

## A Structural Equation Model for Physiochemical Variables of Water, Benthic Invertebrates, and Feeding Activity of Waterbirds in the Sitsao Wetlands of Southern Taiwan

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**Shih-Hsiung Liang, Bao-Sen Shieh and Yaw-Syan Fu (2002)** A structural equation model for physiochemical variables of water, benthic invertebrates, and feeding activity of waterbirds in the Sitsao wetlands of southern Taiwan. *Zoological Studies* 41(4): 441-451. We used structural equation modeling to explore the relationships between benthic invertebrates and physiochemical variables of water, and investigated their direct and indirect effects on waterbird feeding activities. Sixteen sites located in the Sitsao wetlands of southern Taiwan were sampled on a monthly basis from Sept. 1997 to Aug. 1998. Factor analysis identified 1 factor for physiochemical variables and 2 factors for benthic invertebrates. We classified waterbirds into 10 feeding groups, and factor analysis of the feeding activities of these groups suggested 3 feeding factors. Therefore, we used 6 factors to construct an initial model examining their causal relationships to each other and then modified the models to obtain more significant paths. Results indicate that water depth affected all 3 waterbird feeding factors, and salinity influenced only the small-invertebrate factor, which in turn directly affected the surface-feeding factor. Daily lowest water temperature affected only the wading-feeding factor in the final model. To further examine the final structural model, we used repeated measures ANOVA to analyze temporal variations in variables among the 4 types of wetlands: unused salt fields, abandoned fish ponds, active fish ponds, and mangroves. Three related variables (salinity, the small-invertebrate factor, and the surface-feeding factor) varied significantly among wetland types, although the differences did not significantly change from month to month. We conclude that the results of structural equation modeling combined with repeated measures ANOVA provide important information that can be useful in managing the Sitsao wetlands for different feeding groups of waterbirds. <http://www.sinica.edu.tw/zool/zoolstud/41.4/441.pdf>

**Key words:** Structural equation model, Water depth, Benthic invertebrates, Feeding activity, Waterbirds.

Wetlands are essential habitats for waterbirds. Waterbirds acquire important nutrients by feeding on benthic macroinvertebrates, the availability of which is influenced by physiochemical variables such as water depth and water chemistry. Benthic invertebrates have been found to be the primary foods of waterbirds (Reeder 1951, Rundle 1982), and these invertebrates have also been found to strongly influence the distribution (Colwell and Landrum 1993) and feeding behavior of waterbirds (Murkin and Kadlec 1986). Waterbirds have been reported to reduce the density of benthic

invertebrates (Mercier and McNeil 1994) and to select habitats with higher densities of benthic invertebrates (Safran et al. 1997).

The physiochemical environment can also directly and indirectly affect waterbird feeding. In a direct way, for example, different species of shorebird are constrained morphologically to forage at specific water depths (Safran et al. 1997, Isola et al. 2000). Indirectly, however, physiochemical variables such as salinity and acidity affect the distribution and richness of benthic invertebrates (Courtney and Clements 1998,

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Leland and Fend 1998, McRae et al. 1998), which in turn can affect the feeding ecology of waterbirds.

Although relationships between invertebrate density and waterbird feeding, between physiochemical variables and waterbird feeding, and between physiochemical variables and benthic invertebrates have been investigated, few studies have simultaneously addressed relationships among these ecologically interwoven variables. Structural equation modeling (SEM), an extension of path analysis, has been used to specify causal relationships among a number of observed variables, making such a study possible. For example, Wissinger et al. (1999) used SEM to explore the relationships among pond morphometry, water quality, water depth, and salamander populations, and to investigate their direct and indirect effects on invertebrate communities. Similarly, we investigated relationships among waterbird feeding activities, benthic invertebrates, and physiochemical variables of water in the Sitsao wetlands of southern Taiwan. First, we classified waterbirds into 10 feeding groups. We then used SEM to explore the relationships between physiochemical variables of the water and benthic invertebrates, and investigated their direct and indirect effects on the feeding activities of these 10 waterbird groups. To further

analyze the final structural model, we examined temporal variations in the variables shown in the final model among various wetland types.

## MATERIALS AND METHODS

### Study site

We conducted this study in the Sitsao wetlands of southern Taiwan (Fig. 1), a 515-ha wetland complex that was first protected as a wildlife refuge in 1994. The area contains active fish ponds, abandoned fish ponds, unused salt fields, and mangroves. In this area, more than 183 bird species, including 160 migratory species, have been recorded, the majority being sandpipers, plovers, herons, and terns (Shuei and Hwang 1997). Sightings of 3 endangered species, the Black-faced Spoonbill (*Platalea minor*), white Spoonbill (*Platalea leucorodia*), and white Stork (*Ciconia ciconia*) have been reported in this wetland area.

### Sampling plan

We sampled 16 sites, including 8 unused salt field sites, two mangrove sites, four active fish

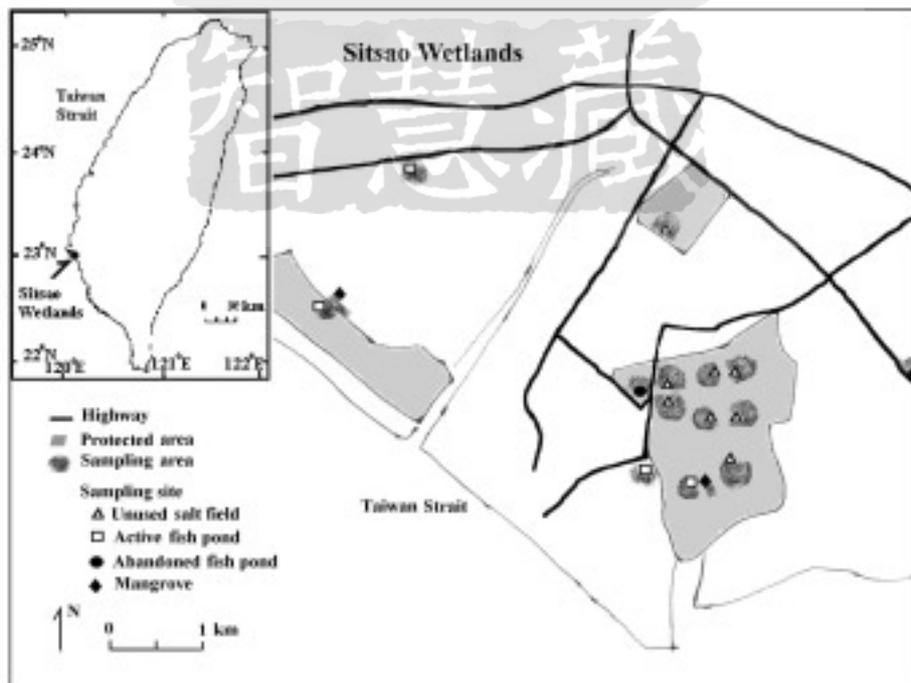


Fig. 1. Location of sampling sites in the Sitsao wetlands of southern Taiwan.

pond sites, and 2 abandoned fish pond sites (Fig. 1), monthly from Sept. 1997 to Aug. 1998. Each sampling period lasted 2 to 3 d. We observed waterbirds twice at each site in each sampling period (once in the morning during 06:30-10:30 h and once in the afternoon during 14:00-18:00 h). Instantaneous scan sampling (Martin and Bateson 1986) was used to record bird species, the number of individual birds, and their behavior (feeding or non-feeding). For every site, we also measured 3 subsamples of water depths and recorded pH (Hanna pH meter), salinity (0‰-100‰) and density (1.00-1.07) (Nippon Optical Work) once at fixed locations (water areas about 1 arm-length from land) in each sampling period. Thermometers were placed at each site for 24 h to record the daily lowest and highest water temperatures. We used acrylic tubes, 15 cm in diameter and 30 cm long, to sample underwater sediments and collected benthic invertebrates which were extracted by washing the sediments with water through 2 metallic screens, one with a mesh size of 0.5 mm and the other 1 mm. Benthic invertebrates were first placed in 10% alcohol for narcotization and then were preserved in 10% formalin. In total, we identified 7 categories of benthic invertebrates: Nereidae, Sabellidae, Goniadidae, Amphipoda, Oligochaeta, Capitellidae, and Insecta (Pennak 1978, Thorp and Covich 1991, Payne 1992, Liao 1994, Hsieh 1995, Lin and Liao 1995). We calculated the density (no./m<sup>2</sup>) of each invertebrate category at each site on a monthly basis and performed the following analyses.

### Data analysis

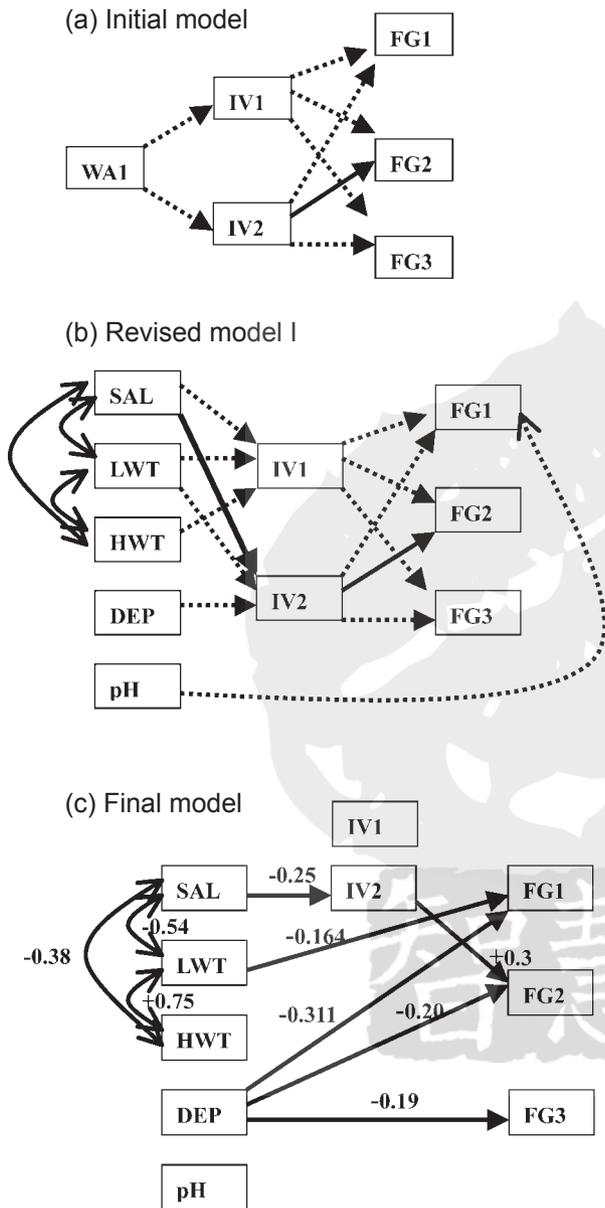
To analyze the data, we used factor analysis, structural equation modeling (SEM), and repeated measures ANOVA. Although we studied 16 sites, fifteen sites were used in factor analysis and SEM because waterbird observations from one of the mangrove sites were not recorded. Repeated measures ANOVA was performed on data obtained from 16 sites. Unfortunately, due to the artificial drying up of certain active fish ponds during various months, values from some of the sites had to be deleted from the repeated measures ANOVA as well as from SEM.

Waterbirds were classified into 10 feeding groups: 1) plovers (Charadriidae); 2) small-billed probers (sandpiper bill length < 1 head length) (Scolopacidae); 3) medium-billed probers (1 head length < sandpiper bill length < 2 head lengths) (Scolopacidae); 4) Black-winged Stilts (*Himantopus*;

*himantopus*; Recurvirostridae); 5) bitterns, herons, and egrets (Ardeidae); 6) surface-feeding ducks (Anatidae); 7) Little Grebes (*Podiceps ruficollis*; Podicipedidae); 8) terns (Laridae); 9) Moorhens (*Gallinula chloropus*; Rallidae); and 10) Black-faced Spoonbills (*Plataea minor*; Threskiornithidae). Feeding activity of each group was defined as the number of feeding birds divided by the total number of birds observed. The reason feeding activity was used rather than the actual number of feeding birds in our analysis was to standardize the data among sites of different-sized areas and to focus on the functional response of waterbirds to prey density. Monthly feeding activity of each feeding group at every site was calculated by combining the morning and afternoon observations that were made each month, and reporting them as the proportion of feeding birds to all observed birds. The binomial proportion of the feeding activity was arc sine transformed (Snedecor and Cochran 1980) for later analysis. Factors were decided separately for the feeding activity of 10 waterbird groups, six physiochemical variables of water, and densities of 7 invertebrate categories by factor analysis using squared multiple correlations as prior communality estimates. The principal factor method with varimax rotation was used to extract the factors, and only factors suggested by scree tests were retained for rotation (SAS Institute 1989). To interpret factors more effectively, we arbitrarily chose 0.2 as a cutoff value to have at least 2 variables with significant loading on each retained factor. Thus, in interpreting the rotated factor pattern, a category or group was said to load on a given factor if the factor loading was  $\geq 0.2$  for that factor and was  $< 0.2$  for the other factors.

Factors retained in the factor analysis were used as variables in an initial model (Fig. 2a). SEM and path analysis were conducted using the SAS system's CALIS procedure (SAS Institute 1989). We evaluated 6 goodness of fit indices: the chi-square statistic, the goodness of fit index (GFI), GFI adjusted for the degrees of freedom, the normed fit index (NFI), the non-normed fit index (NNFI), and the comparative fit index (CFI). The NFI may range from 0 to 1, where 0 represents the goodness of fit associated with a null model specifying that all variables are uncorrelated, and 1 represents the goodness of fit associated with a saturated model that perfectly reproduces the original covariance matrix. The NNFI and CFI are variations on the NFI. Values for the NFI, NNFI, and CFI over 0.9 indicate an acceptable fit between the model and data; the fitness of

the model and significance of the paths were examined according to the methods suggested by



**Fig. 2.** Variables and paths of (a) the initial model, (b) the revised model I, and (c) the preferred final model. Arrows represent the direction of influence of variables. Dashed lines indicate a non-significant path ( $t$ -test,  $p > 0.05$ ). Solid lines indicate a significant path ( $t$ -test,  $p < 0.05$ ). The number located next to the curved 2-headed arrow indicates the correlation between 2 variables. WA1 indicates the factor for physiochemical variables of water. IV1 and IV2 indicate the 1st and 2nd benthic invertebrate factors, respectively. FG1, FG2, and FG3 indicate the 3 factors for feeding activity of waterbirds. LWT, daily lowest water temperature; HWT, daily highest water temperature; DEP, water depth; SAL, salinity.

Hatcher (1994). Moreover, to modify the model by placing more paths in the model, we used Spearman's rank correlation to investigate relationships among original physiochemical variables of water and the factors. Those variables with a significant correlation ( $p < 0.05$ ) were chosen as possible variables to be used in the revised models. Paths were deleted and added also based on the output of path analysis (modification option), and modification indices were used to determine how the model should be changed. The final accepted model was justified by its fit indices and the number of significant paths.

Repeated measures ANOVA was used to investigate the effects of month and wetland types (unused salt field, active fish pond, abandoned fish pond, and mangroves) on the variables shown in the final model. When the effects of month and the interaction between wetland type and month were tested, we used a conservative number of degrees of freedom instead of the original number, and the original number of degrees of freedom was listed in the following results to show the actual sample size.

## RESULTS

### SEM models

In total, six factors were found. One factor was suggested for physiochemical variables. This factor (WA1) had higher loadings on daily lowest water temperature (LWT), daily highest water temperature (HWT), and salinity (Table 1). Two factors were suggested for benthic invertebrates, three categories of which (Nereidae, Sabellidae, and Goniadidae) were found to load on the 1st factor, labeled the medium-large-polychaete factor (IV1) (Table 1), and 2 of which (Capitellidae and Insecta) were found to load on the 2nd factor, labeled the small-invertebrate factor (IV2). Three factors were suggested for feeding activity of waterbirds. Five feeding groups loaded on the 1st factor, labeled the wading-feeding factor (FG1) (Table 1). Two feeding groups (Moorhens and surface-feeding ducks) loaded on the 2nd factor, labeled the surface-feeding factor (FG2). Two feeding groups (Little Grebes and Black-faced Spoonbills) loaded on the 3rd factor, labeled the underwater-feeding factor (FG3) (Table 1).

The 6 factors, extracted from the physiochemical variables of water, benthic invertebrates, and waterbird feeding activity, were used as variables

in the initial model (Fig. 2a). Although the initial model was not rejected as an inadequate representation of the observed data (Chi-square test,  $p > 0.05$ ) (Table 2) and had rather high fit indices, only one of 8 paths was significant ( $|t| > 1.96$ ,  $p < 0.05$ ). To have more than 1 significant path in the model, therefore, we replaced the WA1 factor with the original physiochemical variables of water (Table 2; Fig. 2b). A final model was accepted by justifying the number of significant paths and fit indices. In the final accepted model, only 1 tree-step path was significant (Fig. 2c), indicating that salinity affected IV2, which in turn positively affected FG2. In addition, in the final model, FG2 was

also influenced by water depth.

Water depth was the only variable that affected all 3 waterbird feeding factors in the final model (Fig. 2c). Moreover, the 3 standardized path coefficients between water depth and the 3 waterbird feeding factors were all negative. The path coefficient between FG1 and water depth was the smallest or the most negative among the 3 coefficients, which means, compared to other waterbirds, wading birds decreased their feeding activity the most as water depth increased.

The daily lowest water temperature (LWT) only affected FG1 in the final model (Fig. 2c). Two variables (pH and IV1) were excluded from

**Table 1.** Variables and corresponding factor loadings

| Rotated factor pattern (%) |                 |                 |                                   |
|----------------------------|-----------------|-----------------|-----------------------------------|
| Factor 1 (WA1)             |                 |                 | Physiochemical variables of water |
| <sup>a</sup> 86            |                 |                 | Daily lowest water temperature    |
| <sup>a</sup> 76            |                 |                 | Daily highest water temperature   |
| <sup>a</sup> -54           |                 |                 | Salinity                          |
| 18                         |                 |                 | pH                                |
| 15                         |                 |                 | Water depth                       |
| -6                         |                 |                 | Water density                     |
| 1.6680                     |                 |                 | Eigenvalue                        |
| 1.0698                     |                 |                 | <sup>b</sup> Cumulative           |
| Rotated factor pattern (%) |                 |                 |                                   |
| Factor 1 (IV1)             | Factor 2 (IV2)  |                 | Invertebrate category             |
| <sup>a</sup> 53            | -1              |                 | Nereidae                          |
| <sup>a</sup> 52            | 3               |                 | Sabellidae                        |
| <sup>a</sup> 21            | -4              |                 | Goniadidae                        |
| 9                          | 1               |                 | Amphipoda                         |
| -6                         | -5              |                 | Oligochaeta                       |
| 8                          | <sup>a</sup> 45 |                 | Capitellidae                      |
| -13                        | <sup>a</sup> 44 |                 | Insecta                           |
| 0.6309                     | 0.4073          |                 | Eigenvalue                        |
| 1.0955                     | 1.8028          |                 | <sup>b</sup> Cumulative           |
| Rotated factor pattern (%) |                 |                 |                                   |
| Factor 1 (FG1)             | Factor 2 (FG2)  | Factor 3 (FG3)  | Feeding groups of waterbirds      |
| <sup>a</sup> 60            | 11              | -10             | Plovers                           |
| <sup>a</sup> 59            | 4               | -2              | Medium-billed probers             |
| <sup>a</sup> 34            | -11             | -1              | Black-winged stilts               |
| <sup>a</sup> 24            | -1              | -5              | Hérons, egrets                    |
| <sup>a</sup> 20            | 4               | 9               | Small-billed probers              |
| -12                        | 5               | -8              | Terns                             |
| 3                          | <sup>a</sup> 41 | 5               | Moorhens                          |
| 3                          | <sup>a</sup> 40 | -7              | Surface-feeding ducks             |
| -1                         | 2               | <sup>a</sup> 41 | Grebes                            |
| -2                         | -3              | <sup>a</sup> 36 | Spoonbills                        |
| 0.9437                     | 0.3607          | 0.3204          | Eigenvalue                        |
| 0.9186                     | 1.2697          | 1.5816          | <sup>b</sup> Cumulative           |

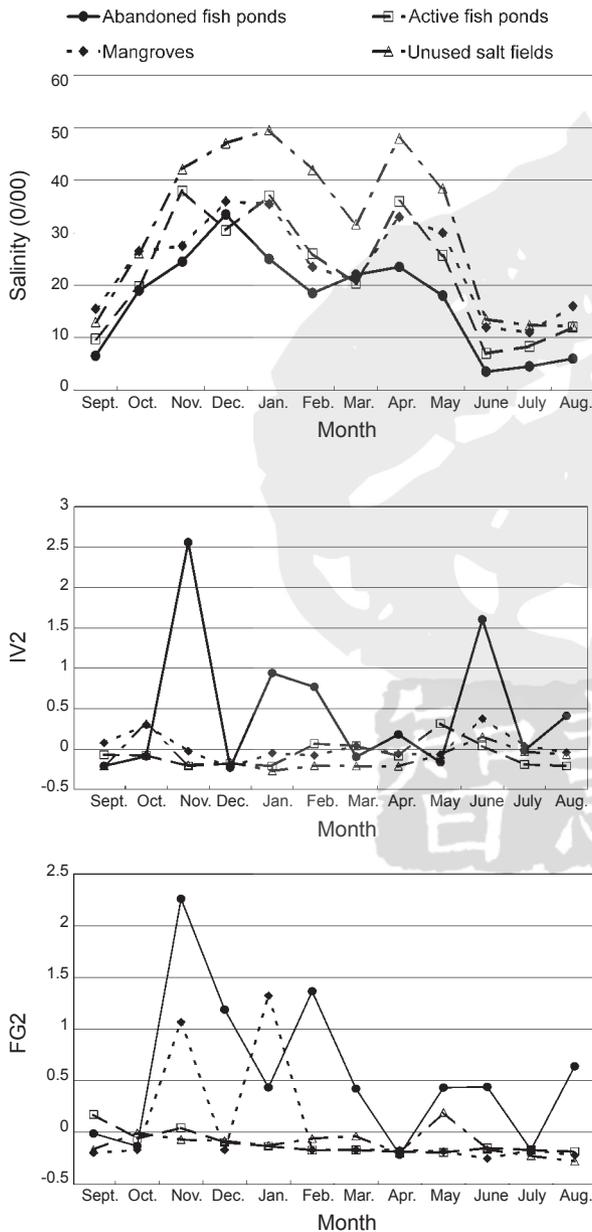
<sup>a</sup>Loading  $\geq 0.2$ .

<sup>b</sup>Cumulative percent of common variance accounted for by the factors. This value might be greater than 100% because the prior communality estimates (squared multiple correlations) were not perfectly accurate (Hatcher 1994).

the final model. Salinity was negatively correlated with HWT and LWT, while HWT and LWT were positively correlated.

### Temporal and spatial variations of variables

In the final model, three related variables: salinity, IV2, and FG2, significantly differed among



**Fig. 3.** Monthly changes in salinity, the 2nd benthic invertebrate factor (IV2), and the 2nd waterbird feeding factor (FG2) among wetland types from Sept. 1997 to Aug. 1998. Lines were drawn according to averages of sampled sites of a particular wetland type.

the various wetland types (Table 3). These differences, however, did not significantly change from month to month (nonsignificant interaction effect: month x wetland type). Among the various wetland types, abandoned fish ponds generally had the lowest salinity and the highest IV2 and FG2 values from month to month (Fig. 3). FG1, but not FG3, significantly varied among wetland types (Table 3). In addition, unused salt fields had the highest FG1 scores among the wetland types, while abandoned fish ponds had the lowest FG1 scores (unused salt fields: mean  $\pm$  standard error of the mean =  $0.2157 \pm 0.0813$ ; mangroves:  $-0.1662 \pm 0.1449$ ; active fish ponds:  $-0.2358 \pm 0.0895$ ; and abandoned fish ponds:  $-0.2996 \pm 0.1059$ ).

Monthly changes in LWT were significant (Table 3; Fig. 4). Monthly changes in water depth were also significant (Table 3; Fig. 4), which affected all 3 waterbird feeding factors in the final model. However, neither LWT nor water depth varied significantly among the various wetland types (Table 3).

IV1, the medium-large-polychaete factor, which was excluded from the final model, varied significantly among the wetland types, and these differences also varied significantly from month to month (Table 3; Fig. 5).

## DISCUSSION

### Implications of the final SEM model

In this study, we extracted variables and factors to construct a structural model, with the intention of describing overall relationships among variables of different levels, including physiochemical variables of water as the abiotic environment, benthic invertebrates as prey, and waterbirds as predators, in a wetland ecosystem. The final SEM model revealed that the original physiochemical variables were better suited than a single prominent factor selected from the factor analysis.

In the final SEM model, only 1 three-step path was significant. In this 3-step path, salinity affected the small-benthic invertebrate factor (IV2), which in turn affected the surface-feeding factor of waterbirds (FG2). The surface-feeding factor of waterbirds was heavily loaded by 2 feeding groups: Moorhens and surface-feeding ducks. Both feeding groups commonly feed on the water surface. Moorhens feed from the surface of the water as they walk about on floating plants, or

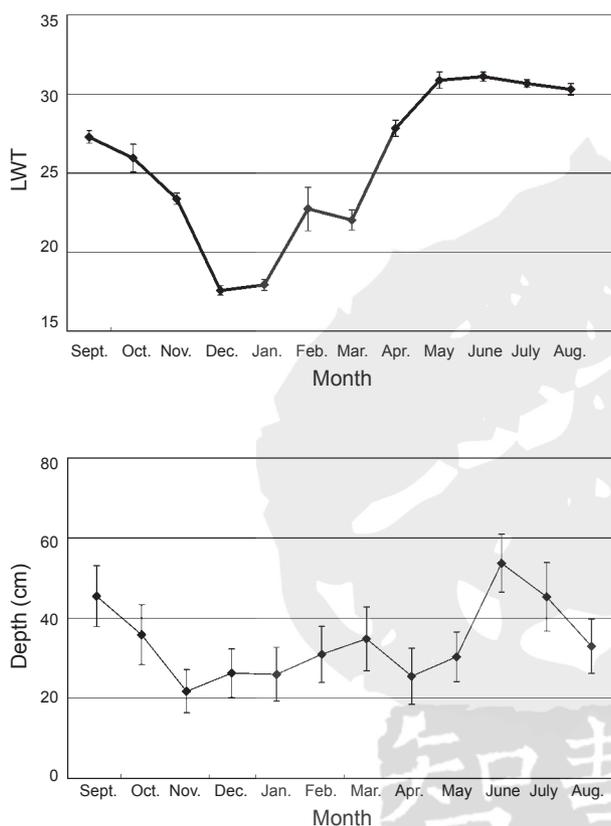
swim and dive for insects and the soft parts of water plants (Terres 1991). Surface-feeding ducks are dabblers (Anatinae) which feed on invertebrates as a vital source of nutrients for growth and reproduction; chironomid larvae are often the most important invertebrates in their diets (De Szalay et al. 1999). The small benthic invertebrates in this

study consisted of the Capitellidae and larvae of such insects as the Chironomidae. Therefore, the relationship between the 2 feeding groups and small benthic invertebrates could be designated as a direct feeding chain.

Studies have found that salinity affects benthic invertebrate communities (Leland and Fend 1998, McRae et al. 1998), and different species of aquatic invertebrates have been found to exhibit differences in salinity tolerance (Euliss et al. 1999, Lovvorn et al. 1999). In this study, salinities ranged from 5‰ to 70‰, and we found that salinity significantly affected the density of small benthic invertebrates, which decreased as salinity increased (a negative path coefficient in the model). Salinity indirectly influenced the surface-feeding factor via the small-benthic invertebrate factor. Furthermore, based on the results of repeated measures ANOVA, these ecological relationships were prominent and temporally consistent in abandoned fish ponds, which generally had the lowest salinities, and the highest IV2 and FG2 values from month to month (Fig. 3).

The medium-large-polychaete factor (IV1) did not appear in the final model for 2 possible reasons. The 1st reason is that we only had samples from 1 mangrove site, where polychaetes were usually most abundant. Therefore, we may have lacked adequate data to show its significance. Thus, the final model in this study should not be viewed as an adequate model for mangroves. Second, the medium-large-polychaete factor spatially differed, and this spatial difference also varied temporally. This changeable property may have made the medium-large-polychaetes an unreliable resource to waterbirds, thus rendering their density a poor predictor of waterbird feeding activity.

Two physical variables, LWT and water depth, affected FG1 (the wading-feeding factor). The



**Fig. 4.** Monthly changes in average daily lowest water temperature (LWT) and water depth from Sept. 1997 to Aug. 1998. Lines (mean  $\pm$  standard error of the mean) were drawn according to sampled sites in a particular month.

**Table 2.** Goodness of fit indices for various models

| Fit index                           | Initial model | Revised model | Final model |
|-------------------------------------|---------------|---------------|-------------|
| Chi-square                          | 10.14         | 57.09         | 18.85       |
| df                                  | 7             | 22            | 16          |
| <i>p</i>                            | 0.18          | 0.0001        | 0.28        |
| Goodness of fit index (GFI)         | 0.98          | 0.93          | 0.97        |
| GFI adjusted for degrees of freedom | 0.93          | 0.84          | 0.94        |
| Comparative fit index (CFI)         | 0.94          | 0.85          | 0.99        |
| Non-normed fit index (NNFI)         | 0.86          | 0.68          | 0.98        |
| Normed fit index (NFI)              | 0.84          | 0.79          | 0.93        |

effect of water depth on FG1 was about twice that of LWT as illustrated by the relative magnitudes of the path coefficients (Fig. 2c). Furthermore, the path coefficients in the SEM model also revealed

that, compared to other waterbirds, wading birds decreased their feeding activity the most as the water became deeper. In general, water depth can directly and indirectly affect feeding activities of

**Table 3.** Repeated measures ANOVA of variables from September 1997 to August 1998 in the Sitsao wetlands

| Salinity ( <i>n</i> = 175)    |     |                |             |         |                 |
|-------------------------------|-----|----------------|-------------|---------|-----------------|
| Source                        | df  | Sum of squares | Mean square | F value | Conservative df |
| Wet                           | 3   | 6092.8         | 2030.9      | 4.21*   |                 |
| Site (wet)                    | 12  | 5784.5         | 482.0       |         |                 |
| Month                         | 11  | 24337.7        | 2212.5      | 57.92** | 1               |
| Month x wet                   | 33  | 2083.3         | 63.1        | 1.65    | 3               |
| Month x site (wet)            | 115 | 4396.8         | 38.2        |         | 10              |
| IV2 ( <i>n</i> = 182)         |     |                |             |         |                 |
| Source                        | df  | Sum of squares | Mean square | F value | Conservative df |
| Wet                           | 3   | 6.40           | 2.13        | 5.76*   |                 |
| Site (wet)                    | 12  | 4.48           | 0.37        |         |                 |
| Month                         | 11  | 4.20           | 0.38        | 1.81    | 1               |
| Month x wet                   | 33  | 16.49          | 0.50        | 2.38    | 3               |
| Month x site (wet)            | 122 | 25.22          | 0.21        |         | 11              |
| FG2 ( <i>n</i> = 180)         |     |                |             |         |                 |
| Source                        | df  | Sum of squares | Mean square | F value | Conservative df |
| Wet                           | 3   | 8.73           | 2.91        | 6.19*   |                 |
| Site (wet)                    | 11  | 5.20           | 0.47        |         |                 |
| Month                         | 11  | 3.624          | 0.329       | 2.04    | 1               |
| Month x wet                   | 33  | 13.599         | 0.412       | 2.56    | 3               |
| Month x site (wet)            | 121 | 19.50          | 0.161       |         | 11              |
| FG1 ( <i>n</i> = 180)         |     |                |             |         |                 |
| Source                        | df  | Sum of squares | Mean square | F value | Conservative df |
| Wet                           | 3   | 9.72           | 3.24        | 4.15*   |                 |
| Site (wet)                    | 11  | 8.57           | 0.78        |         |                 |
| Month                         | 11  | 13.37          | 1.22        | 2.60    | 1               |
| Month x wet                   | 33  | 8.15           | 0.25        | 0.53    | 3               |
| Month x site (wet)            | 121 | 56.53          | 0.47        |         | 11              |
| FG3 ( <i>n</i> = 180)         |     |                |             |         |                 |
| Source                        | df  | Sum of squares | Mean square | F value | Conservative df |
| Wet                           | 3   | 0.474          | 0.156       | 0.26    |                 |
| Site (wet)                    | 11  | 6.486          | 0.590       |         |                 |
| Month                         | 11  | 1.962          | 0.178       | 0.66    | 1               |
| Month x wet                   | 33  | 5.881          | 0.178       | 0.66    | 3               |
| Month x site (wet)            | 121 | 32.44          | 0.268       |         | 11              |
| LWT ( <i>n</i> = 163)         |     |                |             |         |                 |
| Source                        | df  | Sum of squares | Mean square | F value | Conservative df |
| Wet                           | 3   | 24.3           | 8.1         | 1.16    |                 |
| Site (wet)                    | 12  | 83.5           | 7.0         |         |                 |
| Month                         | 11  | 3260.9         | 296.4       | 49.4**  | 1               |
| Month x wet                   | 33  | 91.1           | 2.8         | 0.47    | 3               |
| Month x site (wet)            | 103 | 618.7          | 6.0         |         | 9               |
| Water depth ( <i>n</i> = 182) |     |                |             |         |                 |
| Source                        | df  | Sum of squares | Mean square | F value | Conservative df |
| Wet                           | 3   | 26365.4        | 8788.5      | 1.23    |                 |
| Site (wet)                    | 12  | 85852.7        | 7154.4      |         |                 |
| Month                         | 11  | 14590.1        | 1326.4      | 15.66** | 1               |
| Month x wet                   | 33  | 5821.6         | 176.4       | 2.08    | 3               |
| Month x site (wet)            | 122 | 1033.6         | 84.7        |         | 11              |
| IV1 ( <i>n</i> = 182)         |     |                |             |         |                 |
| Source                        | df  | Sum of squares | Mean square | F value | Conservative df |
| Wet                           | 3   | 35.0           | 11.7        | 27.2**  |                 |
| Site (wet)                    | 12  | 5.11           | 0.43        |         |                 |
| Month                         | 11  | 2.12           | 0.19        | 1.36    | 1               |
| Month x wet                   | 33  | 17.31          | 0.52        | 3.71*   | 3               |
| Month x site (wet)            | 122 | 17.46          | 0.14        |         | 11              |

Wet: wetland type; \*\* $p < 0.01$ ; \* $p < 0.05$ .

wading birds. Wading birds in our study included small shorebirds such as plovers and sandpipers, which are ground-dwelling feeders, and large wading birds such as herons and egrets, which feed on fish. Shorebirds may be too small to walk and feed in deeper water; therefore, water depth has a direct effect on their feeding activities. Large wading birds with long legs and big body size, however, are less constrained morphologically by water depth than are shorebirds; water depth may not play a direct but an indirect role in affecting their feeding activities. Young and Chan (1997) pointed out that large wading birds such as herons and egrets choose feeding sites in drained fish ponds where water is shallow and fish are more concentrated. Because herons and egrets were frequently seen with fish in their bills during our observations, we suggest that water depth affects the feeding activities of large wading birds via fish densities.

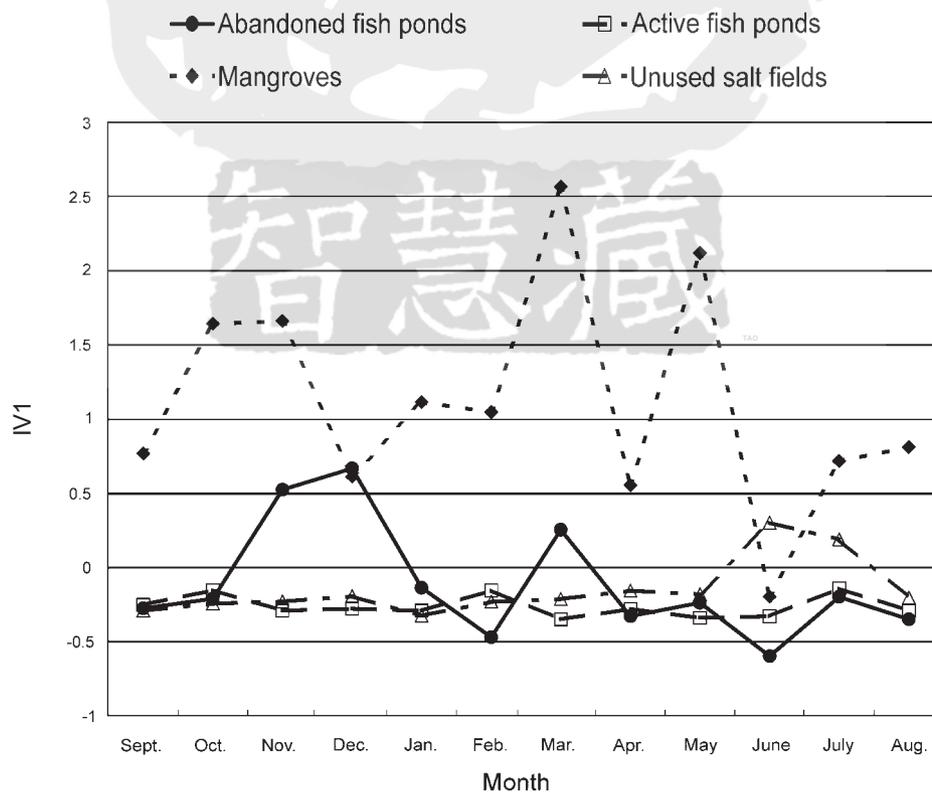
In the final model, only the feeding activities of surface-feeding ducks and Moorhens (FG2) were related to prey density (IV2), while wading bird feeding activity was not for 2 possible rea-

sons. First, as Safran et al. (1997) suggested, species possessing greater mobility such as waterfowl and Moorhens can choose feeding sites based on food abundance, while small shorebirds such as plovers and sandpipers, constrained morphologically by water depth, can not. Second, large wading birds such as herons, egrets, and Black-faced Spoonbills feed on fish, which were neither sampled nor included in the modeling.

### Implications for management of waterbird feeding habitat

The only significant 3-step path in the SEM model was the salinity/small benthic invertebrate/surface-feeding factor of waterbirds. In addition, these ecological relationships were prominent and temporally consistent in abandoned fish ponds. Based on these results, the goal of having more Moorhens and ducks feeding in the Sitsao wetlands could be easily achieved through increasing the number of abandoned fish ponds.

Water depth has been reported to be an important factor affecting the distribution of water-



**Fig. 5.** Monthly changes in the 1st benthic invertebrate factor (IV1) among wetland types from Sept. 1997 to Aug. 1998. Lines were drawn according to averages of sampled sites of a particular wetland type.

birds. Our results show that water depth affected the wading-feeding factor the most. In addition, water depth varied temporally but not spatially. Based on these results, we recommend an increase in overall shallow-water areas in the Sitsao wetlands during winter to provide feeding habitat for wintering and early spring migratory wading birds such as shorebirds, sandpipers, herons, and egrets. Furthermore, our results show that the 2nd lowest wading-feeding factor occurred in active fish ponds, and this might indicate that wading bird feeding habitat is limited in active fish ponds. Twedt et al. (1998) pointed out that aquaculture facilities periodically draw down ponds as an integral part of their management regime and suggested that the management of drawing down ponds could be used to increase the feeding habitats of waterbirds. To provide additional feeding habitat for wading birds in the Sitsao wetlands, we recommend that managers should encourage owners of fish ponds to drain ponds during late autumn and early winter when migratory birds are most abundant and feeding habitats are limited.

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## 利用線性結構模式探討四草溼地水深及化學變數、 底棲無脊椎動物和水鳥進食活動的關係

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本研究利用線性結構模式探索底棲無脊椎動物與水深及化學變數的關係，並進而瞭解它們與水鳥進食活動的直接和間接關係。我們於1997年9月至1998年8月每月到四草溼地的16個樣點進行野外調查。水域及底棲無脊椎動物資料經由因子分析分別得到一個水域因子和兩個底棲無脊椎動物因子；我們先將水鳥歸類成十個食群，再經由因子分析得到三個水鳥進食活動因子。利用這六個因子組成最初模式，然後經由線性結構模式及路徑分析結果，修改這初始模式。最終模式顯示水深影響所有三個水鳥進食因子，鹽度只有影響小型底棲無脊椎動物因子，小型底棲無脊椎動物因子進而影響紅冠水雞及水鴨進食因子。為進一步檢視最後接受的模式，我們利用重複測量變方分析探討模式中變數的時空變化。在最後模式中三個相關的變數（鹽度、小型底棲無脊椎動物因子、紅冠水雞及水鴨進食因子）在不同的溼地形式有顯著的差異，且此差異並不隨月份不同而改變。我們並根據結構模式與重複測量變方分析的結果，提出增加四草溼地不同覓食鳥群的棲地經營建議。

**關鍵詞：**線性結構模式，水深，底棲無脊椎動物，進食活動，水鳥。

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