > 0$, the odds of population growth are greater than the odds of population decline and when $y < 0$, the reverse is true. The point where Eq. (3) crosses the x-axis (dark rectangle), therefore, should represent a threshold value for Resource R. Variation in the threshold estimate can be included by plotting the confidence interval (Table 3; columns 8 and 9) around the function and determining where confidence intervals cross the x-axis. In Fig. 4, the threshold point for standardized Resource R = -0.03 (dark rectangles) and the corresponding 95% CI was -2.3 and 0.25 (gray rectangles). If the goal is to manage the population such that the odds of population growth is equal to the

Table 3 – Annual availability of resource R and corresponding estimates of λ for a hypothetical population during 1981–2002

Year	R availability (ha)	Standardized R	Estimated λ	λ LCL	λ UCL	$\ln(\lambda)$	$\ln(\text{LCL } \lambda)$	$\ln(\text{UCL } \lambda)$
1981	503.10	−0.45	0.98	0.90	1.07	−0.02	−0.11	0.07
1982	530.46	−0.23	1.01	0.95	1.08	0.01	−0.05	0.08
1983	635.76	0.60	1.15	1.06	1.24	0.14	0.06	0.21
1984	690.93	1.04	1.22	1.08	1.38	0.20	0.08	0.32
1985	524.79	−0.28	1.01	0.94	1.08	0.01	−0.06	0.08
1986	442.26	−0.93	0.91	0.79	1.05	−0.09	−0.23	0.05
1987	486.00	−0.58	0.96	0.87	1.07	−0.04	−0.14	0.06
1988	393.30	−1.32	0.86	0.72	1.04	−0.15	−0.33	0.04
1989	427.77	−1.05	0.90	0.77	1.05	−0.11	−0.26	0.05
1990	464.13	−0.76	0.94	0.83	1.06	−0.07	−0.19	0.06
1991	575.01	0.12	1.07	1.02	1.12	0.07	0.02	0.11
1992	711.45	1.20	1.25	1.09	1.44	0.23	0.09	0.37
1993	734.76	1.38	1.29	1.10	1.52	0.25	0.09	0.42
1994	758.70	1.57	1.33	1.10	1.59	0.28	0.10	0.47
1995	676.53	0.92	1.20	1.08	1.34	0.18	0.08	0.29
1996	622.89	0.50	1.13	1.06	1.21	0.12	0.06	0.19
1997	628.20	0.54	1.14	1.06	1.22	0.13	0.06	0.20
1998	641.97	0.65	1.16	1.07	1.25	0.14	0.07	0.22
1999	590.31	0.24	1.09	1.04	1.14	0.08	0.03	0.13
2000	447.12	−0.89	0.92	0.80	1.05	−0.08	−0.22	0.05
2001	273.51	−2.27	0.75	0.55	1.01	−0.29	−0.59	0.01

odds of population decline, then managers could focus efforts on maintaining Resource R at levels between −2.3 and 0.25 standardized units.

Real values of Resource R that represent the range of standardized X_i values can be determined by back transformation. In our example, we standardized all covariates prior to demographic analyses by subtracting the mean and then dividing by the standard deviation:

$$X_i = \frac{X_{\text{real}} - X_{\text{mean}}}{X_{\text{S.D.}}}$$

Therefore, the real value of Resource R at the threshold level equals:

$$X_{\text{real}} = -0.03 \times 126.46 + 559.59, \quad X_{\text{real}} = 555.80 \text{ ha}$$

The corresponding 95% CI equals:

$$X_{95\% \text{ CI}} = -2.3 \times X_{\text{SD}} + X_{\text{mean}}, \quad X_{\text{real}} = 0.25 \times X_{\text{S.D.}} + X_{\text{mean}},$$

$$X_{95\% \text{ CI}} = -2.3 \times 126.46 + 559.59, \quad X_{\text{real}} = 0.25 \times 126.46 + 559.59,$$

$$X_{95\% \text{ CI}} = 268.73, \quad 591.21 \text{ ha}$$

4. Discussion

Understanding resource limitation is critical to effective management and conservation of wild populations (Leopold, 1933). One way to model resource limitation is to augment resource availability for an animal population and estimate demographic response (Hubbs and Boonstra, 1997; Hoodless et al., 1999; Hart et al., 2006); however, resource augmentation is not always logistically feasible and experimentation, as well as resulting inferences, have limited spatial and temporal scope (Stephens et al., 2003). The method we propose to understand resource limitation differs from augmentation models

in that variation in resource availability occurring during a study period is explicitly modeled and considered a state variable.

Demographic numerical response models, which link rates of change in consumer abundance to food availability (Caughley, 1976; May, 1981) are also commonly used to evaluate resource limitation (Pennycuik, 1969; Skogland, 1985; Messier, 1991; Langvatn et al., 1996; Ghosh and Sarkar, 1998; Mduma et al., 1999). Most numerical models, however, do not consider multiple resources as does our method and, therefore, they are relatively unrepresentative of natural systems (Roelke, 2000). Importantly, a resource that is limiting at one time may become non-limiting at another time, depending upon changes in its availability and changes in the availability of other resources. Even if numerical models were used to consider multiple resources, current interpretation of results would yield little about resource limitation as a dynamic process in terms of changing availabilities of resources, such as that demonstrated in Figs. 2 and 3. We found one study that used multiple limiting resources and a demographic numerical response model, but the model was not intended to be used as a predictive tool for management primarily because simulation results represented hypotheses to be tested (Roelke, 2000). Alternatively, results from our method are not based on simulation analyses; they are based on empirical data collected during a study. By evaluating results in terms of y-intercepts and rates of change, our method may be a powerful tool for managers interested in understanding resource limitation as a dynamic process in real-life scenarios. In addition, our method can be used to evaluate multiple competing hypotheses that stem from simulation studies.

Individual-based models are also used to understand resource limitation (Griebeler and Seitz, 2002; Rashleigh and Grossman, 2005). For example, Wang and Grimm (2007) evaluated resource limitation for a population of the common

shrew (*Sorex araneus*) using individual-based models via sub-models of shrew behavior. Although the global model and simulation analyses were very complete, the simulations were based on assumptions regarding the effects of resources on shrew response. Specifically, the relationships between food resources or habitats and shrew responses were specified *a priori* as sub-models. Our method for evaluating resource limitation differs substantially from individual-based models because our method makes no *a priori* assumptions regarding the relationships between resources and vital rates. Indeed, the main purpose of our method is to incorporate empirical data collected during a study to determine the effects of resources on vital rates.

Another method for understanding resource limitation is to use population-level models. Stage-based vital rates for populations are often estimated based on life table experiments, these rates are used to populate matrix models, λ is projected over time, and an algorithm is used to link estimates of λ with estimates of predictor variables (e.g., resources). For example, Meng et al. (2006) evaluated the effects of a chemical on a population of killifish (*Oryzias latipes*). They evaluated the effects of the chemical on individual survival and fecundity in the lab, used these results to populate matrix models, and then projected λ over time under different chemical levels. Our method for understanding resource limitation differs from traditional population-level models because our method evaluates realized λ and results regarding the relationship between λ and resources are not based on simulation analyses.

Models that use capture-recapture data to estimate vital rates and which link predictor variables to vital rates (e.g.,

Grand et al., 1998; Franklin et al., 2000; Armstrong et al., 2001; Doherty and Grubb, 2002; Jones et al., 2002) can yield information regarding which variables affect demography, but current methods for interpreting results from such models fall short in terms of yielding insights into resource limitation as a dynamic process. Conceptually, our method incorporates capture–recapture data to estimate demographic parameters, after which annual estimates of resource availabilities are incorporated as covariates to parameter estimates (Fig. 5). Using an information theory approach for model selection within a hypothesis testing framework (e.g., AIC), models are ranked in terms of their ability to explain the data. Model weights and slope estimates for variables are examined to determine the magnitude and direction of resource effect. Importantly, current approaches for interpreting results of demographic modeling stop here (i.e., the dashed line in Fig. 5). Further evaluation of results from model selection in terms of odds ratios, y-intercepts, x-intercepts, and rates of change can yield information regarding resource limitation and resource thresholds.

The dynamics represented in Figs. 2 and 3 are similar to elasticity and sensitivity analyses (Demetrius, 1969; Caswell, 1978), respectively. Unlike traditional elasticity and sensitivity analyses, which provide single values corresponding to relative or absolute changes in a_{ij} , multiple rates of change in demographic estimates can be evaluated over a range of resource availability values (Figs. 2 and 3). This may be important given the effect of a 0.5 standardized unit increase of Resource A on survival in Fig. 2 differs depending on whether the Resource A increases from A_3 to A_1 or whether it increases from A_1 to A_2 .

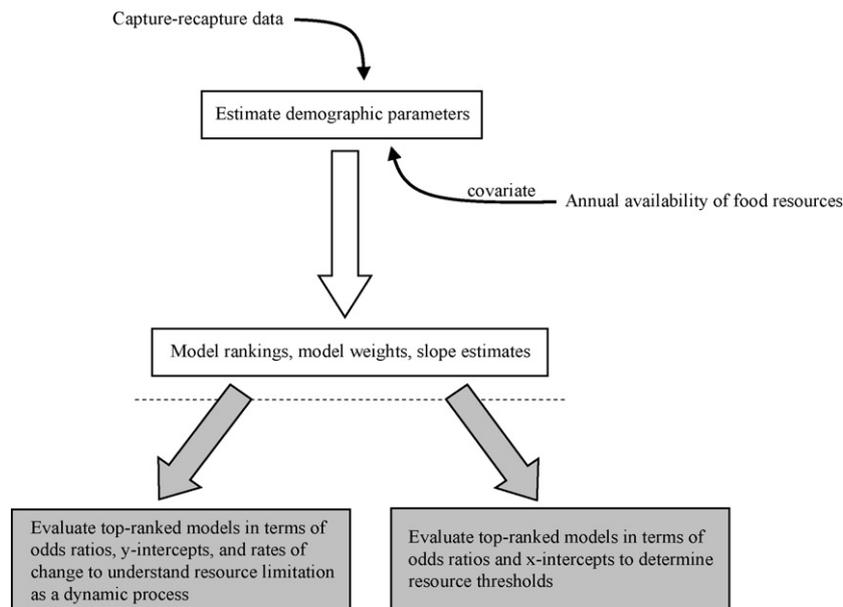


Fig. 5 – Conceptual diagram of proposed method for evaluating results from demographic modeling. Capture–recapture data are used to estimate demographic parameters, estimates of annual availabilities of resources are incorporated as covariates to parameters, and information theory model selection is used to rank models in terms of their ability to explain the data. Current approaches for evaluating demographic models stop at the dotted line. We propose that top-ranked models can be evaluated in terms of odds ratios, y-intercepts, and rates of change to understand resource limitation as a dynamic process. In addition, odds ratios and x-intercepts can be evaluated to understand resource thresholds.

5. Summary

Our approach builds on current methods for analyzing results of demographic modeling when logistic regression is used to link demographic parameters with estimates of resource availability. Within a hypothesis testing framework, critical first steps toward understanding resource limitation include evaluating model rankings, model weights, and slope estimates. Comprehensive understanding of resource limitation, however, requires knowing not only which resources affect demography but also how a resource affects demography as its availability changes or when availability of other resources changes. We propose that researchers can exploit information regarding odds ratios and intercepts, which are part of results stemming from using logistic regression, to understand resource limitation as a dynamic process and to yield insight into resource thresholds.

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