# Characterizing the strength of density dependence in at-risk species through Bayesian model averaging

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ABSTRACT

Developing effective conservation plans for at-risk species requires an understanding of the relationship between numbers of breeding adults and their subsequent offspring. In particular, establishing the degree to which density-dependent effects limit population size can be difficult due to errors in the data themselves, uncertainty in model parameters, and possible misspecification of model structure. Here we develop a Bayesian model averaging framework to fit four simple models of adult-offspring production and estimate the probabilities that negative (i.e., decreasing survival with increasing density) and positive (i.e., Allee effects) density dependence exists. As an example, we analyzed 48 at-risk populations of anadromous Chinook salmon (*Oncorhynchus tshawytscha*) from the northwestern United States. We found strong evidence that more than two-thirds of the populations exhibit negative density-dependent effects of adults. This result was somewhat unexpected given the large reductions in adult numbers relative to historical benchmarks, indicating that carrying capacity of spawning habitat has been reduced considerably. Approximately two thirds of the populations also had non-zero probabilities of positive density-dependent effects of adults, which could suggest that cumulative losses of spawning adults over the past century has led to decreased nutrient and energy subsidies from semelparous carcasses, and diminished bio-physical disturbance from nest-digging activity. Importantly, our analysis highlights the utility of Bayesian model averaging in a conservation context wherein errors in choosing the best model may have more severe consequences than errors in estimating model parameters themselves.

## 1. Introduction

One of the cornerstones of conservation biology is establishing the relationship between the numbers of parents and the offspring they produce. In particular, the degree to which organisms are affected by population density has important implications for individual fitness and population growth. Negative density dependence (NDD) occurs when density is relatively high and any further increases in density lead to increased competition for resources (e.g., food, breeding locations) or transmission of diseases, ultimately causing reductions in per capita survival (Hixon et al., 2002; Brook and Bradshaw, 2006). Conversely, positive density dependence (PDD), or the "Allee effect", arises when density is relatively low and the loss of more individuals causes decreased per capita survival because of cooperative foraging or defensive behaviors, decreased probability of finding a mate, or combinations of these factors (Courchamp et al., 1999; Berec et al., 2007; Gregory et al., 2010a). The strength of both NDD and PDD in wild populations has practical management implications. For example, the presence of NDD could indicate limited habitat availability (i.e., insufficient total area) whereas the existence of PDD might suggest a high degree of habitat fragmentation; rectifying those two types of habitat deficiencies could require rather different actions. When combined with historical knowledge about the population, insights about the combined roles of NDD and PDD are also useful for reintroduction planning (Anderson et al., 2014). Understanding whether NDD and PDD occur and if so, to what extent, is thus particularly valuable for determining the best options for population management and the conservation of at-risk species.

Density-dependence has been studied extensively in fish populations because of its importance to both the management of healthy and
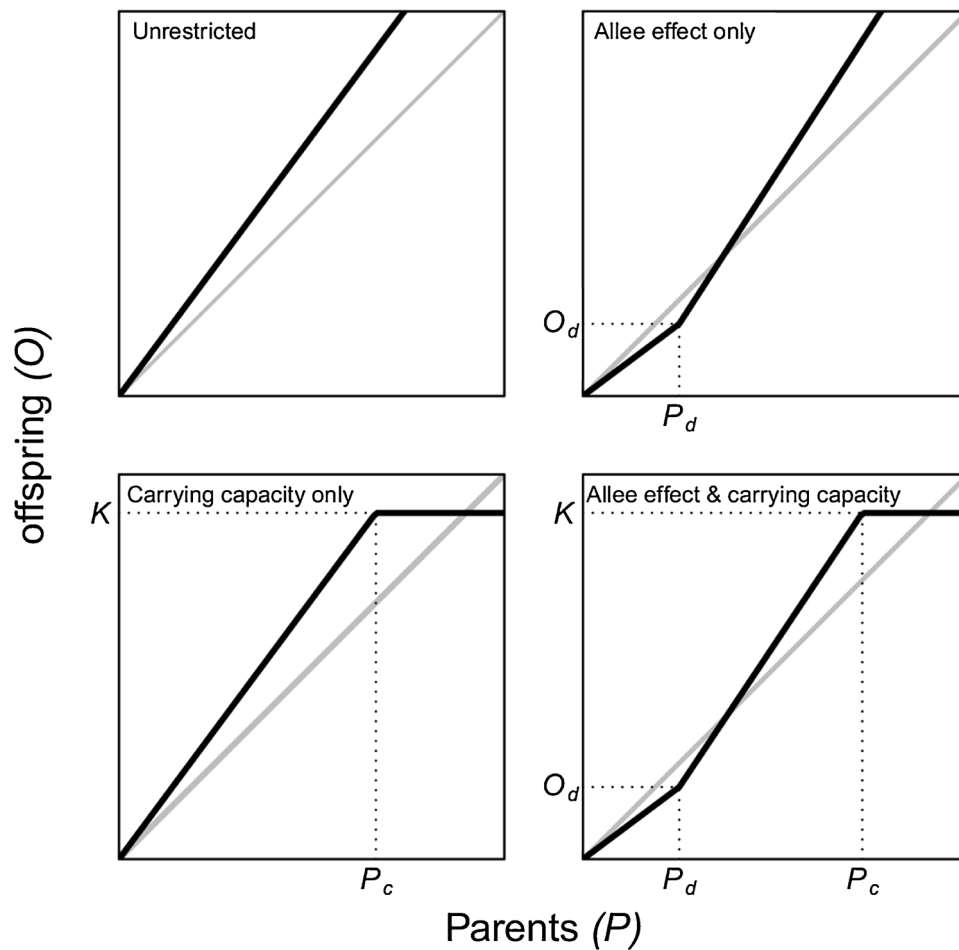
**Fig. 1.** Shape of the four alternative population production models described in the Methods with $P_c$ the number of parents leading to reaching the carrying $K$ and $O_d$ the number of offspring corresponding to the parents depensation breakpoint $P_d$. Thin grey line is the 1:1 replacement line.

economically valuable stocks and the conservation of imperiled populations (Liermann and Hilborn, 1997; Barrowman and Myers, 2000, Barrowman et al. 2003). In classical fisheries management, NDD within a stock implies parental biomass should be harvested to the point where the surplus production of new recruits to the fishery is maximized relative to replacement (Hilborn and Walters, 1992). Conversely, the degree of PDD mortality will determine the rate at which overfished stocks will recover when harvest is reduced. Most conservation practitioners concentrate on the possible existence of PDD. However, NDD at relatively low abundance can exist, implying diminished carrying capacity from factors like habitat loss/modification or the presence of non-native species (Achord et al., 2003), but this is often ignored in conservation contexts.

Models of population dynamics offer a formal means for estimating both positive and negative density dependence (Boyce, 1992). For example, Beverton and Holt (1957) and Ricker (1954) models of density dependence have been used to estimate the relationships between parents and offspring for decades. Approaches allowing for flexibility in curves shapes but not process based, such as splines or Gaussian process models, have also been developed (Bravington et al., 2000; Munch et al., 2005). Meanwhile Barrowman and Myers (2000) introduced a form of piecewise regression model known as the "hockey stick" (HS) model, which is similar to the Ricker and Beverton-Holt curves. The HS model offers potential advantages over these other models in a conservation context because it provides more conservative estimates of the maximum density-independent survival (i.e., slope at the origin) and carrying capacity (Barrowman and Myers, 2000). In addition, the breakpoints in the HS segments may provide natural reference points

for management decisions. However, the HS model does not allow for PDD.

Although statistical modeling is a powerful tool, three main types of uncertainties can hinder our ability to infer the true underlying relationship between parents and their offspring. First, observation errors arise in the form of sampling and measurement errors. Second, model parameters are rarely known without error and instead must be estimated from the data. Third, uncertainty about the structure of the model itself affects inference about the form of the parent-offspring relationship. The first two concerns are often addressed through appropriate sampling designs and explicit consideration of both process and observation/sampling errors. However, possible misspecification of a particular model is typically ignored and instead the "best" model is chosen based on some model selection measure such as Akaike's Information Criterion (Burnham and Anderson et al., 2002). In such cases, two models with nearly identical support from the data could produce widely divergent predictions, especially when confronted with new data (Pascual et al., 1997; Richards, 2005). As a guard against this likely possibility, model averaging (MA) offers a formal means for explicitly addressing model-selection uncertainty in problems of inference and prediction (Burnham and Anderson et al., 2002; Wintle et al., 2003). In particular, model averaging can produce more robust estimates by combining results from an ensemble of multiple independent models (Banner and Higgs, 2017). As a cautionary note, however, averaging expectations from models that are capable of producing an important spectrum of different results may confuse interpretations (Galipaud et al., 2014; Cade, 2015). Thus, the set of models to consider should be carefully chosen.