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2	Brian Dennis, José Miguel Ponciano. 201X. Density dependent state space model for population
3	abundance data with unequal time intervals. Ecology VOL: pp-pp.
4	Appendix. Confidence intervals, hypothesis tests, and model selection for the Ornstein-
5	Uhlenbeck state-space model.
6	The Ornstein-Uhlenbeck state-space (OUSS) model is given by $Y(t_i) = X(t_i) + F_i$,
7	$dX(t) = \theta[\mu - X(t)]dt + \beta dW(t)$, where $Y(t_i)$ is the observed or estimated log-abundance of
8	the population at time t_i , $X(t_i)$ is the actual (unobserved) log-abundance, where F_i has a normal
9	distribution with mean 0 and variance τ^2 , with F_i , F_j uncorrelated $(i \neq j)$, $dW(t)$ has a normal
10	distribution with a mean of 0 and a variance of dt (where the correlation between $dW(t_i)$ and
11	$dW(t_j)$ is equal to 0 if $t_i \neq t_j$), μ is a real-valued parameter, and θ , β^2 , and τ^2 are positive real-
12	valued parameters.
13	Confidence intervals for the model parameters are readily obtained using parametric
14	bootstrapping. For the OUSS model, parametric bootstrapping involves simulating 2000 or so

data sets from the estimated OUSS model (the OUSS model equations evaluated at the maximum
likelihood (ML) or restricted maximum likelihood (REML) estimates) and reestimating the
model parameters for each simulated data set. Percentiles (or alternatively, median-adjusted
percentiles) of the 2000 bootstrap parameter values form the ends of the confidence intervals (see
Manly 1997).

20 Confidence intervals obtained with parametric bootstrapping are in general not symmetric 21 and tend to have better coverage properties than intervals based on large sample ML theory 22 (Pawitan 2001). Also, parametric bootstrap intervals are easily obtained for functions of 23 parameters (such as the stationary variance of X(t) given by $\beta^2/(2\theta)$) just by calculating the value of the particular function for each set of bootstrap parameter values. One of the R
 programs accompanying this paper (Supplementary Material online) calculates parametric
 bootstrap confidence intervals.

4 A statistical hypothesis test of density independence versus density dependence can be 5 performed for the OUSS model with parametric bootstrapping. The exponential growth state-6 space (EGSS) model serves as the null hypothesis of density independence, and the OUSS model 7 serves as the alternative hypothesis of density dependence. The procedure represents an 8 extension of the method of Dennis and Taper (1994), which used only process noise and equal 9 time intervals. The procedure is to simulate 2000 or more data sets from the EGSS model that 10 has been fitted to the data with ML estimates (as described in Humbert et al. 2009). The EGSS 11 and the OUSS model are then fitted to each simulated data set with ML estimation, and a likelihood ratio statistic ($-2 \log (\hat{L}_{EGSS} / \hat{L}_{OUSS})$) is then calculated for each simulated data set. 12 13 Here \hat{L} represents a multivariate normal likelihood maximized under the EGSS or OUSS model. 14 The proportion of the 2000 (or more) simulated likelihood ratio values that exceed the value of 15 likelihood ratio statistic calculated for the data constitutes the P-value for the test. One of the R 16 programs accompanying this paper (Supplementary Material online) calculates the parametric 17 bootstrap likelihood ratio test of the EGSS model versus the OUSS model. The procedure 18 basically tests for the presence of a tendency toward equilibration (or stationarity), and the 19 ecological interpretation of such a test as biological density dependence requires caution (Wolda 20 and Dennis 1993) in the absence of other biological information about the population.

Model selection can be performed among submodels, or among alternative model forms, with information criteria such as AIC and its variants (Burnham and Anderson 2002). The model selection indexes typically require the values of the maximized log-likelihoods for the various

1	models under question (or at least the differences of the maximized log-likelihoods for every pair
2	as in Ponciano et al. 2009). For the OUSS model and its submodels, the maximized log-
3	likelihood values are readily available as byproducts of model-fitting. However, one should not
4	compare models with likelihoods arising from fundamentally different data, such as the raw
5	observations for ML estimates and the differenced observations for REML estimates (or even
6	first differences for OUSS/REML and second differences for EGSS/REML). Rather, the
7	likelihoods for the models being compared should be defined for the same unique observations,
8	which usually means comparing ML with ML.
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