Quantifying Hydrologic Constraints

on the Population of Cape Sable Seaside Sparrow

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Running head: Sparrows and water depth in the Everglades marshes

Abstract

In wetlands, hydrology is considered the primary determinant of the abundance and distribution of organisms. However, very few studies have quantified the hydrological effects on population performances. In this study, we used the data of an annual survey of all potential habitats over more than a decade and quantile regression to quantify the limiting effect of water depth on of the Cape Sable seaside sparrow (*Ammodramus maritimus mirabilis*). We focused our evaluation on the two most applicable models. Our analysis showed that the water depth clearly is a constraint on the number of the breeding male sparrows. The effect of water depth on the number of bird count can be described by: count = exp(1.1 – 0.1 * water depth).

Introduction

In wetlands, hydrology is considered the primary determinant of the abundance and distribution of organisms (Mitsch and Gosselink 1993, Sharitz and Batzer 1999, Keddy 2000). Survival and reproductive success of many microbes, animals and plants are sensitive to hydrological conditions. Many studies have documented these hydrological effects. However, most accounts are qualitative, and very few studies have quantified the hydrological effects on population performances.

The Cape Sable seaside sparrow (*Ammodramus maritimus mirabilis*), is a wetland species that responds sensitively to hydrological conditions (Nott et al. 1998). It nests near the ground in seasonally inundated marl prairies. The sparrow is a federally listed endangered subspecies, endemic to the southern Everglades, Florida, USA (Kushlan and Bass 1983, Curnutt et al 1998). Its current distribution lies almost entirely within the federally protected lands of Everglades National Park and Big Cypress National Preserve (Figure 1). Thus, the subspecies is protected from habitat loss and degradation caused by direct human land use and from direct human persecution, such as harvesting and collecting. Despite this level of protection, some local populations of the sparrow have suffered declines and are still facing stress from malpractices of human hydrological controls. For example, extended or reversed flooding has rendered some previously well used breeding habitats unsuitable. Hydrology is a predominant environmental factor that determines both directly and indirectly the habitat suitability for sparrows (Nott et al. 1998, Pimm et al. 2002).

Hydrological harassment is one of the most common anthropogenic impacts on populations and communities of wetlands (Mitsch and Gosselink 1993). In the last century, anthropogenic hydrological alternation has significantly degraded the ecosystem conditions in the Everglades (Davis and Odgen 1994). As a result, many species suffered population declines, including the sparrow. To prevent further ecological degradation and to reverse the undesirable trends, an extensive large plan of ecological restoration is underway in southern Florida (the 106th Congress, 2000). This restoration plan is

currently the most expensive wetland restoration effort in the world and uses hydrological control as a major means to restore the Everglades ecosystems. One objective of the plan is to reverse the declining trend of populations, particularly endangered species. The performance of Cape Sable seaside sparrow is considered a measure or indicator of restoration success. We need to know the quantitative relationship between hydrology and sparrow performance, to project how sparrow populations respond to hydrological restoration options and to guide restoration designs. Such quantitative knowledge is lacking now.

This article reports a study of the Cape Sable seaside sparrow based on an annual survey of all potential habitats over more than a decade. We used quantile regression to quantify the limiting effect of water depth on sparrow density. Quantile regression is a relatively new statistical method that provides biologically meaningful estimates of the limiting effects of environmental factors (Cade et al. 1999, Cade and Noon 2003). This new statistical approach and the large amount of data available allowed us to determine a quantitative relationship presented in the form of specific models. We focused our evaluation on the two alternative models. Both models appeared to be applicable in describing the quantitative relationship, but may have different implications.

Methods

Sparrows and Field Survey

Beginning in 1981, and then continuing from 1992 to 2001, an extensive annual survey of the Cape Sable seaside sparrow was conducted in the breeding season. Point-counts were carried out along a one-kilometer grid in all potentially suitable areas (Figure 1). The number of sites surveyed varied through years, and a total of 1061 sites were visited. A particular care was taken to cover all sites that potentially hold sparrows. The Cape Sable seaside sparrows are found in six local populations (Figure 1). These local populations are separated by unsuitable habitats, such as sloughs and wooded areas (Curnutt et al. 1998). Breeding male sparrows are territorial, defending and feeding in a home range

roughly about 2 ha (Lockwood et al. 2001). The sparrows retain affinity to their natal site. Movement between local populations was infrequent (Dean and Morrison 1998, Lockwood et al. 2001). Thus, local conditions directly determine the selection of breeding sites and nesting success.

The count sites were visited by helicopter. At each site, after the helicopter flew off and the noise subsided, the observer listened, looked, and recorded the number of birds seen, or heard singing, over a seven-minute interval. These bird counts typically took place between sunrise and 10:00am from April to early June. All sites were referenced with latitude/longitude coordinates generated from a Global Positioning System. Water depth was recorded at six points in each site during each survey. Other information was also recorded, such as plant community and percentage of vegetation cover. Curnutt et al. (1998) and Kushlan and Bass (1983) provide a more detailed account of the methods and assumptions of these counts.

More than 10,000 point counts were recorded. In our regression quantile analysis, we excluded count records with missing values and sites where the sparrow was never found. Most of these sites were probably unsuitable habitats. The conditions of some currently unknown, unmeasured environmental variables may have made these sites unsuitable for sparrows. Our analysis used n = 4,615 bird counts.

Regression Quantile Analysis.

1. The models.

The sparrow counts were modeled as an exponential function and as a linear function of water depth:

a) the linear model,

$$\text{count} = \beta_0 + \beta_1 \times \text{water depth} + \varepsilon,$$

and

b) the exponential model,

$$\text{count} = \exp(\beta_0 + \beta_1 \times \text{water depth}) + \varepsilon,$$

where, ε is the random error. Both models have two parameters β_0 and β_1. The unit of water depth is cm and the average depth at six points at each site was used.

2. Regression quantile analysis.

Regression quantile analysis was used to estimate the strength of hydrological constraints with alternative models. Regression quantiles provide a comprehensive description of changes in all portions of the count distribution with respect to an environmental limiting factor and require minimal assumption about the form of error distribution (Cade and Noon 2003). The upper bounds of the response distribution often provide better estimates of the strength of constraint when other unmeasured factors may be limiting in some samples (Cade et al. 1999). Cade et al (1999, in press) and Cade and Noon (2003) provide a detailed description of regression quantile analysis. We estimated the regression quantiles from the minimum ($\tau = 0$) to the maximum ($\tau = 1$) and graphically presented $\tau =$ 0.99, 0.95. 0.90, 0.75 quantiles (Fig 2).

3. Coefficient of determination and $\Delta AIC_c(\tau)$

We used two measures in the model comparison. The first was the coefficient of determination, $R^1(\tau)$, comparable to R^2 in the mean-oriented least squares regression (Koenker and Machado 1999). The second measure is the difference in the Akaike Information Criterion, $\Delta AIC_c(\tau)$. Here, based on Hurvich and Trsai (1990), as modified for any quantile (τ) in Cade (2003):

$$AIC_c(\tau) = 2\, n \times \ln(\, SAF(\tau) / n\,) + 2\, p\, (\, n / (n - p - 1\,)\,),$$

where, n is the sample size, $p = 2$ for both models and is the number of model parameters to be estimated in regression, and $SAF(\tau)$ is the weighted sum of absolute deviations minimized in estimating the τth quantile regression. Both $R^1(\tau)$ and $\Delta AIC_c(\tau)$ were calculated using the simplest model with just an intercept. The details of calculation and justification of $R^1(\tau)$ and $\Delta AIC_c(\tau)$ are described in Cade (2003). We used AIC_c, which won't differ much from AIC because of the large n.

4. We also conducted the conventional mean-oriented regression analysis with SigmaPlot

8.0 (SPSS 2002) for comparison with the quantile regression.

Results

Visual examination of the scatter plot revealed major patterns in the field observations. The visual examination suggested: a) the number of breeding males were highest when the land is dry, high numbers only occur with little or no surface water; b) the high numbers decrease rapidly as the water depth increases; c) the rate of decrease in counts declines and approaches zero with the increasing water depth; d) very few or no sparrows were found when water depths exceeded 20cm; and f) the majority of counts is zero, and the low sparrow counts occurred across all water depth (Figure 2). These observations indicated: 1) water depth was a constraint on the potential number of breeding male sparrows, and these birds prefer little or no surface water; 2) the decline of bird counts with respect to water depth is nonlinear (exponential) rather than linear; and 3) the variation in bird counts is greatest with shallow water and least with deep water.

The regression quantile analyses provided statistical support for these three propositions. First, the upper quantiles (τ >0.65) of both linear and exponential models had negative slopes (Figure 2), demonstrating that the breeding male sparrows stayed away from deep water.

Second, the rapid decline in counts with little surface water and the decreasing negative rates of decline in counts with increasing water depths were captured well by the nonlinear model (Figure 2). The use of exponential model rather than the linear model was supported by both model selection criteria, $R^1(\tau)$ and $\Delta AIC_c(\tau)$ (Figure 3). The steep slope in the exponential regression curve suggested that the sparrow is sensitive to the presence of surface water and depth increase. This response by sparrow was much more sensitive than indicated by the average slope.

Third, the quantiles of both linear and exponential models showed that the differences among quantile regression curves were larger for shallow water and decreased with

increasing water depth. Higher quantiles had steeper regression slopes of bird response to water depth (Figure 2). Note that upper quantiles best describe the environmental constraints, when it is reasonable to assume that all other important, unmeasured factors could only reduce the demographic performance and lead to a hidden bias in estimation of response (Cade et al. 1999). Lower quantiles, including the central portion (median or mean), depict the reduced rates of response due to the confounding with unmeasured factors. The steep slope of higher quantiles suggested that the sparrows responded to water depth much more sensitively than the central tendency would suggest.

It is interesting to point out the influence of zero counts on our regression analysis. First, the regressions of quantiles <0.65 all had zero slope and zero intercept, for both linear and exponential models. Second, the mean-oriented regressions produced very flat slopes and low intercepts in regression curves for both linear and exponential models. If we had relied on these mean regression models we might have concluded that sparrows were insensitive to water depth. Table 1 shows the parameter estimates from both quantile regression and mean-oriented regression for both linear and exponential models. Large differences can be seen between estimates from quantile regression and mean-oriented regression. Conventional mean regressions have generated a misleading indication of the effect of water depth. The true influence of water depth has been diluted by the influence of unmeasured variables, and this led to an underestimate of hydrological effect in the mean regression model. Note that conventional mean regressions assumed normal distribution and constant variance of the errors. The normality tests and constant variance tests all failed ($P<0.0001$) for both linear and exponential models in mean-oriented regressions. The heteroscedasticity and the violation of normal assumption further add more biases in parameter estimation and ambiguity in statistical interpretation. Figure 4 shows that the estimates for parameter β_1 changed with quantiles, consistent with decreasing heteroscedasticity associated with increasing water depth.

Excluding zeros is a common practice when using the conventional mean-oriented regression to analyze the data set that contains many zeros. We excluded zeros and

conducted mean-oriented regressions. Again, the resultant regression curves were flat and the slope of regression curves was much underestimated. Large biases appeared to occur in parameter estimation. According to these regression curves, bird counts would not change sensitively as water depth increases in the habitats with no or little surface water. In addition, sparrows might have stayed in the habitats with high water, in strong contrast of field observations. Apparently, the conventional mean-oriented regression failed to reveal the hydrological effects due to the preponderance of zero counts. Nevertheless, a large amount of zero does imply that sparrows may not respond to favorable hydrological changes when other factors are limiting.

In short, if other conditions were favorable, water depth alone constrained the number of male sparrows at a breeding site. Bird numbers likely responded to the depth of surface water in a nonlinear fashion, where negative influence of increasing water depth occurred most for slight depth increases from no surface water.

Discussion

The hydrological constraint has been widely considered as the most important abiotic environmental factor in wetland ecosystems (Mitsch and Gosselink 1993, Sharitz and Batzer 1999, Keddy 2000). Nevertheless, quantitative descriptions of hydrological constraints are rare and are much desirable and needed. This study quantitatively demonstrated the hydrological constraint on the Cape Sable seaside sparrow, using a large amount of data and a relatively new statistical technique. We focused on evaluating two competing models. We found that the sparrow responded to water depth very sensitively and the exponential model best represents the sensitive response.

We used the regression quantiles to quantify the hydrological constraint. We demonstrated that the upper quantiles can depict the constraint better than the conventional central-tendency oriented statistics for both biological and statistical reasons. Central-tendency oriented statistics either missed the limiting relationship or drastically underestimated the hydrological constraint. The preponderance of zeros is

much responsible for the great difficulties in the application of conventional central-tendency oriented regression. The central-tendency oriented statistics excluding zero counts often overestimate bird numbers and underestimate the severity of hydrological constraint of low water level. The quantile regression technique may apply to many similar datasets, which did not display clear hydrological constraints with conventional statistical analyses. The large amount of zero counts and the divergent quantile regression curves indicated that other unmeasured habitat conditions may be actively limiting the sparrows to reach their abundance potential that was solely set by water depth and the territoriality of sparrows. Thus, we need to identify the important unmeasured limiting factors to protect the birds.

What are the most important unmeasured limiting factors? Two kinds of candidates deserve further investigation: 1. hydrological conditions that were not measured by snapshot field survey and 2. non-hydrological variables. Among unmeasured hydrological conditions, hydrological history and ground water level appeared to be important. Ecological systems often experience historical memories (Peterson 2003), and hydrological memories may register in sparrow individuals and populations. The sparrows may choose not to stay in a site or may have not visit the site lately, simply because the water was deep sometime ago. This is the ghost of the past, in terms of either local hydrological conditions not long ago or the regional hydrological conditions in one or a few previous breeding seasons. Note that water recession rate is usually low in natural situations. Human controls have created excessively fast recession and ascension rates in southern Everglades and may have extended the importance of the historical effects. Ground water level also may affect the occurrences of sparrows. In this study, we only measured surface water and not ground water. Our models suggest that dry ground is preferred by the sparrows. However, our model can not be interpreted simply as drier is better for sparrows. Our data showed that a large number of dry sites was not occupied by sparrows. Low ground water, particularly low water table for a long term, may deteriorate the habitats and render the habitats unsuitable (Curnutt et al. 1998, Nott et al. 1998). If the range of water depth had been expanded into negative values to include ground water level measurements, our monotonous curve probably could not be

extrapolated much into the low water side and a hump-shaped curve may better depict the relationship.

Hydrological history and ground water level in long term may bring up many indirect influences. For example, vegetation structures and fire frequencies clearly affect the numbers of birds (Curnutt et al. 1998, Nott et al. 1998). Further, the indirect hydrological damages via vegetation changes and fires extend much longer than the duration of damaging hydrological episodes (Nott et al. 1998, Jenkins et al. 2003). Thus, the sparrows fail to show at some sites with apparently suitable hydrological conditions.

The regressions with all quantiles quantitatively describe the population response to hydrology in terms of probability distribution. Quantitatively accurate description of species response to hydrology can contribute our general understanding of populations, communities, and ecosystem processes. In particular, the protection of Cap Sable seaside sparrow is a legal responsibility in USA. How to improve the status of Cap Sable seaside sparrow under our current comprehensive ecological restoration plan is an imminent task. Because of the intricate balance of seemingly conflicting hydrological demands of many species, we need quantitatively most accurate models to identify the optimal plans. The quantitative description of hydrological constraints is much needed in our construction of predictive ecological models. Thus, model selection is inevitable. Using models based on AIC can reduce uncertainty cause by model structural biases and should be considered in statistical modeling. We hope this study provide a much needed description and our development of predictive ecological models will contribute much to restoration design.

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Table 1. Parameter estimates of different models from regression analyses

Model	Parameter	0.95 quantile estimates	Mean-oriented regression with 0s	Mean-oriented regression without 0s
Exponential	β_0	1.10	–0.29	0.70
	β_1	–0.10	–0.24	–0.049
Linear	β_0	3.0	0.72	2.02
	β_1	–0.097	–0.046	–0.074

Linear model : $y = \beta_0 + \beta_1 x$; Exponential model: $y = \exp(\beta_0 + \beta_1 x)$. Note that, for the exponential model, the intercept is $\exp(\beta_0)$, which is extremely close to the intercept of linear model, for each regression method respectively. The curve slope of 0.95 quantile regression is steeper than that of conventional mean regression without records of 0 bird counts, which is steeper than the curve slope of the conventional mean regression with records of 0 bird counts, when water is shallow (< 21cm). When water depth >21cm, the slope of regression curves are very flat.

Figure 1. The distribution of the Cape Sable seaside sparrow and the survey sites. Circles are the sites surveyed. Crosses are the sites where the sparrow has been found at least once in our survey. The dotted line is the boundary of the Everglades National Park.

Figure 2. The sparrow count and water depth: data points and models. a. The 0.99, 0.95, 0.90, 0.80, and 0.70 quantile regressions with the exponential model, count = $e^{\beta 0 + \beta_1 * \text{water depth}}$. b. The 0.99, 0.95, 0.90, and 0.80 quantile regressions with linear model, count = $\beta_0 + \beta_1$* water depth. Sample size, n = 4,615.

Figure 3. The Coefficient of determination, $R^1(\tau)$, and $\Delta AIC_c(\tau)$. The $\Delta AIC_c(\tau)$ is scaled to show the net improvement from the simplest model, therefore, larger differences are for better models. Consistently, the exponential model performed better than the linear model, among all quantiles and for both criteria.

Figure 4. The parameter estimates with different quantiles for the model y = exp($\beta_0 + \beta_1$* water depth).

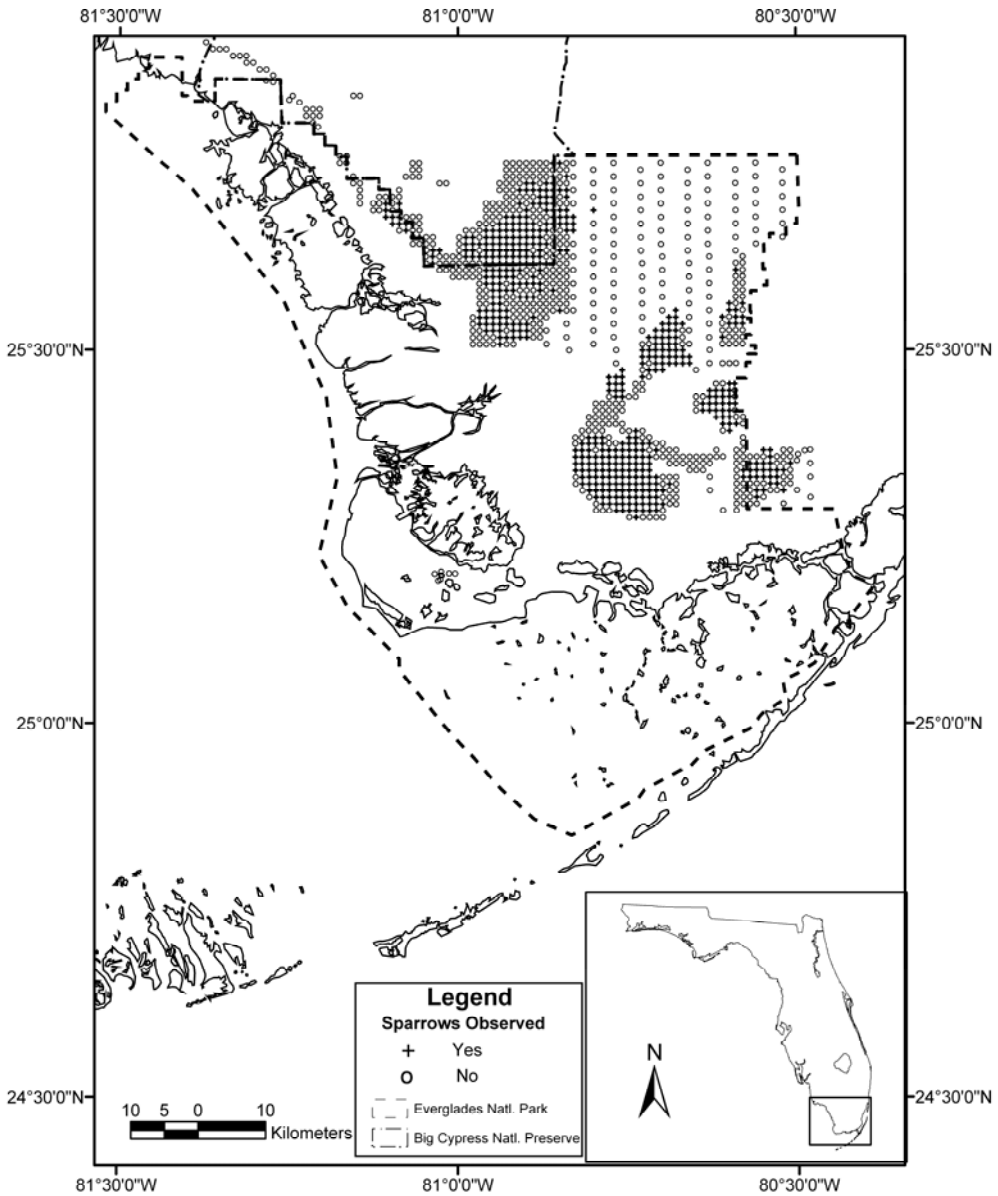

81°30'0"W
81°0'0"W
80°30'0"W
25°30'0"N
25°0'0"N
24°30'0"N
Legend
Sparrows Observed
+ Yes
o No
Everglades Natl. Park
Big Cypress Natl. Preserve
10 5 0 10
Kilometers
N

Figure 1.

Figure 2.

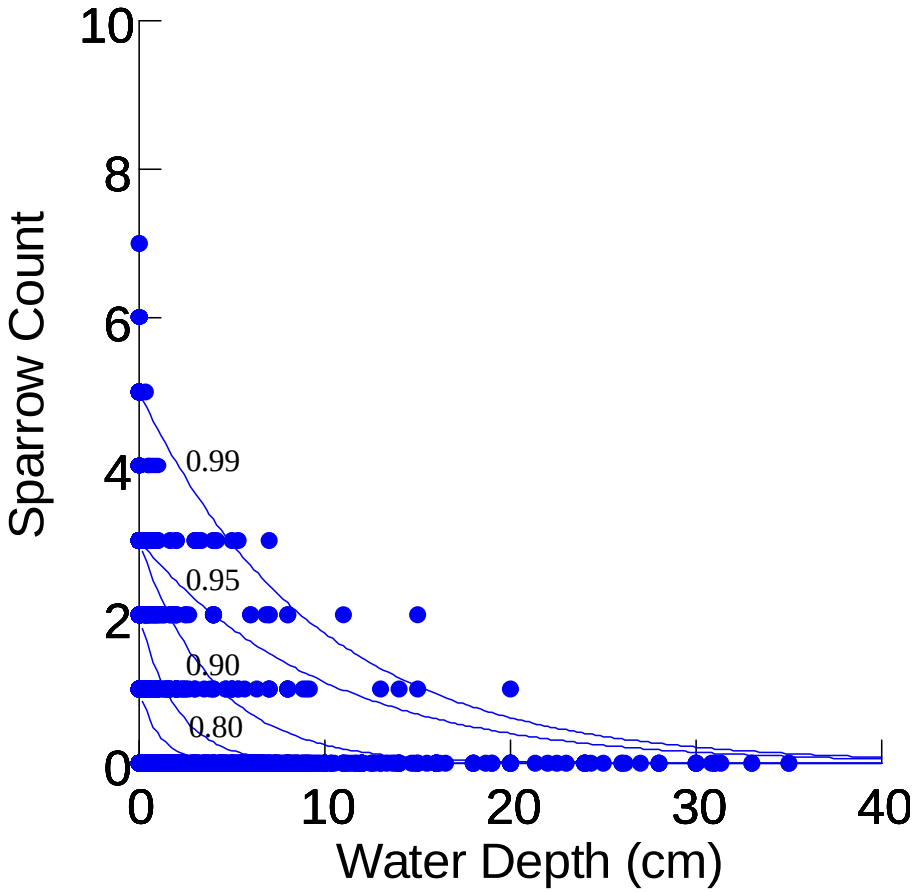
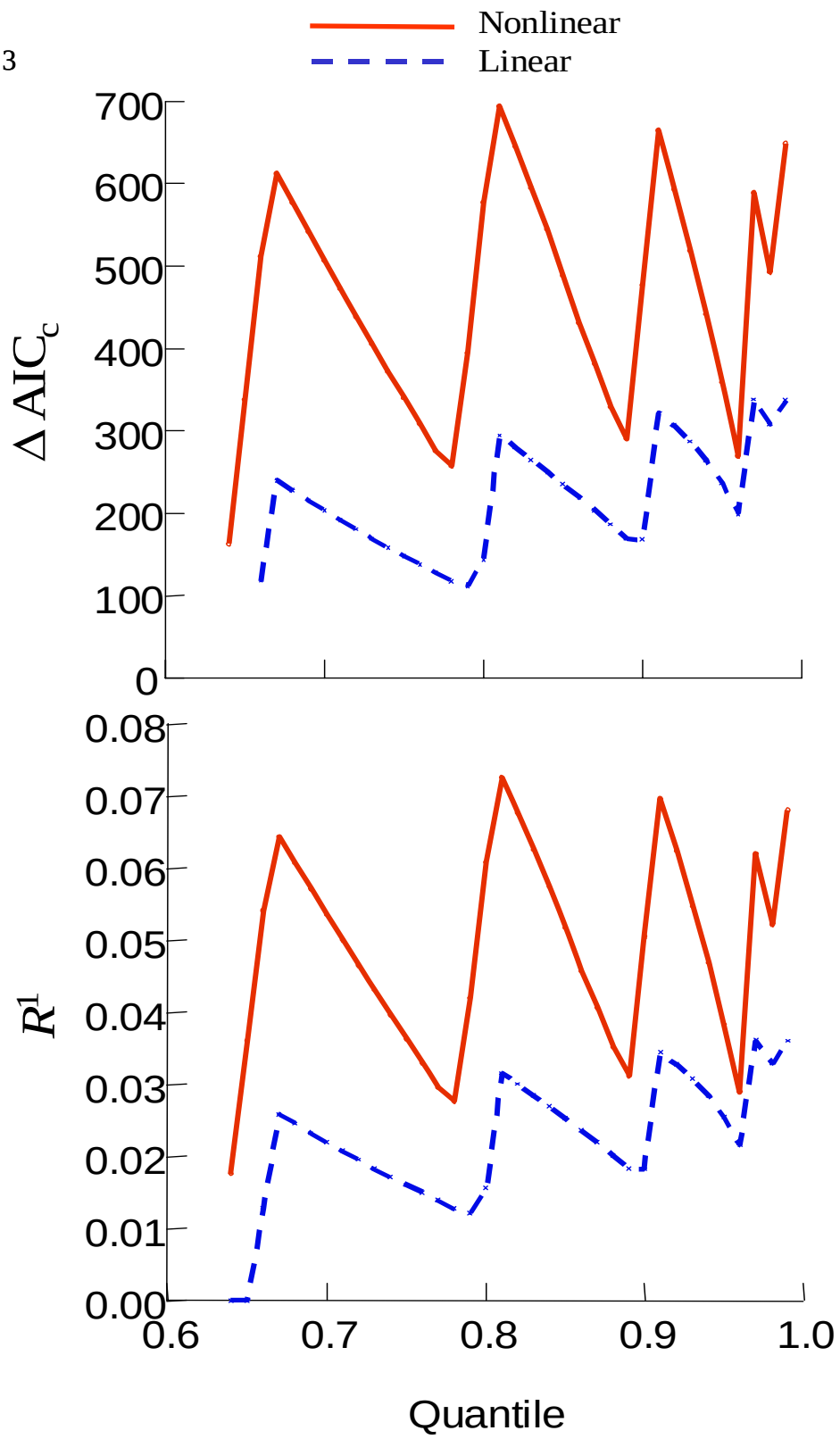

10
8
6
4
2
0
Sparrow Count
0.99
0.95
0.90
0.80
0
10
20
30
40
Water Depth (cm)

Figure 3


Nonlinear
Linear
700
600
500
400
300
200
100
0
Δ AIC$_c$
0.08
0.07
0.06
0.05
0.04
0.03
0.02
0.01
0.00
R^1
0.6
0.7
0.8
0.9
1.0
Quantile

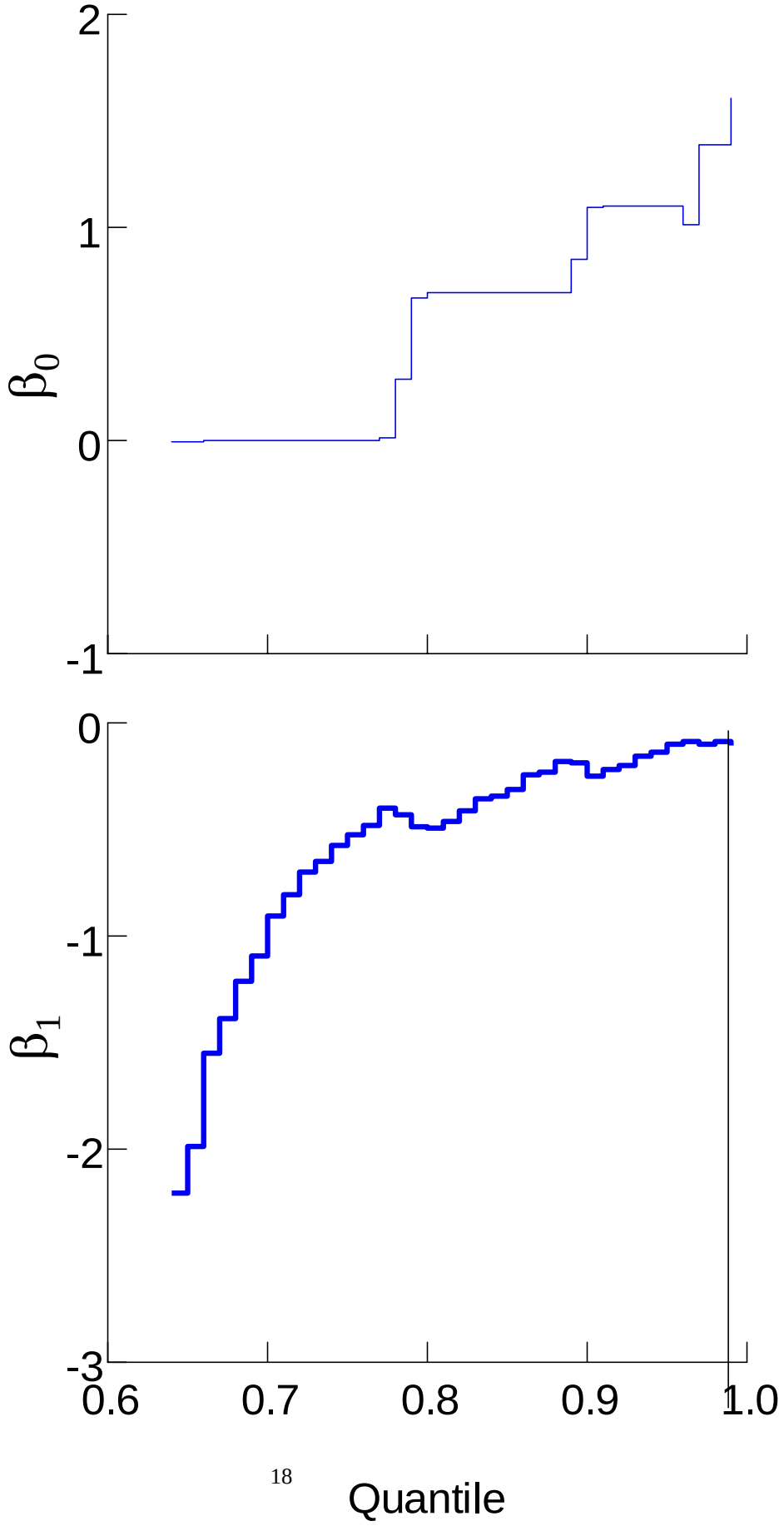



Figure 4.