Abstract

Models of population dynamics play a central role in theoretical and applied ecology where they are used for purposes such as testing hypotheses about density dependence and predicting species' responses to future environmental change or management actions. State-space models, are widely used for these purposes, and they allow for estimating parameters of classical growth models, such as exponential, logistic, and Gompertz, while accounting for demographic stochasticity and observation error. Conventional state-space models, however, have three important limitations: (1) the parameters are not identifiable in many common situations, (2) they do not admit spatial variation in population dynamics, and (3) there is no clear interpretation of the observation error. We demonstrate how each of these problems can be resolved using a class of hierarchical models for spatially-replicated time-series data recently proposed by Dail and Madsen (2011, Biometrics). We expand this class of models to accommodate classical growth models, zero-inflation, and random effects such as observer-specific detection probabilities. Furthermore, we describe classical and Bayesian methods of parameter estimation. These new developments will allow researchers to apply these methods to address important questions regarding the factors affecting spatial and temporal variation in abundance. We demonstrate these developments by analyzing data from the North American Breeding Bird Survey. Code to fit these models using the R package unmarked and JAGS is also provided.

Key words: abundance, Dail and Madsen model, density-dependence, Gompertz model, immigration, open population point count models, random observer effects, range, Ricker model, zero-inflated

Theoretical ecology requires robust models for testing hypotheses regarding density dependence and spatial variation in population dynamics. Such models are also required in applied ecological research for predicting species' responses to environmental change or management actions. For example, many researchers are currently investigating the influence of weather on population dynamics so that predictions can be made about the effects of future climate change. Several complicating factors must be confronted when addressing these questions. First, deterministic models of population dynamics are virtually always inadequate due to "process variation", the inherent stochasticity in demographic parameters and environmental conditions. Second, abundance—the natural state variable in studies of population dynamics—can rarely be observed perfectly in field studies because of "observation error", such as imperfect detection. Failure to account for and heterogeneity in observation error can bias the estimators of abundance and related parameters.

State-space models have become the most widespread approach for studying population dynamics while accounting for process variation and observation error (de Valpine and Hastings, 2002; Buckland et al., 2004; Dennis and Taper, 1994; Dennis et al., 2006). Conventional state-space models are simply time-series models in which the true state of the system is observed imperfectly. Originally developed for xxx (cite Kalman filter papers), the ability to model both the ecological state process and the observation process has made them relevant in numerous ecological applications [need to clean this up]. State-space models have been defined differently by different authors, but we follow Buckland et al. (2004) the definition : "xxx" . Typically, the ecological process is described by a Markovian model that includes a deterministic description of population change as well as two random sources of variation for "process variation". The model for the observation process is typically phenomenological in the sense that observation error is not defined explicitly. As an example, let N_t be the abundance of a species during year t, and X_t be the observed data, which differs from due to observation error (ζ). A simple state space model that includes exponential growth and process variation ($\grave{o}$) could be written as:

$$N_t = N_{t-1} \exp(r) + \grave{o}_t \tag{1}$$
$$X_t = N_t + \zeta_t \tag{2}$$

Here is the intrinsic rate of increase. Typically, both random effects are assumed to follow normal distributions: $\grave{o}_t \sim \mathrm{N}(0, \sigma)$ and $\zeta_t \sim \mathrm{N}(0, \tau)$ (de Valpine and Hastings, 2002; Dennis et al., 2006). Even though this is the most widespread approach for modeling population dynamics using time-series data, several problems are immediately evident. First, if abundance is a non-negative integer, as it always is, there is clearly a problem with this formulation because the normally distributed random effects violate this constraint. To avoid this issue, ecologists often replace N_t with $\log(Y_t/A)$ where A is the area surveyed—i.e., abundance is replaced by the natural log of population density, which is assumed to normally distributed. This is desirable because this allows for the fitting of models assuming normally distributed residuals, which are computationally much less intensive than most alternatives. However, this transformation is problematic since abundance may be zero and thus $Y_t = \log(0) = -\infty$. Generally, zeros are replaced with some small, but positive number, although the effect of this is rarely discussed.

The problems mentioned thus far are minor in comparison to the more serious issue that the parameters of the model are often not identifiable. Specifically, the Markovian nature of the model implies the following likelihood

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The first term is the probability density for the first observation in the time series, Y_t, yet it is intuitively not possible to estimate the parameter(s) of this distribution using only a single observation. This problem has resulted in several papers with interesting names like "multi-modal likelihoods and ridges etc..." The workaround here is to assume that the population is at equilibrium so that that the x can be replaced with the equilibrium distribution. However, assuming equilibrium defeats the objective of many studies of population dynamics, namely determining if and why a population is at equilibrium.

A third problem with these models is that they do not admit spatial variation. This is not a fair criticism because this lies beyond the scope of traditional state-space models, but it does restrict the utility of their since it is typically impossible assess the impacts of factors such as habitat fragmentation or climate change on a population without considering spatial variation. Indeed many populations are regulated by spatial processes such as source-sink dynamics.

Dail and Madsen (2011) developed a model (henceforth the DM model) that resolves each of these problems with traditional state-space models. The DM model allows for inference about spatial and temporal dynamics in abundance while accounting for observation error using only spatially and temporally replicated count data. Their model is an extension of the closed-population N-mixture model (Royle, 2004), which was designed specifically to address the problem of modeling spatial variation in abundance when detection probability is less than unity. The DM extension relaxes the assumption of population closure and includes explicit parameters describing population change as a first-order Markovian process. [more details]

[applications / potential etc...] The DM model is relevant to a huge number of problems confronting basic and applied ecological research. Answering questions about climate change etc... require spatially and temporally extensive datasets such as result from the North American Breeding Bird Survey (BBS) (Robbins et al., 1986). However, most of the datasets of the appropriate scale are collected by volunteers and using protocols that are not amenable to traditional approaches of modeling abundance and detection probability based on standard capture-recapture methods. Instead they have, at best, simple count data for which, when it can be interpreted as counts of unique individuals, the DM model can be applied.. Yadi ya

Although the DM model was designed explicitly for these purposes, the original formulation of the model makes strict distributional assumptions and does not acknowledge many of the sources of variation inherent to existing ecological time-series data. We propose variations on these models that are likely to be more realistic and useful in many cases. We demonstrate the usefulness of these new models with simulated and real BBS data.

1 Methods

1.1 Model Development

As originally formulated, the DM model includes submodels for four conditionally related processes: the initial abundance state, apparent survival, recruitment, and detection probability. Dail and Madsen proposed two options for initial abundance (Poisson and negative binomial): (2) (3) where N_{i1} is the abundance at site i during year 1 and Λ is the expected abundance. The negative binomial model includes the overdispersion parameter α. The survival and recruitment terms allow abundance to change over time: (4) where ω is the survival probability and γ is the arrival rate (which can depend on Nit-1). Dail and Madsen propose three models for γ: the con-

stant model, where γ does not depend on Nit-1, and which simulates a "propagule rain" of recruitment; the autoregressive model , which simulates geometric or density independent growth; and the "no-trend" model, which keeps abundance fixed over time. The number seen is a function of detection probability: (5) Initial abundance, apparent survival, recruitment, and detection can all be modeled as functions of covariates, allowing fairly sophisticated inference about population processes and dynamics from point count data. Range model of initial abundance Dail and Madsen (2011) suggested two distributions for modeling initial abundance: Poisson and negative binomial. We have extended their model to include another distribution, the zero-inflated Poisson. This could be useful when, for example, one is modeling the abundance of several bird species with the same set of BBS routespoint count surveys for all species, but this set includes routes sites outside the range of some of the bird species. The distribution of initial abundances can be represented as: (6) where ψ represents the proportion of extra zeros. These models allow three sources of zero counts by observers: a species was at a route but not detected; the route was within the species' range but there were no birds at that site in that year; and the route was outside the species' range. Furthermore, detection, abundance, and zero-inflation can be modeled separately as functions of different (or the same) covariates. For example, detection of species x at site y in year z might depend on wind speed, abundance on forest type and weather, and zero-inflation upon elevation and climate. This approach combines elements of occupancy modeling (MacKenzie et al. 2006) and abundance modeling, and could prove useful for distinguishing species' fundamental and realized niches (Hutchinson 1957). The zero inflation factor can also affect recruitment or population dynamics (see below). We also considered a zero-inflated negative binomial model of initial abundance, but this model did not perform well in preliminary tests. Population growth models Preliminary DM model runs for several species tended to lead to estimates of survival that were unrealistically high and recruitment that were unrealistically low, or the reverse (compared to independent demographic analyses). The DM models are able to partition changes in abundance to survival and recruitment in part by making strong distributional assumptions (Dail and Madsen 2011). When those assumptions are heavily violated the models may proportion population growth incorrectly into survival and recruitment, even if they estimates population growth accurately. Although partitioning population growth into survival and recruitment is informative, it is not needed for all applications. Furthermore, a simpler model would have several merits: faster running time, fewer total model combinations, and possibly more realistic estimates. Therefore, we developed a version of the DM model that estimates and models population growth directly. In this model, equation 4 is simplified to: (7) where r represents the instantaneous population growth rate. This, like the autoregressive version of the model, is a variant on a simple density-independent exponential model of population growth. Density-dependent versions of the model are also possible. For example: (8) where K is the stable equilibrium of the population and r is the instantaneous population growth rate at low population densities, and both parameters are constrained to be positive. This model is based on Ricker's (1954) discrete time version of the logistic population growth model. We also implemented Gompertz's (1825) density-dependent model: (9) where the log of Nit-1 is only taken when Nit-1 is greater than 0 (when Nit-1 is 0, the full expression simplifies to 0 anyway). Here the interpretations of r and K are similar to in the Ricker model, but K is constrained to be greater than one. Because a single Poisson distribution controls the distribution of Nit in each of these models, the discrete convolution used by Dail and Madsen (2011) is not required, speeding up processing time. Immigration and colonization models The autoregressive, population growth, Ricker, and Gompertz versions of the DM

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models all share a common feature (or bug): once the population at a site reaches 0, it must remain at 0. This is because all contributions to population growth are local in these models. We generalized each these models that include both internal and external (immigration) contributions to population growth. The population growth + immigration model is: (10) or (11) where ι represents the immigration rate (equations 10 and 11 are equivalent). This model is close to the constant DM model (equation 4), with exp(r) instead of ω and ι instead of γ, except that the first process is Poisson distributed instead of binomial. Similarly, the Ricker + immigration model can be represented as: (12) the Gompertz + immigration model as: (13) and the autoregressive + immigration model as: (14) These immigration models are based on the assumption that numbers of immigrants are not dependent on local density. Other versions of these models with different assumptions are possible. The Ricker + immigration and Gompertz + immigration models can be justified by the further assumption that immigrants arrive as adults immediately before the point-count survey (so that density-dependent processes do not have a chance to act on the numbers of immigrants; Otto and Day 2007 p. 161). Deterministic versions of these models do reach stable equilibriums, but the equilibriums are not at K and cannot be solved for analytically (Otto and Day 2007). We have implemented all preceding models in a maximum likelihood framework by extending the unmarked package (Fiske and Chandler 2011) in R (R Development Core Team 2011). Random eEffects of oObservers Differences in observers' ability to see, hear, or identify birds has long been recognized as a potential source of error in avian point count surveys such as the BBS (Robbins et al. 1986, Sauer et al. 1994, Diefenbach et al. 2003, Alldredge et al. 2007, Campbell and Francis 2011). Estimating a separate detection probability for each observer can be difficult and reduces one's ability to estimate the quantities of interest. This problem is compounded by the fact that observers differ greatly in the number of surveys they have run (so that many observers' separate detection probabilities could not be accurately estimated). Current BBS trend estimators deal with this problem by treating observer identity as a random (as opposed to a fixed) effect (Link and Sauer 2002, Sauer and Link 2011). This allows observer-specific differences in detection probability, but assumes that observers are selected at random from a pool of potential observers. Models that contain both random and fixed effects are referred to as mixed models. Often in mixed models (as in this case), the random effect is modeled not because it of interest in itself, but to avoid bias in the estimates of the fixed effects. To include random observer effects in DM models and these extensions, equation 5 can be modified to: (15) (16) where nijt is the number of bird recorded at site i by observer j in year t, pj is observer-specific detection probability, μ_p is the mean detection probability (on the logit scale), and σ_p is the standard deviation of the random observer effects (also on the logit scale). We have implemented random observer effects in the Bayesian framework using program JAGS (version 3.2.0; Plummer 2003) with the R (R Development Core Team 2011) package rjags (Plummer 2011) as an interface. Dynamic range models The zero-inflated Poisson distribution can be applied to not only initial abundance but also to recruitment and population growth terms. For example, the recruitment term of the constant DM model (equation 4) can be modified as follows: (17) When both initial abundance and dynamics are modeled as zero-inflated, ψ can be modeled as time-varying or not (in either case, ψ can also be modeled as varying over space). In the latter case, it makes sense for the model to "remember" which sites are inside the range of the species between the initial abundance stage and each time step of the dynamics stage (see code sample?). Adding zero-inflation to the dynamics of the autoregressive, trend, Ricker, or Gompertz models (without immigration) should have no effect when initial abundance is also zero-inflated unless ψ is time-varying

(because these dynamic models cannot recover from zero abundance). We have implemented zero-inflated dynamics in the Bayesian framework using program JAGS (version 3.2.0; Plummer 2003)

2 Applications

2.1 Simulation Study

We simulated data for 100 sites over 40 years. All simulations assumed initial abundance was Poisson distributed and no covariates affected initial abundance, dynamics, or detection probability. Our first series of simulations assumed dynamics were exponential. We ran 500 simulations for each combination of low, medium, and high Λ, r, and p (Table 1; 27 total combinations).

Our second series of simulations changed dynamics to the Ricker model. We used an initial abundance of 10, a maximum growth rate of 0.005, and a detection probability of 0.25, and simulated low, medium, and high values of equilibrium abundance, each with 500 simulations (Table 1). Our third series of simulations was based on the Ricker + immigration dynamics model; here we fixed all parameters the same as the Ricker model (with K = 10) and simulated low, medium, and high values of immigration rate with 500 simulation each (Table 1).

We estimated the parameters for each simulation using the same initial abundance (Poisson) and dynamics models as were simulated, implemented in the unmarked library in R. When run in a maximum likelihood framework, these models require a maximum abundance to integrate over (Royle 2004, Dail and Madsen 2011); we used 150. We report bias of estimates, root mean squared error, and coverage (percentage of 95Ideas: I. Test importance of random effects modeling, and other differences between JAGS and unmarked II. Model with low p values, or a range of p values III. Ability to distinguish correct initial abundance and dynamics models IV. When can you detect DD if it exists (power)? V. Building on the last two: what if your model set doesn't include the correct DD model? When will the wrong DD model be favored over the wrong DID model?

2.2 Analysis of Breeding Bird Survey Data

We applied these models to North American Breeding Bird Survey (BBS) data from 1966-2010 for two species in the bordering US states Maryland and Virginia. For our focal species, we selected ovenbirds (Seiurus aurocapilla), an abundant and widespread forest breeding migrant with a stable or increasing trend in the region (CITE) and golden-winged warblers (Vermivora chrysoptera), which only breeds in the western parts of these states and has been declining in the region (CITE). MORE INFORMATION ABOUT THE SPECIES?

GENERAL ABOUT BBS DATA. We only used data marked as acceptable for use in the annual BBS analysis. We summed the total birds of each species seen on each route and year and used the routes (rather than the individual stops) as our sites. Strong winds can interfere with point count observers' ability to hear birds (Simons et al. 2007)(cite); we tested the effects of wind speed on detection probability. BBS volunteers record wind conditions at the beginning and end of each route on the Beaufort Scale (start and end wind; Robbins et al. 1986)(start and end wind; 0-9; cite). When start or end wind was not recorded we imputed those values with the start or end mean. We took the mean of start and end wind for each route and put this average wind scale value into four categories: $0 \leq$ wind < 1; $1 \geq$ wind < 2; $2 \leq$

wind < 3; and wind ≥ 3 (maximum of 3.5). Following Link and Sauer (2002), we also included the first time an observer ran a route as a predictor variable for detection probability.

HOW WE OBTAINED AND MANIPULATED PRISM DATA We ran a series of maximum-likelihood based models for each species, and then a series of Bayesian models. We started by testing three models of initial abundance (Poisson, negative binomial, and zero-inflated Poisson) with population growth dynamics (equation 7) and no covariates. We selected the minimum Akaike's Information Criterion (AIC) model from that set to test three additional models for p: wind, first, and wind + first. We selected the minimum AIC model from that set to test eight additional models of dynamics: constant, autoregressive, Ricker, Gompertz, autoregressive + immigration, population growth + immigration, Ricker + immigration, and Gompertz + immigration. We then tested the effect of average minimum temperature for June and July on all dynamics parameters from the minimum AIC dynamics model. When run in a maximum likelihood framework, these models require a maximum abundance to integrate over (Royle 2004, Dail and Madsen 2011); we used 600 for ovenbirds and 350 for GWWA.

We ran the top ranked models from the maximum likelihood analyses in a Bayesian framework. We added random observer effects and, where appropriate, zero-inflated dynamics. WILL ADD MORE HEREWe used non-informative priors. We tested for lack of convergence using X Markov chains for each model (Gelman and Rubin 1992). For each chain we sampled the MCMC for Y iterations, after Z tuning samples. Latent inclusion factors for temperature effects?

Results

The negative binomial distribution was strongly supported for ovenbird initial abundance over the Poisson and zero-inflated Poisson (Table 1A, models A.1 - A.3). Even compared to the Poisson, there was no evidence to support a zero-inflation factor for this species. The best supported model for p was additive effects of wind speed and first run (Table 1A, model A.4). First run and increasing wind speeds both decreased p. All dynamics models with immigration were better supported than models without immigration (Table 1A, models A.8 - A.16); the best supported of these was the Ricker + Immigration. The best supported model of those without immigration was the Gompertz, and the autoregressive and the constant model had the least support. There was little support for an effect of minimum June and July temperature on dynamics parameters of the Ricker + Immigration model (Table 1A, models A.17 - A.18).

Estimates for the top ranked model for OVEN (NB[$\Lambda(.)\alpha(.)$]Ricker+Imm.[$r(.)K(.)\iota(.)$]p(wind+1st)) were similar when run in the Bayesian framework, except that the estimate of r more than halved (from 0.026 ± 0.006 to 0.011 ± 0.005 [for Bayesian model estimates we present mean and SD]). When random observer effects were added, estimates for Λ and K increased dramatically (from 31.6 ± 4.9 to 42.5 ± 7.3 and from 56.2 ± 18.2 to 101.8 ± 21.1, respectively), and the estimate for r was intermediate (0.018 ± 0.006). The estimate of the intercept for p (on the logit scale) dropped from -1.5 ± 0.1 to -2.0 ± 0.1, and the estimate of σ_p was 0.35 ± 0.03. [Richard, I ran the temperature model in the Bayesian framework (w/ and w/o random effect) too. Should we include those results? As earlier, very little evidence for an effect of temperature on any of the parameters, although I couldn't get the latent inclusion parameter to work for r.] Gelman and Rubin diagnostics and visual examination of the ? plots provided some evidence for a lack of convergence in estimates of the intercept for p for all Bayesian models ran.

There was slightly more support for the ZIP distribution for initial abundance of GWWA than for the negative binomial; both were strongly supported over the

Poisson (Table 1B, models B.1 - B.3). The best supported model for p was an effect of first run (Table 1B, model B.4). The best supported dynamics model was population growth (Table 1B, model B.8); the estimate of r from this model was -0.058 ± 0.017 (SE). There was no support for immigration added to the population growth or autoregressive models (Table 1B, models B.10 and B.13). However, the Gompertz + immigration and Ricker + immigration models were supported over the corresponding models without immigration (Table 1B, models B.11, B.12, B.14, and B.15), despite low estimates of ι from these models (0.003 ± 0.003 and 0.003 ± 0.002, respectively). There was considerable support for an effect of average minimum June and July temperature on r in the population growth model (Table 1B, model B.17), with a negative slope.

Because of the closeness of rankings for the ZIP and negative binomial distributions for GWWA, we also ran the subsequent models with the negative binomial initial abundance. Rankings of subsequent models were similar, but with a p covariate (first) the negative binomial distribution outranked the ZIP.

STILL WORKING ON JAGS GWWA RESULTS Estimated detection probabilities were generally low. For OVEN, the estimated probability of detecting a bird with no wind and not the first time an observer had run a route varied between 0.046 ± 0.002 (model A.16) and 0.192 ± 0.015 (model A.11), among models that accounted for both. For GWWA, the estimated probability of detecting a bird by a non-first time observer varied between 0.025 ± 0.008 (model B.18) and 0.141 ± 0.027 (model B.16), among models that accounted for first but not wind.

For both species, constant dynamics models estimated very high survival probabilities ($\omega = 1 \pm 1.3e{-}05$ for OVEN and 0.935 ± 0.011 for GWWA). The autoregressive and autoregressive + immigration models estimated very low survival probabilities for OVEN ($\omega = 0.058 \pm 0.046$ and 0.026 ± 0.060, respectively), but not for GWWA ($\omega = 0.715 \pm 0.288$ for both models).

3 Discussion

We made four important developments of the open population N-mixture model proposed by Dail and Madsen that make the model more applicable to long-term data such as is collected by the North American Breeding Bird Survey. First, we have reconciled the objectives of traditional state-space models with open population N-mixture models by illustrating how classical models of population dynamics can be embedded within the framework. Second, we have demonstrated methods of accounting for zero-inflation in the time-series. Third, we have illustrated how additional random effects such as observer-specific detection probabilities can be accommodated. Fourth, we presented a Bayesian analysis of the model, which makes it much easier to estimate parameters and to fine tune the model for specific purposes.

A unique aspect of the Dail and Madsen model as originally devised was that it allowed for the estimation of demographic parameters under strict distributional assumptions and with the assumption of geographic closure. Clearly, estimating demographic parameters from count data is a loftyn ambitious goal, and the required assumption will not be valid in many cases. Nonetheless, their approach is important because it allows for the combination of count data with other data types such as capture-recapture data , which offers a means of making inferences about demographic processes at broad spatial scales. Models combining count data and demographic data are often referred to as integrated population models, and This topic has received much attention lately under t

In the absence of direct information about demographic parameters, and when

the original assumptions of the model do not hold, we have offered extensions of the model to estimate derived parameters such as population growth rate. This has been the traditional emphasis of state-space models, and our approach resolves many of the factors limiting ...

[paragraph on zero-inflation]The zero-inflated models for initial abundance and dynamics allow one to estimate and model the proportion of sites outside of the range of a species. This could be especially useful when different factors control the range than the abundance or dynamics within the range. [some examples where that is the case?]

[paragraph on random effects] [paragraph on Bayesian] In spite of the new extensions we have proposed, several aspects of the model could be improved. First, the precision with which the parameters of the state process can be estimated ultimately depends upon how well detection probability is estimated. When there is only a single survey per primary period, the information about detection probability comes from deviations from the parametric assumptions about population dynamics. Thus, without direct information about detection probability, the estimates will be determined by model based assumptions. Furthermore, there are multiple components of detection probability that should be accounted for to minimize bias and yield valid estimates of population size. [Nichols EURING paper] .

Fortunately, it is easy to incorporate direct information about detection probability and we recommend that this be done whenever possible. The original method for proposed in the original paper was to collected replicated counts within the primary periods during a period in which the populations could be assumed to be closed. a robust design could be used to combine multiple surveys per primary period to increase the precision of the estimates. We envision that multiple other options are available as well. For instance, there should be no difficulty extending the model to accommodate traditional capture-recapture data collected during each primary period. Removal or time of detection etc.. Distance-related heterogeneity in detection probability is another source of variation that can bias estimators of abundance. Show some equations for the alternative observation models.

[paragraph on spatially-explicit dispersal] [Other possible extensions we could mention: Spatially hierarchical model (so can use individual stops) Other models of variability in growth or recruitment (such as negative binomial) Add density dependence to survival and recruitment models] [Discuss causes of low p values (and other BBS results) here or in BBS results?]

The modeling framework we described can be used to address many of the most pressing issue in ecology and conservation biology. For example, it is possible to test hypotheses about temporal and spatial population regulation. Furthermore, the Bayesian approach is very useful in that it can be used to combine multiple sources of data to develop mechanistic models of population dynamics. Thus one can test hypotheses about the effects of climate change on either explicit demographic parameters or in derived parameters such as population growth rate. Furthermore, under the Bayesian approach , population viability analysis is trivial because projecting populations into the future can be done as a component of the MCMC analysis. This allows for the computation of posterior distributions of parameters such as quasi-extinction probability.

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