

# **Evaluating Population Trend Models for a Hawaiian Forest Bird Species**

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of a writing project submitted by

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This writing project has been read by the writing project advisor and has been found to be satisfactory regarding content, English usage, format, citations, bibliographic style, and consistency, and is ready for submission to the Statistics Faculty.

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# 1 Introduction

## 1.1 Background

Native bird populations were declining at many locations on Hawai'i islands due to diseases, introduced competitions and habitat loss. The Hakalau Forest National Wildlife Refuge (Hakalau) was established in 1985 on the island of Hawai'i as a test case for habitat restoration as a tool for restoring populations of native Hawaiian forest birds. Federal management agency and university researchers have both conducted studies monitoring the population of forest birds at Hakalau; however, their conclusions did not always agree. Scientists from the federal management agency (Camp et al. 2010) assessed the bird population by estimating density annually for 21 years. Using a linear regression model, they concluded that long-term population trends in Hakalau are stable and increasing. On the other hand, researchers from University of Hawai'i (Freed & Cann 2010) suggested that the single-slope regression used by Camp et al (2010). missed an environmental change and misrepresent the population trends. Freed & Cann suggested using a piecewise regression to capture the change in environment. They concluded that the populations at Hakalau were declining despite the restoration efforts. The population trend lines fitted using both models for a single bird species, Hawai'i 'akepa (*Loxops c. coccineus*), were plotted in Figure 1.

In this report, I will present the results of all models using data for density estimates of Hawai'i 'akepa in open-forest study area (see nest section for study areas). The goal is to critique each model through model evaluation techniques such as model convergence and posterior predictive check, and to compare models in question with results from different models and simulations. I will also provide some suggestions on improving model fit, and a discussion on assessment of a population trend.

## 1.2 Study Design/Data collection

### 1.2.1 Study Area

Bird population surveys were conducted at Hakalau on the windward slope of Mauna Kea on the island of Hawai'i. The montane forest at middle elevations (600-1900 m) is dominated by native 'ohi'a and koa, where as the high elevation (>1900 m) it consisted of open grassland, mature koa trees, and recently planted forest.

The refuge was divided into three study areas that reflect the history of management at Hakalau (Figure 2): 1) the pasture study area (1650-2000 m), 2) the open-forest study area (1400-1920 m), and 3) the closed-forest study area (1400-1700 m).

### 1.2.2 Bird Species

Density and population trends were estimated for eight native and four introduced species by authors of the original study (Camp et al. 2010). I focus mainly on assessing models and estimates for Hawai'i 'akepa.

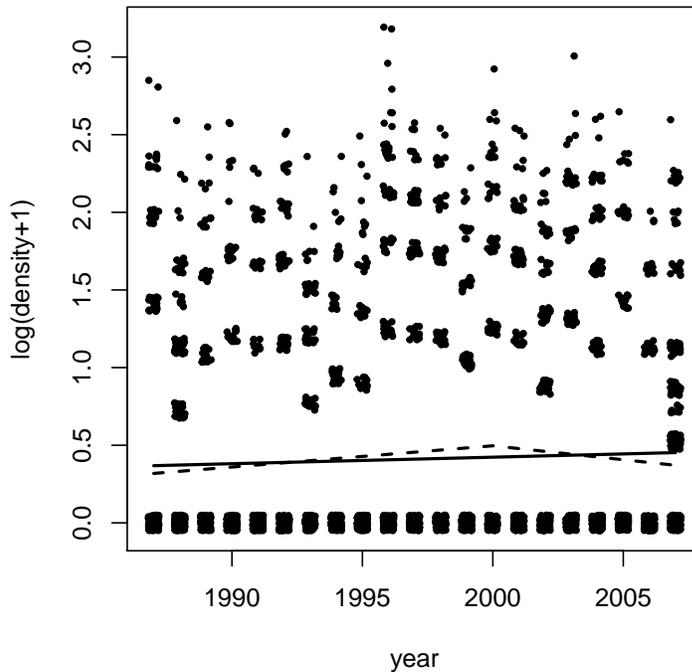


Figure 1: Scatter plot shows the population trend of a particular bird species, Hawai'i 'akepa, in Hakalau. Density estimates (birds per hectare) for stations surveyed are jittered and plotted in log scale from year 1987 to 2007. The solid line represents the linear regression line for the 'akepa population density estimates, and the dashed line represents the trend line fitted using piecewise regression.

### 1.2.3 Bird Sampling

Bird count surveys were conducted at a total of 15 transects, with a range of 196 to 343 stations across the refuge. At each station, surveyors recorded the detection type and horizontal distance from the station's center to individual birds detected during an 8-min count. Surveyors also noted the weather information and time of surveys. The surveys were typically conducted between dawn and 11 am, and halted when weather exceeded prescribed levels. The authors restricted the bird surveys within breeding season because the detectability of forest birds varies through the year. The surveys were conducted yearly and there were 21 years of survey data ranging from 1987 to 2007. Point-transect methods, a form of distance sampling, were used to estimate bird density at each station. Distance sampling was not the focus of this writing project, but Buckland et al. (2001, 2004) described the procedures and analyses in details.

### 1.2.4 Trend Detection

Camp et al. (2010) assessed long-term trends in bird density in the open-forest and pasture study areas over 21 years of survey data. Using a Bayesian framework, they fitted a normal

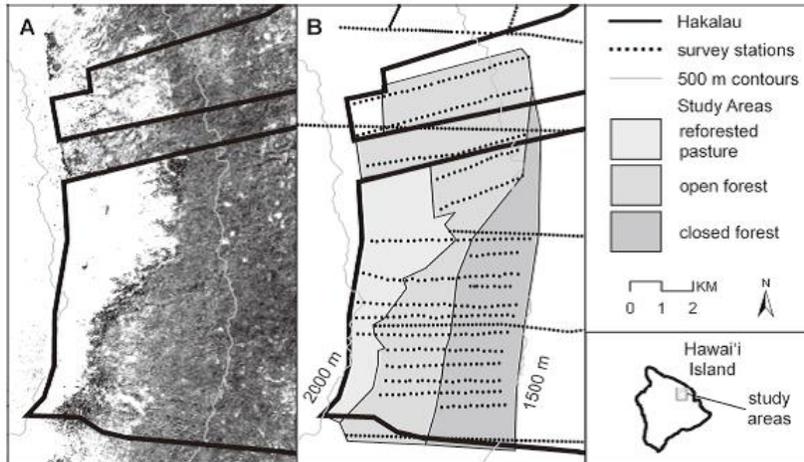


Figure 2: Study site from Camp et al. 2010 research.

log-linear regression model for each bird species using density as the response variable and sample years as a continuous explanatory variable. The years were centered on 1997 for the period 1987-2007. The slope estimate would be considered the rate of change in log density. The parameter  $\alpha$  (intercept),  $\beta$  (slope), and  $\sigma^2$  (variance) were given uninformative prior distributions. The model is defined below:

$$\begin{aligned}
 \text{density}_i &\sim N(\mu_i, \sigma^2), \quad i = \text{number of station} \\
 \log(\mu_i) &= \alpha + \beta \cdot \text{year}_i \\
 \alpha &\sim N(0, 0.000001) \\
 \beta &\sim N(0, 0.000001) \\
 \sigma^2 &\sim \text{inv} - \text{gamma}(0.001, 0.001)
 \end{aligned}$$

## 2 Model Checking and Evaluation

### 2.1 Normal Log-linear Regression Model

#### 2.1.1 Model Convergence

I ran the model in JAGS (Plummer 2013) through an R environment (R Core team 2015) using ‘akepa density estimates data provided by Camp et al. (2010). The sampling included 50 000 iterations, with 3 chains, thinning of 5, and a burn-in period of 10 000. I assessed convergence using Gelman’s diagnostics ( $\hat{R}$  and effective size; Gelman & Rubin 1992), trace-plots, and Hellinger distances between the distributions of three chains for each parameter. Hellinger method estimates the distance between two distributions in order to assess similarity (and thus convergence) between two distributions, which can be thought of as chains in the MCMC setting. Once we have a list of Hellinger’s distance for each possible chain combination, we can consider whether these distances are large enough to indicate dissimilarities between chains or not (Boone et al. 2014).

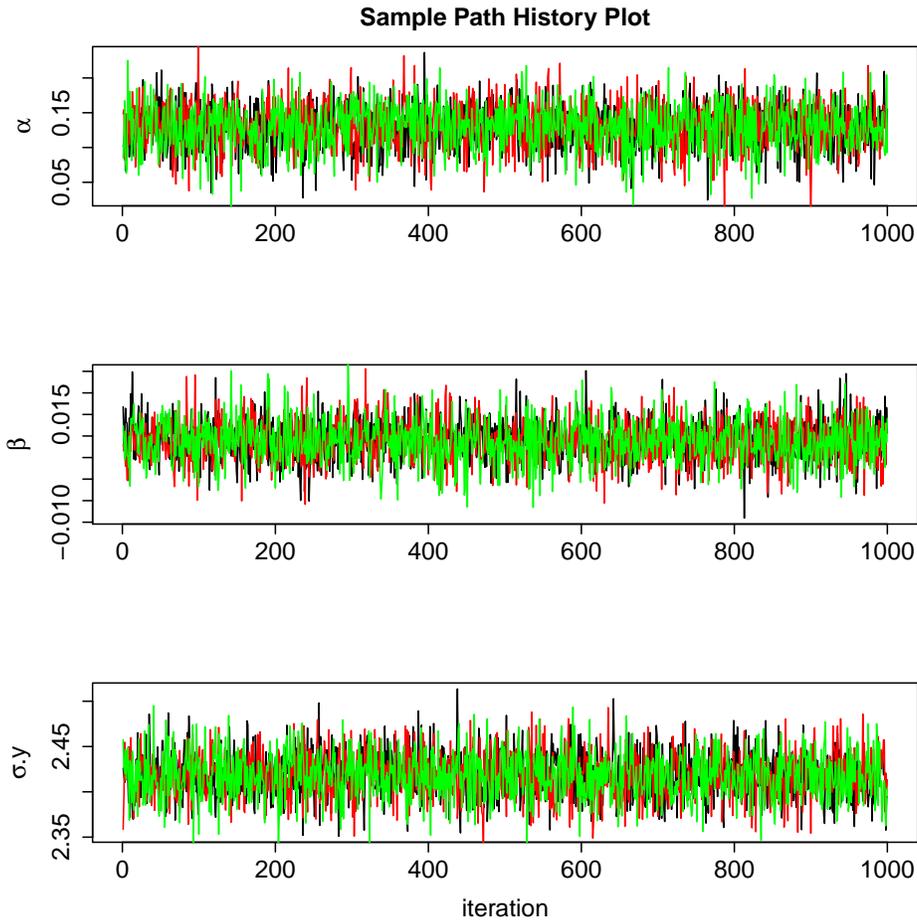
Gelman's diagnostics and traceplots showed no major concerns for model convergence.  $\hat{R}$  values were all equal to 1, and effective sizes were large (Table 1 and 2, and the corresponding figures below). The values for Hellinger distances were small for all, indicating no concerns for convergence.

	R.hat	R.hat.upper.CI	n.eff
alpha	1	1	29860.52
beta	1	1	28882.94
sigma.y	1	1	30000.00

Table 1: Gelman's diagnostics

	chain.1vs2	chain.1vs3	chain.2vs3
alpha	0.02	0.02	0.02
beta	0.02	0.02	0.02
sigma.y	0.02	0.02	0.02

Table 2: Hellinger distances



### 2.1.2 Posterior Predictive Check

The idea of posterior predictive model check is to compare the hypothetical future value of an observation (simulated using Bayesian model) to the actual observed value. The approach is first due to Rubin (1984), using test statistics or other discrepancy measures that summarize departures of the assumed model from the observed data. If the model is correct, the random samples drawn from the posterior predictive distribution of observation should be similar to the observed data (Gelman et al. 2014). In this case, the observation is the estimated density of ‘akepa (denoted as “*density*”). The posterior predictive observations are denoted as “*density<sup>rep</sup>*.”

Posterior predictive check suggested potential violations in model assumptions for Camp et al. (2010). Figure 4 contains a histogram matrix, where the first plot on the first row is the distribution of the estimated population densities for ‘akepa. The estimated population densities for ‘akepa are enlarged and shown in Figure 3. The remaining histograms show the sampling distributions of *density<sup>rep</sup>* of 11 selected iterations. These 11 *density<sup>rep</sup>* histograms all contained negative values, which indicated that a normal log-linear regression model did not model the population density very well, especially when values were close to 0. Figure 5 shows the histogram of proportion of negative densities, and the vertical line at 0 indicates no negative density in the data. All simulated *density<sup>rep</sup>* distributions contained negative values.

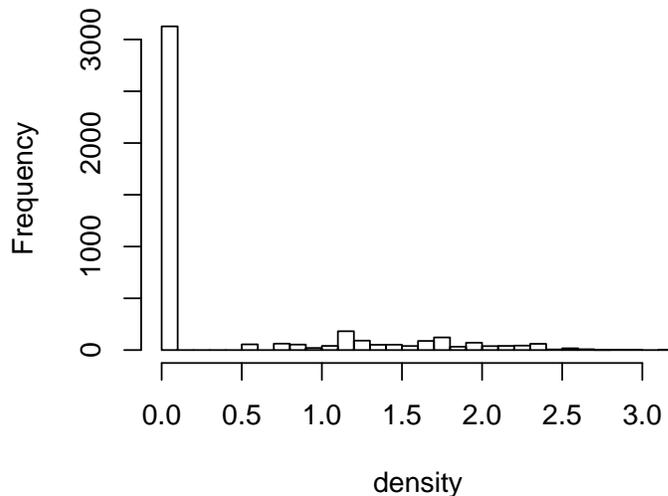


Figure 3: Histogram of the estimated population densities for ‘akepa.

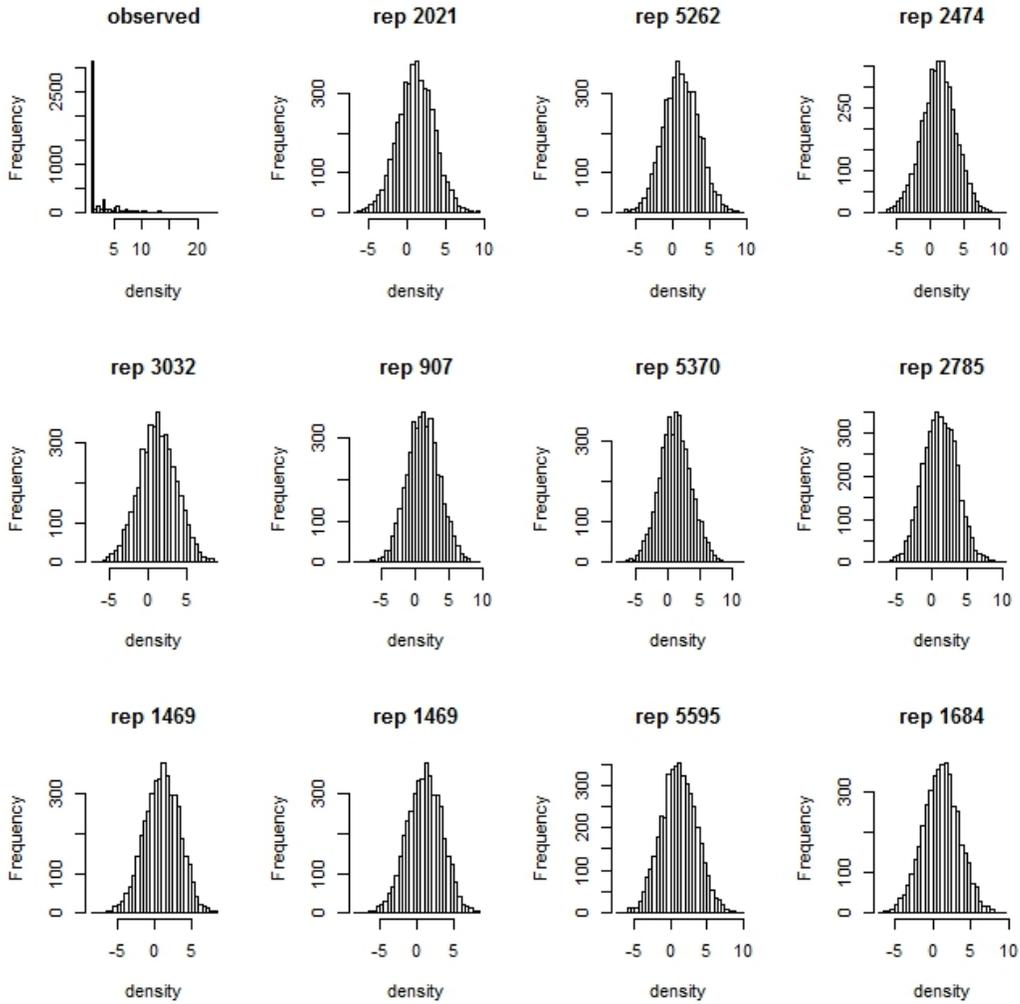


Figure 4: Approximations of posterior predictive distributions for 11 iterations all contain negative density values.

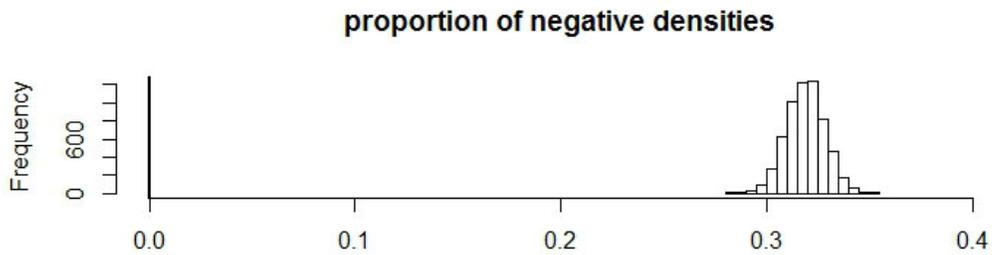


Figure 5: Histogram of the proportion of negative densities within all simulated  $density^{rep}$  distributions.

## 2.2 Hurdle Model

### 2.2.1 Model Fitting

I modified the model from Camp et al. (2010) using a hurdle model. The model consisted of two parts. In the first part, the data were considered as zeros vs. non-zeros, and a binomial model was used to model the probability that a zero value was observed. In the second part, the non-zero densities were modeled with a lognormal model. The support of a lognormal distribution must be greater than zero, so they could not produce zero densities. The response and explanatory variables of the hurdle model remained the same as the log-link normal model from Camp et al. (2010), but I allowed the intercept to vary between years. The hurdle model is described below:

If  $density_i = 0$ ,

$density_i \sim bin(1 - \pi_i)$ , where  $\pi_i$  is the probability of observing  $density_i > 0$ ,

and  $i =$  number of station,

$logit(\pi_i) = \alpha_{year[i]}^1 + \beta^1 \cdot year_i + \epsilon_i$ ,

$\alpha_{year}^1 \sim N(\mu_{\alpha 1}, \sigma_{\alpha 1}^2)$ , for  $year = 1987$  to  $2007$ ,

$\mu_{\alpha 1} \sim N(0, 0.000001)$ ,

$\sigma_{\alpha 1}^2 \sim inv - gamma(0.001, 0.001)$ ,

$\beta^1 \sim N(0, 0.000001)$ ,

$\epsilon_i \sim inv - gamma(0.001, 0.001)$ ,

If  $density_i > 0$ ,

$density_i \sim lognormal(\mu_i \cdot \pi_i, \sigma^2)$ ,  $i =$  number of station,

$\mu_i \cdot \pi_i = \alpha_{year[i]}^2 + \beta^2 \cdot year_i$ ,

$\alpha_{year}^2 \sim N(\mu_{\alpha 2}, \sigma_{\alpha 2}^2)$ , for  $year = 1987$  to  $2007$ ,

$\mu_{\alpha 2} \sim N(0, 0.000001)$ ,

$\sigma_{\alpha 2}^2 \sim inv - gamma(0.001, 0.001)$ ,

$\beta^2 \sim N(0, 0.000001)$ ,

$\sigma^2 \sim inv - gamma(0.001, 0.001)$ ,

I kept the same weakly informative prior distributions as the Camp et al. (2010) model. The sample size was relatively large in this case, and prior information should have little influence on the posterior distribution. I ran the hurdle model using JAGS with 50 000 iterations, 3 chains, thinning of 5, and a burn-in period of 10 000. I assessed convergence using Gelman's diagnostics ( $\hat{R}$  and effective size), traceplots, and Hellinger distances.

With the hurdle model, the median of  $\beta$  was estimated to be -0.007, with 95% Bayesian credible interval = (-0.011, -0.002). The conclusion changed compared to the original results from log-link normal model (median = 0.009, 95% credible interval = (-0.001, 0.018)).

## 2.2.2 Model Evaluations

Gelman’s diagnostics and traceplots showed no major concerns for model convergence.  $\hat{R}$  values were all close to 1, and effective sizes were large. The values for Hellinger distances were small for all, indicating no concerns for convergence. To save space, the results were not shown here.

Figure 6 shows a histogram matrix of observed *density* and  $density^{rep}$  plotted in the same format as the previous model. Figure 7 shows the same as Figure 6 but without the zero density estimates. No negative  $density^{rep}$  was drawn from the posterior predictive distribution of density using hurdle model, indicating a better fit than the normal log-linear model. However, the distribution of  $density^{rep}$  overestimated the zeros in the observed density. Figure 8 shows the histogram of the proportion of zero densities in the sampling distribution of  $density^{rep}$ , and the thick vertical line indicates the proportion of zero densities in the observed data.

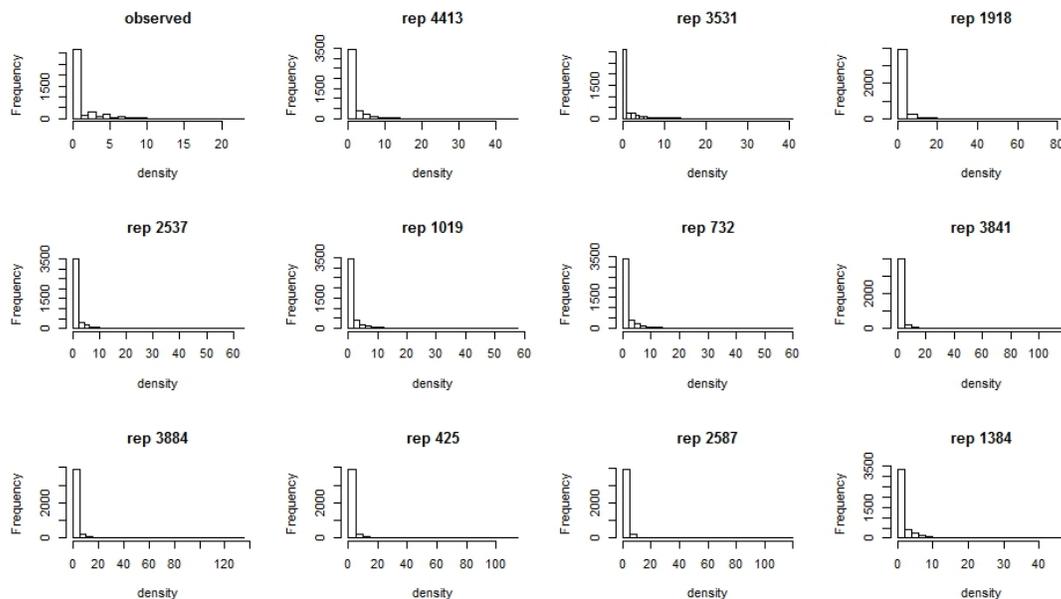


Figure 6: Random drawings from the posterior predictive distributions of hurdle model. The distribution of  $density^{rep}$  seemed more comparable to the observed *density*, indicating better fit than the log-link normal model.

A posterior predictive model check revealed that the distribution of  $density^{rep}$  may have a longer tail than the observed densities. Figure 9 plotted the observed densities on the first left, and 11 randomly selected sampling distributions of  $density^{rep}$ . The random draws from  $density^{rep}$  showed a wider range (longer tails) than the observed densities, suggesting overdispersion in the model.

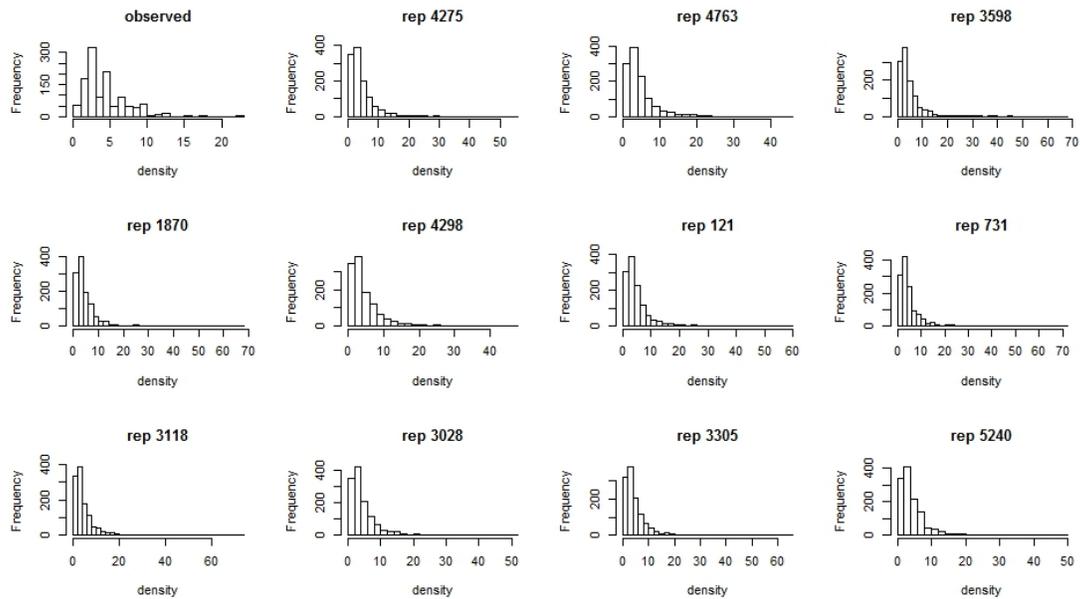


Figure 7: Random drawings from the posterior predictive distributions of hurdle model plotted without zeros.

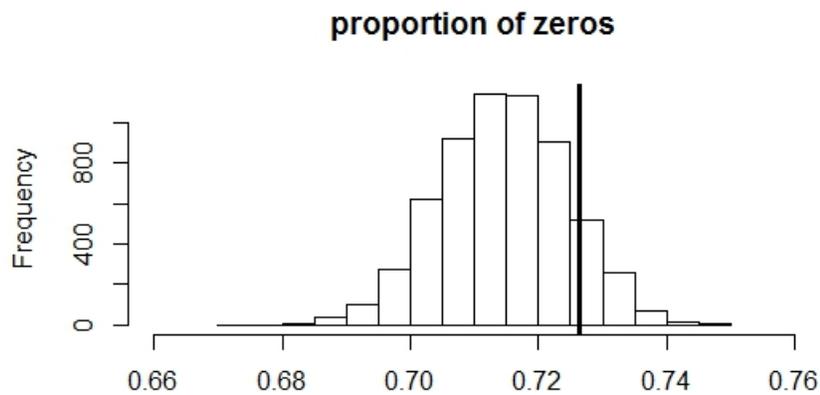


Figure 8: Proportion of zero densities in the random draws of posterior predictive distribution for  $density^{rep}$ . The vertical line represents the observed statistic, and the histogram shows the model overestimated the zeros.

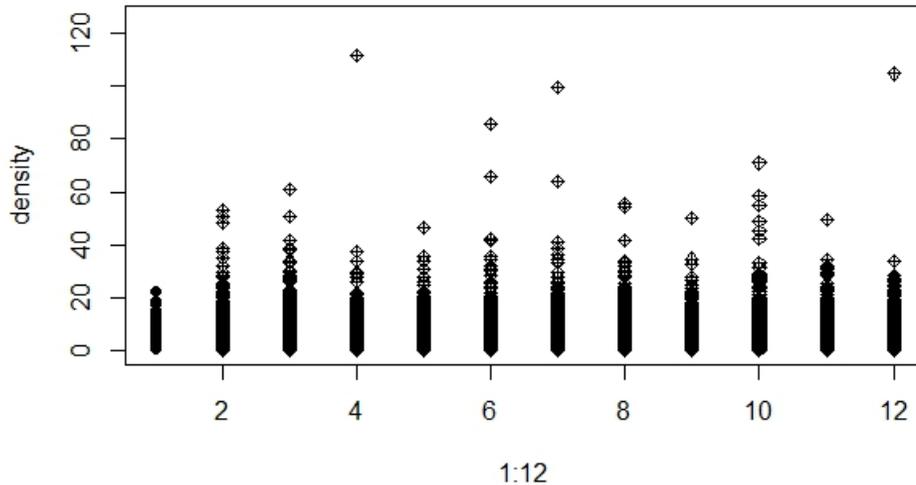


Figure 9: The observed densities are plotted on the first of the left on the plot, and the rest are randomly selected from the simulations of  $density^{rep}$ . The simulated  $density^{rep}$  show a wider range (longer tails) than the observed densities, suggesting overdispersion in the model.

## 2.3 Population Projection

### 2.3.1 Growth Rate

Another way to assess population trend was to evaluate population growth rate ( $\lambda$ ). If we start with  $N$  individuals at time  $t$ , then at time  $t + 1$  the number of individuals is  $N_{t+1} = N_t \cdot \lambda_t$ . I calculated the annual average density, and the growth rate between all 21 consecutive years.  $\lambda_t$  was calculated using:  $\frac{N(t+1)}{N(t)}$ . The result was 20  $\lambda$ 's for discrete time from 1987 to 2006.

For population change in continuous time, we used the equation  $N_{t+1} = N_t \cdot e^r$ , where  $r$  is the instantaneous growth rate. Comparing the above two equations, we see that  $e^r = \lambda$ , and  $r = \ln(\lambda)$ . I fitted a simple linear regression using the  $\ln(\lambda_t)$  as the response and year as the explanatory. I found no relationship between  $\ln(\lambda_t)$  and year; in other words, there was no evidence suggesting that densities change over the years ( $p = 0.93$ , 95% CI = (-0.05, 0.05), Figure 10).

### 2.3.2 Simulations

Using the estimated  $\lambda$ 's, I simulated 50 population growth projections. Starting at the estimated mean density of 1987, I randomly sampled with replacement from the 20  $\lambda$ 's as the intrinsic growth rate for each time step, and projected the density to 2007 (20 years).

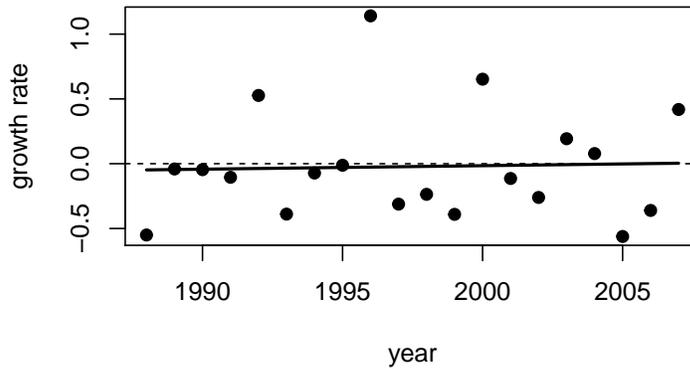


Figure 10: The plot shows the estimated growth rates of average densities for 21 consecutive years. The assumptions for independent and equally weighted observations are not adequately met in this regression analysis, but a flat regression line suggests no evidence of a relationship between growth rate and year. Growth rate below 0 indicates a shrinking population.

The simulations were plotted in Figure 11. Because this represents outcome from a random process, a variety of patterns can manifest in the population trend.

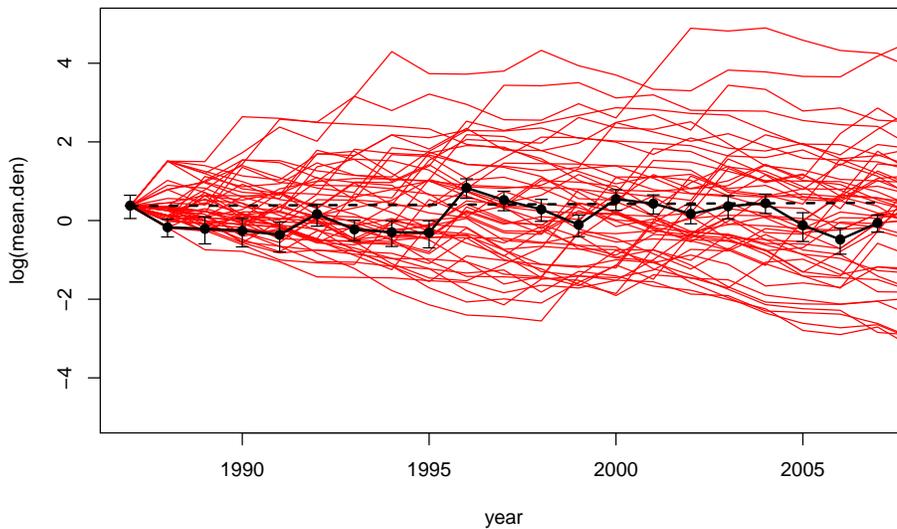


Figure 11: The plot shows the intrinsic population projection using simulation. Each density projection is plotted in a red line. The black dash line represents the slope from the log-normal regression model. The estimated mean density of each year is plotted in black dots connected with a solid black line. I use 10 000 bootstrap simulations to obtain a 95% CI for mean density for each year.

## 2.4 Piecewise

Freed and Cann (2010) did not document the details of their model fitting process. Judging from their plots in the paper, Freed and Cann constructed their models by fitting two separate regression slopes through the estimated mean densities of surveyed year (Figure 12). There was no mention of a transformation of density, so I reproduced their results by fitting a linear regression using density as the response, and two time periods (1987-1999 and 2000-2007) as the explanatory variables. Residual vs. fitted and normal q-q plots showed the constant variance assumption was adequately met, but the normality assumption was violated due to abundant amount of zeros in the density estimates. (Figure 12).

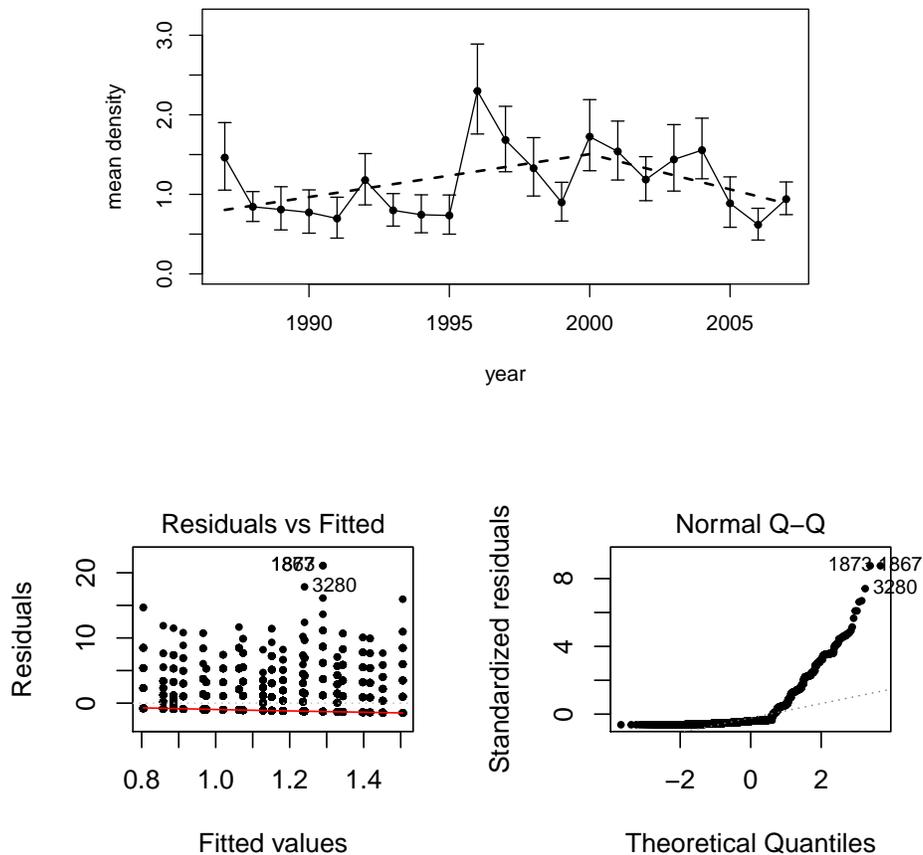


Figure 12: The top plot shows fitted values from piecewise regression with a break at year 14 (dash line). Solid circles connected by continuous line represent estimated mean density of Hawai'i 'akepa over 21 years (1987-2007) in the middle-elevation stratum of Hakalau Forest National Wildlife Refuge. Density data are from Camp et al. (2010). Residual vs. fitted and normal q-q plots show that the constant variance assumption is adequately met, but the normality assumption is not.

Because other models in this report were all fitted using density in log scale, I also reproduced the results from Freed and Cann using a log transformed density ( $\log(\text{density} + 1)$ ), in addition to their original results. The piecewise regression in log scale was shown in Figure 13. Residual vs. fitted plot showed the constant variance assumption was adequately met. However, normal q-q plot still showed clear violations to the normality assumption, even after log transforming the density estimates (Figure 13).

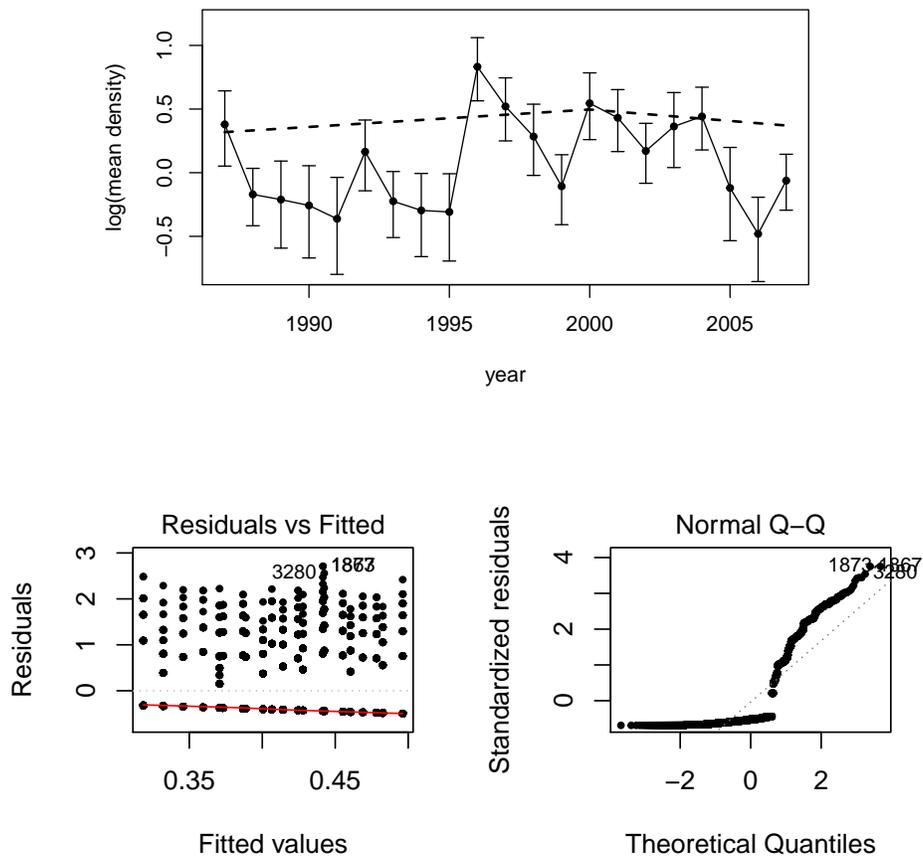


Figure 13: The results of piecewise regression are shown in log scale. Residual vs. fitted indicates no major concerns for violation of the constant variance assumption, but normal q-q plots shows that the normality assumption is not improved after log transforming density estimates.

Instead of requiring a linear form for the population trend (or log trend in a log-normal model), I fitted a generalized additive model (GAM) which allowed shapes ranging from a straight line, through a smoothing function, to unconstrained annual estimates (Fewster et al. 2000). For the GAM, I used  $\log(\text{density} + 1)$  as the response, and year as the explanatory with a smoothing function utilizing thin plate regression spline (Figure 14). I assessed the evidence for change in slope in year 2000 by comparing the smoothed curve fitted by GAM and the two-piece regression line fitted by piecewise regression. The fitted curve using GAM was plotted below.

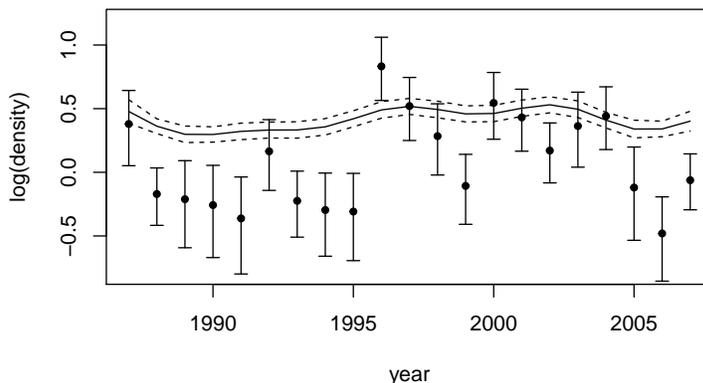


Figure 14: The plot shows estimated log (mean density) of Hawai'i 'akepa in Hakalau from 1987 to 2007, with 95% confidence interval obtained using bootstrap method. The smoothed trend line was obtained by fitting a generalized additive model to  $\log(\text{density})$ . The dashed lines define an approximate 95% confidence envelope around the smoothed curve.

## 3 Discussion

### 3.1 Camp et al. model: Normal log-linear regression

#### 3.1.1 Normal log-linear regression vs. hurdle model

The main concern for the normal log-linear model was that the model assumed a normally distributed 'akepa density. Random draws from the posterior predictive distribution showed negative values for 'akepa density, indicating normal distribution assumption was not reasonable. It was possible that Camp et al. (2010) meant to fit a model with a log transformed response, but somehow a log-link normal model was mistakenly chosen.

Interpretation of results would be straight forward if we fitted the population trend model in log scale, because the model assumed an exponential growth in population. If we plotted

the natural log of population, rather than population in the original scale, the curve in population growth would become a straight line. Log transforming the estimated population density allowed us to estimate population growth over time through a linear relationship. In a continuous time, population at time  $t$  was expressed as  $N(t) = N(0) \cdot e^{rt}$ , where  $r$  was the instantaneous rate of population change. After taking log on both side of the equation, the exponential growth model became a linear regression with slope ( $\beta_1$ ) representing the growth rate ( $r$ ):

$$\ln(N(t)) = \ln(N(0)) + rt \Rightarrow y = \beta_0 + \beta_1 x$$

The estimated population densities of ‘akepa seemed to have a mixture distribution with an inflated amount of zero’s (Figure 3). Camp et al. (2010) have considered fitting a mixture model due to inflated zero density. They found that a mixture model would only make a difference on a large scale sampling frame. In an area such as Hakalua, the sampling frame was small enough that most of the models they fitted across bird species showed results that were consistent with their normal log-linear model (email communication, June 2014). Still, I fitted a hurdle model using data for ‘akepa densities in open-forest. The model fit showed an improvement, and the conclusion changed from positive population trend to negative for ‘akepa, although the change was not drastic.

I modified the normal log-linear model and fitted a hurdle model with log-normal distribution for the non-zero densities, mainly based on the assumption that the population trend follows an exponential growth. The resulting fit was improved, with no negative values in random draws from posterior predictive distribution for ‘akepa density. However, a model check showed that the hurdle model over-predicted ‘akepa densities (Figure 9) and proportion of zeros (Figure 8).

Two suggestions for improving the hurdle model are proposed. First, ‘akepa densities can be converted into actual counts using station areas. A hurdle model with Poisson counts may not have a long-tailed density distribution as in a log-normal distribution. The tail length of a log normal increases with variance, while the tail size of a Poisson distribution does not depend on the variance. Second, a hurdle model does not distinguish between real or fake zeros, thereby possibly causing overestimation of zeros in ‘akepa densities. Including habitat measurements in the model may help in identifying optimal habitats for ‘akepa, and using a mixture model may help distinguish real zero and fake zero detection.

### 3.1.2 Hierarchical level

The bird density at time  $t$  was dependent on the previous population density at time  $t-1$ , and a simple linear regression model would not estimate the correlation between densities in successive years. To properly estimate the variance-covariance, one should fit a hierarchical model allowing both intercepts and slopes for year to vary. However, in this data set, there was only one level in time (year), which only allow the intercepts for time to vary. If we want to vary the slopes for time, we would need to add another level in the time series, such as

sample month. However, logistically it might not be feasible to conduct bird counts multiple times a year.

## 3.2 Freed & Cann model: piecewise regression

### 3.2.1 Model fit

Freed and Cann (2010) fitted a piecewise regression on the population density of ‘akepa in Hakalau. It was not clear from the description of Freed and Cann’s paper, but it seemed to me that they fitted their regression using average density per year as the response. Linear regression, including piecewise, assumed that each observation was equally weighted and independent of each other. Although these were not the case in Freed and Cann’s model, they failed to discuss the limitations of their inference.

I reproduced Freed and Cann’s model using the whole dataset provided by Camp et al. (2010). Although the results were comparable to the results of Free and Cann, it did not serve as a justification for fitting a regression using average densities. I evaluated the model fit using the original data. Normal q-q plots indicated that the model did not adequately meet the normality assumption (Figure 12). Even after log transforming the estimated population densities of ‘akepa, the same assumption was still badly violated (Figure 13).

### 3.2.2 Population growth rate and stochastic process

I fitted a simple linear model to the estimated growth rates of average densities for 21 successive years (section 2.3.1). The growth rates were most likely not independent for the successive years, and the estimated growth rates were not equally weighted due to different amount of observations per year. However, as an exploratory analysis, we can still get a crude assessment on the overall trend for the change of rate in ‘akepa density. The results provided no evidence suggesting a changing trend in growth rate around year 2000. Also, from the results of GAM, there was little evidence suggesting a change in population trend in year 2000. Both assessments provided no support for Freed and Cann’s decision for a year 2000 break point.

Freed and Cann provided ecological evidence (in separate studies) that there was an environmental change in year 2000, which they used as the break point in their population trend piecewise model. They suggested that there was an environmental change that may have had a negative effect on the population trend of ‘akepa. However, from a statistical perspective, choosing a break point at year 2000 seemed arbitrary. As demonstrated earlier, simulations of ‘akepa population density projection over 21 years showed that a variety of patterns can manifest in population trends by random process (section 2.3.2). It can be difficult to tease apart the environmental process and the random process in a population trend.

Still, Freed and Cann’s observations regarding an environmental change could signal a latent effect that has not yet manifested in the ‘akepa population trend. However, using a

population trend model might not be the most convincing approach to show the relationship between environment and population growth. Instead, researchers can model population more directly through vital rates such as survival and fecundity (Caswell 2001). By adjusting vital rates of different age classes through model simulations, researchers can assess sensitivity and elasticity of these vital rates to the population trend. The results will provide quantifiable estimates of environmental effect on the ‘akepa and other native Hawaiian forest bird populations.

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## 5 JAGS Models

```
## JAGS model for Camp et al model
model{
  for(i in 1:N){
    density[i] ~ dnorm (mu[i], tau)
    log(mu[i]) <- alpha + beta * (year[i] - 1997)
  }

  tau ~ dgamma (0.001, 0.001)
  sigma.y <- pow(tau, -0.5)
  alpha ~ dnorm (0, 1e-06)
  beta ~ dnorm (0, 1e-06)
}

## posterior predictive check for Camp et al model
model{
  for(i in 1:N){
    density[i] ~ dnorm (mu[i], tau)
    log(mu[i]) <- alpha + beta * (year[i] - 1997)

    den.rep[i] ~ dnorm (mu.rep[i], tau)
    log(mu.rep[i]) <- alpha + beta * (year[i] - 1997)
  }

  tau ~ dgamma (0.001, 0.001)
  sigma.y <- pow(tau, -0.5)
  alpha ~ dnorm (0, 1e-06)
  beta ~ dnorm (0, 1e-06)
}
```

```

## Hurdle model posterior predictive check
model{
  for( i in 1 : N ) {
    r[i] ~ dbin(p[i],1)
    b[i] ~ dnorm(0.0,tau)
    logit(p[i]) <- alpha1[year[i]] + beta1 * (year[i] - 1997) + b[i]

    density[i] ~ dlnorm (mu[i], tau)
    mu[i] <- (alpha2[year[i]] + beta2 * (year[i] - 1997)) / p[i]

    r.rep[i] ~ dbin(p.rep[i],1)
    b.rep[i] ~ dnorm(0.0,tau)
    logit(p.rep[i]) <- alpha1[year[i]] + beta1 * (year[i] - 1997) + b.rep[i]

    den.rep2[i] ~ dlnorm (mu.rep[i], tau)
    mu.rep[i] <- alpha2[year[i]] + beta2 * (year[i] - 1997)
    den.rep[i] <- den.rep2[i]*r.rep[i]/p.rep[i]
  }

  beta1 ~ dnorm (0, 1e-06)
  beta2 ~ dnorm (0, 1e-06)
  tau ~ dgamma (0.001, 0.001)
  sigma.y <- pow(tau, -0.5)

  for (j in 1987:2007){
    alpha1[j] ~ dnorm (mu.a1, tau.a1)
    alpha2[j] ~ dnorm (mu.a2, tau.a2)
  }
  mu.a1 ~ dnorm (0, 1e-06)
  tau.a1 ~ dgamma (0.001, 0.001)
  sigma.a1 <- pow(tau.a1, -0.5)

  mu.a2 ~ dnorm (0, 1e-06)
  tau.a2 ~ dgamma (0.001, 0.001)
  sigma.a2 <- pow(tau.a2, -0.5)
}

```