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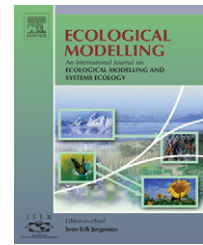
Monitoring waterbird abundance in wetlands: The importance of controlling results for variation in water depth

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ABSTRACT

Wetland use by waterbirds is highly dependent on water depth, and depth requirements generally vary among species. Furthermore, water depth within wetlands often varies greatly over time due to unpredictable hydrological events, making comparisons of waterbird abundance among wetlands difficult as effects of habitat variables and water depth are confounded. Species-specific relationships between bird abundance and water depth necessarily are non-linear; thus, we developed a methodology to correct waterbird abundance for variation in water depth, based on the non-parametric regression of these two variables. Accordingly, we used the difference between observed and predicted abundances from non-parametric regression (analogous to parametric residuals) as an estimate of bird abundance at equivalent water depths. We scaled this difference to levels of observed and predicted abundances using the formula: ((observed − predicted abundance)/(observed + predicted abundance)) × 100. This estimate also corresponds to the observed:predicted abundance ratio, which allows easy interpretation of results. We illustrated this methodology using two hypothetical species that differed in water depth and wetland preferences. Comparisons of wetlands, using both observed and relative corrected abundances, indicated that relative corrected abundance adequately separates the effect of water depth from the effect of wetlands.

1. Introduction

Waterbirds comprise a large group of species including anseriformes, charadriiformes, ciconiiformes, gaviiformes, gruiformes, pelecaniformes, podicipediformes, and procellariiformes. These species display a variety of adaptations for exploiting wetland habitats. In non-diving waterbirds, variation in morphological features, such as bill length and shape, bill lamellae distance, neck length, leg length, and body size, allow species to forage at different depths and on different foods (Baker, 1979; Pöysä, 1983; Nudds and

Bowlby, 1984; Zwarts and Wanink, 1984). Accordingly, water depth is paramount in explaining waterbird density, and determining whether or not habitat is available; waterbird diversity generally is highest at low water depth and correlated to hydrological diversity (Powell, 1987; Taft et al., 2002; Bolduc and Afton, 2004a; Kingsford et al., 2004; Robertson and Massenbauer, 2005; Holm and Clausen, 2006).

Thus, it is reasonable to assume that waterbird communities differ among areas showing different hydrological regimes at a given time. Such differences ultimately describe the confounded effects of resource availability (via water depth) and

resource abundance, and one cannot ascertain the extent to which of the two factors affect the observed bird abundance. Indeed, several researchers have compared bird abundances among wetlands, while admitting a confounding effect of the variation in water depth on wetland comparisons, but did not include water depth in their predictive models (Hands et al., 1991; Frederick and McGehee, 1994). If water regimes are fairly predictable, as for tidal wetlands, comparing these communities can be straightforward. However, there often is a large variation in wetland hydrology among consecutive days, months or years (Mitsch and Gosselink, 1993; Bolduc and Afton, 2004b), which precludes generalizing on the short-time water depth of a given wetland, unless one examines the long-term wetland hydroperiod (defining the seasonal pattern of water levels in a given wetland type and the vegetation that developed therein). Ecological studies generally are conducted over a few consecutive years at best and use sampling techniques to optimize efforts in the field. Consequently, such studies necessarily are susceptible to unpredictable short-term events, such as sudden hydrological events in wetlands, which cause problems for census (e.g., Warnock et al., 1998). Accordingly, water depth and wetland type effects need to be controlled for and estimated separately in analyses with objectives of providing unbiased conclusions on how these habitats provide resources preferred by waterbirds.

As noted above, the general biological relationship between water depth and waterbird abundance is clear; however, its mathematical functions have not been explored thoroughly. Researchers who have examined the influence of water depth on the abundance of non-diving waterbirds generally report the average water depth used by each species (Weber and Haig, 1996; Safran et al., 1997; Isola et al., 2000) or the range of water depths used (Davis and Smith, 1998; Ntiamoa-Baidu et al., 1998). The relationships of water depth and several biotic components of wetlands previously have been analyzed in several ways. For example, variation in bird abundance and water depth sometimes are analyzed separately and their relationship discussed afterward (e.g., Connor and Gabor, 2006). Also, water depth may be transformed into categories (ranges) and the latter compared (Hoover, 2006). When possible, an experimental setup can be used with the study's subjects enclosed at specific water depths (Angeler et al., 2005). Wetlands also can be divided in cells where water depth is manipulated (Murkin et al., 2000), or water depth can be manipulated in laboratory experiments (Miller and Zedler, 2003). Often, water depth is considered as a separate environmental factor and incorporated in multivariate models to predict effects on biotic components (Bolduc and Afton, 2004a; Özesmi et al., 2006; Vincent et al., 2006). Finally, univariate models of the effect of water depth on bird abundance have been explored using linear, exponential, quadratic and S-shaped models (Bancroft et al., 2002; Boertmann and Riget, 2006; DesGranges et al., 2006).

Some researchers have reported negative correlations between water depth and bird abundance (Epstein and Joyner, 1988; Colwell and Taft, 2000), even though the end result of this is biologically unrealistic because it implies that maximum waterbird abundance is found where water depth is zero. In general, there should be a water depth that maximizes resource exploitation, and consequently bird abundance, and a range of water depths that a species uses, which depend

on the interaction among feeding strategy, morphological features and resource abundance at various water depth. Quadratic models generally follow the above pattern, but there are no bases for a parametric function between bird abundance and water depth. Although useful to identify the cutoff point where the relationship between bird abundance and water depth changes rapidly, the S-shaped model of Boertmann and Riget (2006) is relevant to local conditions only.

In this paper, we argue that the relationship between water depth and bird abundance is non-linear in most non-diving waterbird species, with low abundance at water depth 0 (except for shorebirds), followed by an increase afterward until a maximum is reached, and then a decrease to abundance 0 when water depth is too deep for a species to forage. Moreover, the mathematical functions of such relationships are unknown, and probably vary among species. We therefore suggest that non-parametric regression be used for modeling relationships between species-specific waterbird abundance and water depth.

Developments in non-linear modeling (Cleveland et al., 1988) and its integration in statistical software facilitate examinations of the relationship between water depth and waterbird abundance. Curve-fitting techniques using non-parametric smoothing (locally weighted regression, LOESS) also can be integrated into parametric analysis using generalized additive models (Hastie and Tibshirani, 1990). Here, we use non-parametric regressions to estimate bird abundance in relation to water depth. We compute differences between observed abundances and those predicted by the non-parametric regression at recorded water depths (analogous to residuals in parametric models) for two hypothetical species. We subsequently compare four hypothetical wetlands, using both observed and corrected abundances within an analysis of variance, to illustrate differences between these two estimates. Finally, we discuss the pros and cons of our method and alternatives, and provide an Appendix A with instructions for use of our method by field biologists.

2. Methods

2.1. Modeling abundance of hypothetical species

To illustrate our methodology, we created hypothetical survey data for two waterbird species that differed in their water depth and wetland selection. Species G (i.e., a generalist species) uses a large range of water depths and its abundance is maximized at a water depth of 15 cm. Species S (i.e., a specialist species) uses a narrow range of water depths and its abundance is maximized at a water depth of 5 cm. We built a curve of maximum abundance by 1-cm water depth classes for depths between 0 and 40 cm for each species, to compute hypothetical bird counts using the following equations:

for G species in water depths $0 - 15$ cm, $\quad MAX = \log(WD)$,

for G species in water depths $16 - 40$ cm,

$MAX = \log(PWD - [\log(PWD)])$,

for S species in water depths $0 - 5$ cm, $\quad MAX = (WD)^3$,

for S species in water depths $6 - 40$ cm, $\quad MAX = ((PWD) - 0.2)^3$,