# Bird ecology and Taylor's variance-mean regression

## Ilkka Hanski & Juha Tiainen

Hanski, I. & Tiainen, J. 1989: Bird ecology and Taylor's variance-mean regression. — Ann. Zool. Fennici 26:213–217.

L. R. Taylor (1986 and earlier) has suggested that the slope $b$ of the regression $\log V = a + b \log x$ of variance $V$ against mean density $x$ is a species-specific constant. We attempt to relate the regression slopes for British birds to 13 life history and population ecological parameters. Spatial regression slopes are found to be unreliable, because the relatively constant average densities across sites in most bird populations do not allow a sufficiently large range of mean densities to be sampled. In temporal regressions, the only parameter apart from overall mean density that unequivocally affected the slope was territoriality, territorial species having significantly lower slopes (1.08) than non-territorial species (1.28). This result demonstrates large-scale population dynamic consequences of territoriality, but we conclude that the variance-mean regression analysis is not a generally useful tool in bird ecology.

*I. Hanski & J. Tiainen, Department of Zoology, University of Helsinki, P. Rautatiekatu 13, SF-00100 Helsinki, Finland.*

## 1. Introduction

Ecologists have often been tempted to reduce the complexity of populations and communities into one or a few numerical indices. The great influx of species diversity studies in the 1960s and 1970s is a case in point (for examples and criticism see James & Rathbun 1981). Another example from population ecology is L. R. Taylor's variance-mean regression analysis (Taylor 1961, 1986, Taylor & Taylor 1977, 1983 and references therein), which aims at reducing population dynamics to a single index, the regression slope of the logarithm of variance against the logarithm of mean abundance. The variances and means are calculated either across many sampling sites separately for several sampling periods (spatial regression), or over many sampling periods but separately for many sites (temporal regression). For a discussion of the two kinds of regression and the appropriate data see Taylor & Woiwod (1980, 1982), Taylor et al. (1980) and Hanski (1982).

Taylor and his co-workers suggest that the regression slope is a species-specific constant (Taylor & Woiwod 1982, Taylor 1986). They have repeatedly asserted that current population dynamic theory and models are unable to explain the interspecific variation in the slope values, and they have invoked complex behavioural mechanisms to account for the observed patterns (Taylor & Taylor 1977, 1979, 1983, Taylor et al. 1983). These conclusions have been challenged by Anderson et al. (1982), Hanski (1982, 1987), Thórarinsson (1986) and Downing (1986) on theoretical, ecological and statistical grounds.

What has been lacking both in Taylor's own and in his critics' works is an attempt to relate the regression slopes to the ecology of the species (though see R. A. J. Taylor 1981b for an unsuccessful attempt to relate the regression slopes to R. A. J. Taylor's Δ-model parameters, which themselves could not be satisfactorily estimated with empirical data: R. A. J. Taylor 1981a). If the slope cannot be related to anything else in the biology of the species, the ecological significance of the slope becomes questionable. If, on the other hand, the slope is correlated with other biological and ecological parameters, it may play a useful role in the study of population ecology. Here we explore the relationships between the variance-mean regression slopes and thirteen life history and ecological parameters in British birds.

## 2. Material

The statistics of spatial and temporal variance-mean regressions for British birds have been published by Taylor et al. (1980) and Taylor & Woiwod (1982), respectively. The data come from the Common Bird Census of the British Trust for Ornithology, conducted between 1962 and 1976 at selected woodland and farmland sites. Data for the two habitat types have been analysed separately, though if the two slopes did not differ significantly from each other only a common regression line was reported. Taylor et al. (1980) and Taylor & Woiwod (1982) should be consulted for details on the regressions and for references to the original data. We excluded 16 rare species prior to the analyses, leaving 95 species. A species was considered to be rare if Taylor et al. (1980) or Taylor & Woiwod (1982) failed to report its spatial or temporal regression, respectively. The following life history and population ecology parameters were included in this study (data are from standard handbooks if not stated otherwise):

1. Taxonomy: Family. Eight families with 5 or more species were included (total 55 species).

2. Global distribution: European (only in Europe: 25 species), Palaearctic or nearly Palaearctic (from the Atlantic Ocean across Siberia to or nearly to the Pacific Ocean: 55), and eastern or northern species (from Siberia and northern Europe to Central Europe including the British Isles; absent elsewhere in western Europe: 15). Classification based on the maps in Voous (1960).

3. Distribution in Britain (Sharrock 1976): southernmost third of the island (1), England and Wales only (13), the whole of Britain (78), lacking from southern parts of Britain (2), and coastal distribution (1). Only categories with >2 species were included in the analysis.

4. Distribution in the British Isles: the logarithm of the number of $10 \times 10$ km$^2$ Atlas squares (maximum 3775; Sharrock 1976).

5. Migratory behaviour: sedentary species (60), partial or short-distance migrants (12), and long-distance migrants (23).

6. Main habitat: woodland (38), nesting in woodland, foraging in the open (24), open habitats (18), and water and shore habitats (15).

7. Territorial behaviour: not clearly territorial (22) and territorial species (73).

8. Nestsite: holes above ground (19), openly in trees (24), bushes (8), and ground (41; three species could not be classified).

9. Clutch size: median of the first clutch in Campbell & Ferguson-Lees (1972).

10. Length of the breeding season in months (Campbell & Ferguson-Lees 1972).

11. Adult survival rate (for 13 species from Dobson 1987).

12. Food: invertebrates (48), vertebrates (7), plants (adults, chicks not considered; 28), and omnivory with mainly animals in summer and plants in winter (28).

13. Log-transformed weight.

## 3. Spatial regressions

The spatial variance-mean regression is estimated from variance-mean pairs calculated across many sampling sites separately for several sampling periods. In the data analysed here, each data point gives the spatial variance and mean density in many populations in one year, and the regression has as many data points as there are years during which sampling was conducted.

Estimation of the spatial variance-mean regression slope involves a difficulty that has become apparent only recently: the range of means sampled is often quite small, say less than one order of magnitude (Downing 1986, Hanski 1987). For statistical reasons, the standard error of the slope estimate is large when the range of the means is small, in other words the slope estimate is unreliable. As expected, extreme values of the spatial slope are commonly found in species with a small range of mean densities sampled (Downing 1986, Hanski 1987).

Turning to Taylor's analysis of the bird data (Taylor et al. 1980), we encounter another difficulty that makes it impossible to evaluate the magnitude of this statistical problem. For nearly half of the species (43 of 95), Taylor et al. (1980) found that the samples from the two habitat types had a "single" regression, the slope and the intercept not being statistically different. For these species they report only one set of parameter values estimated from the pooled data points for the two habitat types. As most bird species are more abundant in one of the two habitat types, their analysis gives misleadingly large ranges and compounds within-habitat and between-habitat variation in numbers. Because the results are not given separately for the two series of data, which themselves are not in the public domain, we do not know how reliable, or unreliable, the slope estimates are.

Amongst the remaining 52 species there are only 8 species with the range of means greater than one order of magnitude in both habitat types. As the slope estimates tend to be unreliable for species with ranges less than this (Downing 1986, Hanski 1987), there is little point in attempting any analysis of the spatial slopes. This situation is, however, indicative of bird ecology: unlike in many insect populations (Hanski 1987), average densities across sampling sites tend to remain relatively stable in bird populations (e.g. von Haartman 1971), and it is uncommon that in the course of 15 years (the length of time covered by Taylor's data) the maximum of the annual average densities is 10 times greater than the minimum. Examples can be found in species occurring in marginal habitats, at the margins of their ranges, and among food specialists depending upon greatly fluctuating food resources such as tree seeds and voles (e.g. Korpimäki 1984, 1987, Virkkala 1989).

## 4. Temporal regressions

A small range of mean densities is not generally a problem with temporal regressions, in which each data point gives the variance and the mean for one site, calculated over the years of the study. When a large and heterogeneous region is sampled, as is the case with the bird data analysed by Taylor & Woiwod (1982), population means are likely to be sufficiently different to generate a range greater than one order of magnitude.

Varying overall mean density can affect the temporal slope (Hanski 1982). The slope is expected to approach one in the rarest species, with the distribution of individuals in samples approaching Poisson (Anderson et al. 1982, Hanski 1982). In common species, the null hypothesis for density-independent dynamics is two (Anderson et al. 1982, Hanski 1982), and in fact it is difficult to distinguish variance-mean regression results for moths and aphids from this null hypothesis (Hanski 1982). In contrast, in birds there is only a slight increase in the slope with mean abundance. The interspecific regression of the slope against the mean was just significant in the farmland data ($P=0.023$) while being nonsignificant in the woodland data, and even in the former only 5% of variation in the slope was accounted for by the regression. Nonetheless, as several of the ecological variables (Section 2) were correlated with mean abundance, we have used below covariance and multiple regression analyses with mean abundance as a covariate.

The following variables had no effect on the slope: migratory behaviour (parameter number 5 in the list in Section 2), global (2) and UK distribution type (3 and 4), food (12), weight (13), clutch size (9) and the length of the breeding season (10). The remaining four variables were correlated with the temporal slope in one or both sets of data.

By far the most significant ($P<0.001$) relationship was found between territoriality (7) and the temporal slope: territorial species ($n=73$) tended to have lower slopes than nonterritorial species ($n=22$; average slopes were 1.08 and 1.28, respectively, in both habitat types; Table 1). The three other variables with less significant relationships with the temporal slope were family (1), habitat selection (6) and survival rate (11). However, further analyses showed that territoriality varied highly significantly between the families ($P<0.001$; Table 2). The data are not suitable for a two-way ANOVA, but in single-way ANOVAs for

the territorial species only (47 of the 55 species in Table 2) the differences between the families were nonsignificant, suggesting that the significant effect of family in all the 55 species is due to territoriality. Habitat selection had a significant effect at the 5% level in the woodland but not in the farmland data, but two-way ANOVAs with habitat selection and territoriality as independent variables strongly suggested that in this case, too, only territoriality significantly affected the slope (Table 3). Finally, survival rate was significantly and positively correlated with the slope in the farmland ($P<0.02$) but not in the woodland data. This result could not be accounted for by territoriality, but as we had data on survival for only 13 species, and as we have run many analyses involving the temporal slope, this result may be due to chance only.

Table 1. ANCOVA of the temporal variance-mean regression slope in the farmland and woodland data.

| Source of variation | Farmland | | Woodland | |
|---|---|---|---|---|
| | F | P | F | P |
| Covariate: mean | 6.17 | 0.015 | 0.88 | 0.361 |
| Main effect: territoriality | 15.16 | 0.0002 | 11.68 | 0.0009 |

Table 2. Statistics of the temporal regression slope (mean±$SE$) and the average degree of territoriality in the bird families with at least 5 species in the data set. Territoriality was coded as 0 (=no territoriality) or 1 (=territoriality). Differences between the families in the slope are significant ($P<0.02$) but most probably due to varying territoriality between the families (see the text).

| Family | No. species | Temporal slope | | Average territoriality |
|---|---|---|---|---|
| | | Farmland | Woodland | |
| Scolopacidae | 6 | 0.95±0.09 | 0.95±0.09 | 1.00 |
| Motacillidae | 5 | 1.01±0.03 | 1.01±0.03 | 1.00 |
| Sylvidae | 11 | 1.13±0.03 | 1.19±0.05 | 1.00 |
| Turdidae | 9 | 1.20±0.11 | 0.99±0.13 | 1.00 |
| Fringillidae | 7 | 1.07±0.03 | 1.10±0.05 | 0.86 |
| Paridae | 6 | 1.10±0.06 | 1.10±0.06 | 0.83 |
| Corvidae | 5 | 1.16±0.17 | 1.16±0.17 | 0.60 |
| Anatidae | 6 | 1.45±0.09 | 1.45±0.09 | 0.33 |

Table 3. ANOVAs of the temporal variance–mean regression slope in the farmland and woodland data.

| Source of variation | df | Farmland | | | Woodland | | |
|---|---|---|---|---|---|---|---|
| | | Mean square | F | P | Mean square | F | P |
| Main effects | 4 | 0.241 | 4.83 | 0.001 | 0.276 | 4.29 | 0.003 |
| Habitat selection | 3 | 0.070 | 1.41 | 0.246 | 0.135 | 2.10 | 0.106 |
| Territoriality | 1 | 0.640 | 12.79 | 0.001 | 0.409 | 6.37 | 0.013 |
| Interaction | 3 | 0.175 | 3.50 | 0.019 | 0.110 | 1.71 | 0.171 |

## 5. Conclusion

The only parameter that unequivocally affects the temporal variance-mean regression slope in birds is territoriality: territorial species tend to have lower slopes than nonterritorial species. This is not a surprising result, as territoriality is a prime example of a density dependent process (Fretwell & Lucas 1969, Krebs 1971, von Haartman 1971, Klomp 1972, Patterson 1980), and more density dependent dynamics are expected to be associated with lower variance-mean regression slopes (Hanski 1982). Territorial birds have slopes only slightly greater than one, in striking contrast to moths and aphids with slopes around two, the null hypothesis for density independent dynamics (Hanski 1982, Taylor & Woiwod 1982).

Although it is satisfying to find that the density dependence of territoriality is "revealed" by the variance-mean regression analysis, this result does not bring much new to bird ecology. Territoriality involves a multitude of behavioural and ecological elements, and it is more fruitful to analyse them thoroughly than to try to reduce the population dynamic consequences of territoriality to a single index, the regression coefficient. See, for instance, O'Connor (1983) and Pimm (1984) for ecological analyses of the same BTO data that have been used by Taylor & Woiwod (1982). It is noteworthy that migratory behaviour did not affect the regression slope at all, though O'Connor (1983) found many population dynamic differences between resident and migratory species.

Most of the variance in the spatial and temporal slopes cannot be related to the ecological parameters included in this study. While it is possible that other parameters could be found that would do better, we feel compelled to conclude, at this point, that the temporal variance-mean regression analysis is not a useful tool in bird ecology.

## References

Anderson, R. M., Gordon, D., Crawley, M. J. & Hassell, M. P. 1982: Variability in the abundance of animal and plant species. — Nature 296:245–248.

Campbell, B. & Ferguson-Lees, J. 1972: A field guide to birds' nests. — Constable, London.

Dobson, A. P. 1987: A comparison of seasonal and annual mortality for both sexes of fifteen species of common British birds. — Ornis Scand. 18:122–128.

Downing, J. A. 1986: Spatial heterogeneity: evolved behaviour or mathematical artefact? — Nature 323:255–257.

Fretwell, S. D. & Lucas, Jr., H. L. 1969: On territorial behavior and other factors influencing habitat distribution in birds. I. Theoretical development. — Acta Biotheor. 19:16–36.

von Haartman, L. 1971: Population dynamics. — In: Farner, D. S. & King, J. R. (eds.), Avian biology. Vol. 1, pp. 391–459. Academic Press, New York.

Hanski, I. 1982: On patterns of temporal and spatial variation in animal populations. — Ann. Zool. Fennici 19:21–37.

—"— 1987: Crosscorrelation in population dynamics and the slope of spatial variance-mean regressions. — Oikos 50:148–151.

James, F. C. & Rathbun, S. 1981: Rarefaction, relative abundance, and diversity of avian communities. — Auk 98:785–800.

Klomp, H. 1972: Regulation of the size of bird populations by means of territorial behaviour. — Neth. J. Zool. 22:456–488.

Korpimäki, E. 1984: Population dynamics of birds of prey in relation to fluctuations in small mammal populations in western Finland. — Ann. Zool. Fennici 21:287–293.

—"— 1987: Timing of breeding of Tengelmalm's owl Aegolius funereus to vole dynamics in western Finland. — Ibis 129:58–68.

Krebs, J. R. 1971: Territory and breeding density in the great tit, Parus major L. — Ecology 52:2–22.

O'Connor, R. J. 1983: Behavioural regulation of bird populations: A review of habitat use in relation to migration and residency. — In: Sibly, R. M. & Smith, R. H. (eds.), Behavioural ecology, pp. 103–142. Blackwell, Oxford.

Patterson, I. J. 1980: Territorial behaviour and the limitation of population density. — Ardea 68:53–62.

Pimm, S. L. 1984: Food chains and return times. — In: Strong, D. R. Jr., Simberloff D., Abele, L. G. & Thistle, A. B. (eds.), Ecological communities, pp. 397–412. — Princeton Univ. Press, Princeton.

Sharrock, J. T. R. 1976: The atlas of breeding birds in Britain and Ireland. — British Trust for Ornithology, Tring.

Taylor, L. R. 1961: Aggregation, variance and the mean. — Nature 189:732–735.

—"— 1986: Synoptic dynamics, migration and the Rothamsted Insect Survey. Presidential Address to the British Ecological Society, December 1984. — J. Anim. Ecol. 55:1–38.

Taylor, L. R. & Taylor, R. A. J. 1977: Aggregation, migration and population mechanics. — Nature 265:415–421.

—"— 1983: Insect migration as a paradigm for survival by movement. — In: Swingland, I. R. & Greenwood, P. J. (eds.), The ecology of animal movement, pp. 181–214. Clarendon Press, Oxford.

Taylor, L. R., Taylor, R. A. J., Woiwod, I. P. & Perry, J. N. 1983: Behavioural dynamics. — Nature 303:801–804.

Taylor, L. R. & Woiwod, I. P. 1980: Temporal stability as a density-dependent species characteristic. — J. Anim. Ecol. 49:209–224.

—"— 1982: Comparative synoptic dynamics. I. Relationships between inter- and intraspecific spatial and temporal variance/mean population parameters. — J. Anim. Ecol. 51:879–906.

Taylor, L. R., Woiwod, I. P. & Perry, J. N. 1980: Variance and large scale spatial stability of aphids, moths and birds. — J. Anim. Ecol. 49:831–854.

Taylor, R. A. J. 1981a: The behavioural basis of redistribution. I. The Δ-model concept. — J. Anim. Ecol. 50:573–586.

—"— 1981b: The behavioural basis of redistribution. II. Simulations of the Δ-model. — J. Anim. Ecol. 50:587–604.

Taylor, R. A. J. & Taylor, L. R. 1979: A behavioural model for the evolution of spatial dynamics. — In: Anderson, R. M., Turner, B. D. & Taylor, L. R. (eds.), Population dynamics, pp. 1–27. Blackwell, Oxford.

Thórarinsson, K. 1986: Population density and movement: a critique of delta-models. — Oikos 46:70–81.

Virkkala, R. 1989: Short-term fluctuations in bird communities and populations in virgin and managed forests in Northern forests. — Ann. Zool. Fennici 26:277–285.

Voous, K. H. 1960: Atlas of European birds. — Nelson, Edinburgh.