Spatial autocorrelation
of ecological phenomena

Walter D. Koenig

Ecological variables often fluctuate synchronously over wide geographical areas, a phenomenon known as spatial autocorrelation or spatial synchrony. Development of statistical approaches designed to test for spatial autocorrelation combined with the increasing accessibility of long-term, large-scale ecological datasets are now making it possible to document the patterns and understand the causes of spatial synchrony at scales that were previously intractable. These developments promise to foster significant future advances in understanding population regulation, metapopulation dynamics and other areas of population ecology.

Walter Koenig is at the Hastings Natural History Reservation, University of California at Berkeley, 38601 E. Carmel Valley Road, Carmel Valley, CA 93924, USA (wicker@uclink4.berkeley.edu).

Most interesting ecological phenomena vary in both space and time: population densities change from year to year and are rarely identical from one locality to the next; dispersal rates vary with population density and thus are different from one year to the next and from one population to another; weather conditions vary both annually and locally depending on physiography. Documenting these kinds of variation and understanding their causes are central to population ecology. However, the significance of spatial structure extends to other fields as well. Almost every major hypothesis for the ecological factor selecting for a particular spatial pattern or mating system rests on some hypothetical spatiotemporal pattern in the distribution of food, resources or some other critical parameter. Examples include Horn's geometric model for coloniality[1], the polygyny threshold model[2], the delayed-dispersal threshold model for the evolution of cooperative breeding[3], and home-range-based models for the evolution of leks[4]. Patterns of population change through space and time directly determine the relevance of metapopulation dynamics and thus are of basic importance to conservation biology[5–7].

Measuring spatial autocorrelation

Discerning patterns of spatiotemporal variation in ecological variables can be difficult[8]. Here I focus on the synchrony exhibited by many biotic and abiotic ecological factors over what can be strikingly large geographical areas or, stated more simply, spatial autocorrelation of ecological phenomena. A typical analysis involves a series of measurements overlapping in time taken at multiple sites over some geographical area, which can be small (e.g. data on annual growth of individual trees within a 1 ha plot) or large (e.g. population density of snowshoe hares at sites spread throughout the northern hemisphere). As a first step, it is often desirable to modify the raw data. Common procedures include log-transformation to reduce the correlation between the mean and the variance, and calculation of residuals from a linear regression to avoid patterns caused by large-scale global trends instead of the regional processes of direct interest[9]. An example of the latter problem would be if densities increased at all sites during the time the data are collected. Pairwise correlations based on the annual raw census data would then all be positive because of the long-term trend. Standardizing the data by using residuals from a linear regression eliminates this long-term trend and focuses the analysis on more regional processes.

The standard method for analysing spatial patterns in this type of data is the Mantel test[10], which tests the overall relationship between distance and similarity between sites. Two matrices are calculated: (1) a 'distance matrix' consisting of the distances between all pairs of sites, and (2) a 'correlation matrix' consisting of the similarity between the annual values across all pairs of sites. An easy way to visualize such data is to plot the correlation coefficients against distance. An example of this is given in Fig. 1 for the standardized mean densities of mountain hares (*Lepus timidus*) surveyed in Finland over a 39-year period. These data represent the standard case in which data are annual measurements, but data taken at shorter or longer intervals merely alter the timescale over which geographical variation in spatial patterns is measured.
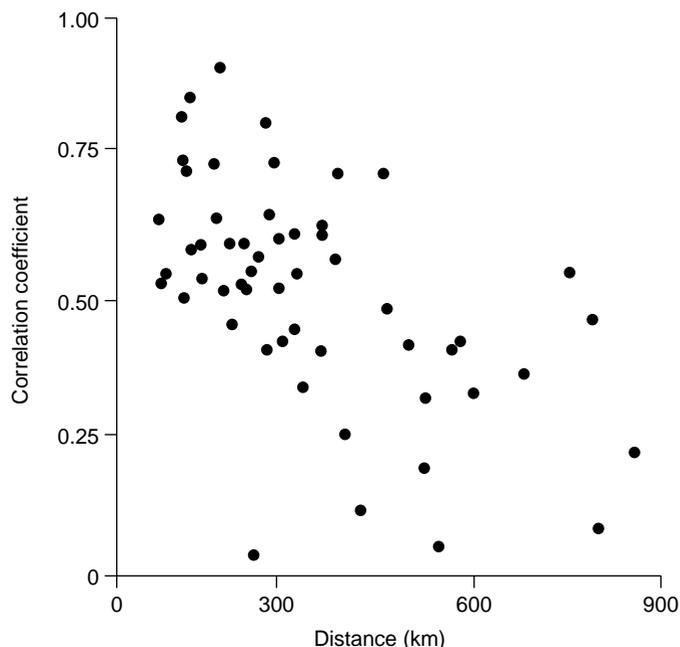
Fig. 1. Synchrony in relative mean density of mountain hares (*Lepus timidus*) among 11 provinces in Finland measured over 39 years (1946–1984) plotted against the distance between the geographical centers of the provinces. The total number of comparisons is 55, corresponding to the number of pairwise comparisons possible between 11 sets of data. Note that synchrony declines with increasing distance between provinces (r = –0.57). *Reproduced, with permission, from Ref. 18.*

The data in Fig. 1 exhibit a common pattern, namely that synchrony declines with distance. The Mantel procedure tests this pattern using a randomization test in which one of the matrices is shuffled, and the resulting regression coefficient compared with the observed (unshuffled) regression. The end-product is a value (Mantel z) indicating whether or not synchrony (or autocorrelation) changes with distance. A modification of this procedure divides distance into categories and tests whether the degree of autocorrelation exhibited by pairwise values within the category is greater than or less than the overall average autocorrelation between sites. Plotting the successive normalized Mantel z-values for each distance category yields a Mantel correlogram. However, it is generally desirable to test statistically not only relative synchrony, as done by Mantel tests, but also absolute synchrony. Various methods for doing this have been suggested (Box 1). However, even with improved analytical methods problems remain, from the unknown effects of measurement error to nonindependence of sites (Box 2).

There are also logistical problems in acquiring sufficient data to analyse spatial patterns. Even a single population study requires a large amount of work, and long-term studies spanning many years are notoriously difficult to fund and maintain. It is consequently not surprising that there are few studies in which workers have acquired many years of demographic data on species at multiple sites covering a large area. Nonetheless, this is exactly what is required to perform robust spatial analyses addressing the question of how synchronous population parameters are over a range of ecologically interesting geographical scales. Those studies that have been done are rarely the product of a single research group; instead, most make use of large, more or less communal datasets acquired as part of long-term monitoring efforts (Table 1).

Patterns and causes of spatial synchrony

What factors drive the spatial autocorrelation observed in ecological phenomena? Answering this question provides critical evidence regarding the importance of various biotic and abiotic factors in the regulation of local populations. Often clues can be extracted from the observed relationship between synchrony and distance. For example, consider the hypothesis that solar activity synchronizes snowshoe hare (*Lepus americanus*) populations via a connection with climate[17]. If this were true, two predictions are that all populations should be synchronous through time and that synchrony should not decline systematically with distance. These follow from the fact that the postulated extrinsic factor (solar activity) is the same, at least relatively, at all points on the globe in a particular year. Comparisons of hare populations within and between continents fail to support this prediction[18]. New and Old World hare populations are asynchronous and there is a clear decline in synchrony with increasing distance between sites in Finland (Fig. 1).

A decline in synchrony between sites as the distance between them increases is the most pervasive pattern emerging from spatial autocorrelation analyses. There are at least three hypotheses that could explain this pattern in various systems[19]: (1) the presence of nomadic predators switching between areas containing high densities of prey; (2) dispersal declining in frequency with increasing distance between sites; and (3) environmental synchrony that declines with distance. A variant of (3) is that the pattern reflects a spatial decline in synchrony in food or some other resource critical to the population. If so, then the factors behind the decline of the critical resource, rather than the species or system directly under study, should be investigated.

Box 1. Testing for spatial autocorrelation: traditional versus new techniques

Mantel correlograms test for autocorrelation relative to the overall dataset. Thus a complete Mantel correlogram always yields approximately the same number of positive and negative values regardless of the underlying pattern of spatial synchrony. By contrast, it is the pattern of absolute, rather than relative, spatial synchrony between sites that is frequently of interest. Various methods for analysing and comparing such data have been attempted, including a regression approach based on all possible 2 × 2 arrays of overlapping data between sites[11], species-specific indices based on the *x*-intercept from the regression of distance on the correlation coefficients[9], and clustering techniques[12,13]. A recent method[14] calculates 'modified correlograms', in which correlation coefficients are divided into distance categories and each set is tested using a randomization procedure in which data from individual sites are used only once. Sets of correlation coefficients derived from randomization trials are averaged and tested for significance based on the proportion of trials yielding mean values greater than (or less than) zero.

This technique yields average correlation coefficients for each distance category and calculates whether they are significantly different from 0. If the ecological factor is being tested against itself (autocorrelation), values cannot be significantly less than zero because multiple sets of data cannot all be inversely correlated with one another. However, if one ecological factor is being tested against another (cross-correlation), values can be either significantly positive or significantly negative. With large datasets, statistically significant values can be obtained even though the absolute degree of correlation is small; whether such low spatial autocorrelation is biologically significant or not must be considered on a case-by-case basis.

Box 2. Statistical nonindependence in spatial autocorrelation analyses

Multiple use of sites: the first source of nonindependence in spatial data stems from the fact that data from N sites yield $[(N*N - 1)/2]$ pairwise correlations despite containing only $(N - 1 + N - 2)$ independent values[15]. Consequently, standard statistical tests using all pairwise values will yield an inflated number of degrees of freedom. Most spatial statistical methods, including Mantel tests and modified correlograms, circumvent this problem using randomization procedures.

Site redundancy: the second source of difficulty is more subtle. Consider 14 sites in two different arrangements: (a) two clumps of seven sites separated by 100 km within which sites are 10 km from each other and (b) a transect in which each site is 10 km from the next:
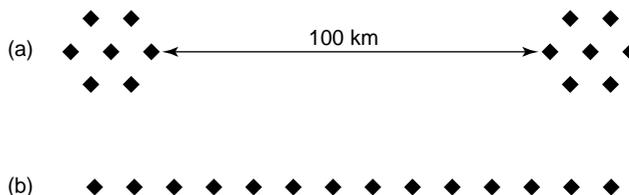
The number of pairwise sites ≤20 km apart is 42 in (a) and 24 in (b), whereas the number of pairwise sites ≥100 km apart is 49 in (a) and 10 in (b). However, assuming that nearby sites (e.g. ≤20 km apart) are highly synchronous, there is little or no additional information regarding either of these distance categories contained in configuration (a), despite the larger sample sizes. In other words, most sites in (a) are redundant.

Site redundancy is general and potentially affects virtually all spatial analyses. In effect, the very phenomenon of interest – spatial autocorrelation – renders sites nonindependent and thus compromises the statistics used to test for its presence. The problem is similar to that of assessing the significance of the correlation between spatially autocorrelated processes[16], but is not as readily circumvented because the procedures affected are randomization tests involving series of correlation coefficients rather than standard parametric tests of individual r values for which the degrees of freedom can be easily adjusted. Site redundancy can be minimized by careful design, such as avoiding large clumps of sites within which autocorrelation is likely to be high. Unfortunately, the spatial scale at which autocorrelation occurs will rarely be known *a priori* and thus optimal design will be possible only after many years of effort have already gone into collecting data.

Because of site redundancy, statistical tests of all spatial processes must be considered with caution. Correcting for multiple comparisons and reducing the probability level needed for rejecting the null hypothesis are ad hoc, but prudent, courses of action.

(Online: Fig. I)

Table 1. Examples of large-scale datasets used or suitable for analysis of spatial autocorrelation

Name	Taxa	Geographical area	Scope	Availability
Christmas Bird Count	Birds	North America	30+ years, 1200+ sites	Can be downloaded from the Web[a]
Breeding Bird Survey	Birds	North America	30+ years, 4000+ sites	Can be downloaded from the Web[b]
Butterfly Monitoring Scheme	Butterflies	UK	20+ years, 120+ sites	Through the Institute of Terrestrial Ecology, UK
Rothamsted Insect Survey	Aphids and moths	Europe	25+ years, 80+ sites	Through the Institute of Arable Crops Research, UK
International Tree-ring Databank	Trees	Worldwide	500+ years, 1200+ sites	Can be downloaded from the Web[c]
Global Historical Climatology Network	Rainfall and temperature	Worldwide	6000+ sites	Can be downloaded from the Web[d]

[a]ftp:// ftp.im.nbs.gov/pub/data/cbc/
[b]ftp://ftp.im.nbs.gov/pub/data/bbs/
[c]http://www.ngdc.noaa.gov/paleo/ftp-treering.html
[d]ftp://ftp.ncdc.noaa.gov/pub/data/ghcn/

All three of these hypotheses have been invoked in particular cases. Predator switching, suggested as a potentially important synchronizing factor of microtine populations[20], has received support largely from theoretical models[21], although multitrophic-level experiments indicate a role for interactions with predators and vegetation in the population fluctuations of snowshoe hares[22]. Greater attention has been focused on the relative importance of environmental perturbations, also known as the Moran effect, compared with dispersal as the cause of the decline in spatial synchrony observed in the population densities of many species. Because dispersal is often locally restricted and always distance dependent to some extent, populations whose synchrony is maintained by dispersal are expected to exhibit a strong decay in synchrony with increasing distance between populations[23]. Thus, the decline in synchrony with distance observed in species as diverse as whitefish (*Coregonus lavaretus*) along the Baltic Sea and capercaillie (*Tetrao urogallus*) in Finland is consistent with dispersal, or connectivity, playing an important role in synchronizing population dynamics[23]. However, dispersal is less likely to play a critical role in synchronizing presumably less vagile species, such as most moths, over distances of hundreds of kilometers[9]. Neither can dispersal be a factor in maintaining synchrony in population fluctuations between populations of sheep on two islands in the St Kilda archipelago[24] (see also p. 1, this issue) nor in statistical synchrony in growth and reproduction of boreal trees between sites 2500 km or more apart[25].

The potential role of environmental factors in the decay in synchrony with distance has been modeled extensively, but conclusions have been mixed. Based on a spatially explicit metapopulation model, Hanski and Woiwod[9] concluded that environmental variation should result in a positive correlation between spatial synchrony and population variability, whereas dispersal should increase synchrony but decrease population variability. Their analyses of spatial synchrony in British moths and aphids generally yielded a positive relationship between these variables, and thus they concluded that spatial synchrony in these taxa was more likely to be due to environmental variation than to dispersal. Ranta *et al.*[23,26] envisioned climatic perturbations acting simultaneously over large areas and resulting in little or no decay of synchrony with distance between populations synchronized by the Moran effect. From this, they concluded that it would be difficult to disentangle the possibilities that dispersal alone determined the patterns of spatial autocorrelation between populations from whether both dispersal and the Moran effect acted in concert. Haydon and Steen[19] modeled the role of environmental perturbations on inter-population synchrony and concluded that synchrony is (1) generated primarily by variation in, rather than the incidence of, extreme large-scale environmental perturbations and (2) unlikely to be maintained by dispersal alone when the coefficients of variation of the environmental processes influencing population dynamics are small.

The pattern of spatial autocorrelation in the environmental factors themselves, such as rainfall and temperature, will determine the role of the Moran effect in synchronizing population dynamics. Surprisingly, there appear to be few published analyses of geographical synchrony in environmental factors, and even fewer of the similarities between such factors and the populations they are likely to influence. Sutcliffe *et al.*[27] suggested that synchrony between UK butterfly populations over distances of 200 km or more resulted from regionally correlated weather patterns, but cited no corroborating data. Lindström *et al.*[28] showed that long-term averages of various regional climatic factors correlated with synchrony in three species of grouse (*Lagopus*) in Finland, but did not attempt to analyse the spatial pattern of year-to-year variation in weather.

What few analyses exist suggest that significant geographical synchrony in environmental factors can extend over large geographical areas[29] but can decline with increasing distance between sites[30] in a similar way to that observed in the populations of many organisms. Recent analyses of three species of oaks (*Quercus*) over a 288 km transect in central coastal California, USA (W.D. Koenig *et al.*, unpublished) indicate that synchrony in annual acorn production between sites closely matches the geographical synchrony observed in spring temperature and rainfall that had previously been demonstrated to correlate with annual acorn production within a site. Further analyses along these lines will be necessary to both disentangle the relative importance of, and eventually determine how best to discriminate between, dispersal and spatially autocorrelated environmental conditions as the main cause of spatial autocorrelation in population dynamics.

Higher-order analyses: drifts, waves and cross-correlations

Analysis of spatial autocorrelation is in its infancy and few studies have gone beyond documenting and attempting to explain basic patterns within species. An exception is a recent analysis of Canadian lynx (*Lynx canadensis*) populations[31]. As in many other species, geographical synchrony in the Canadian lynx is widespread and declines with distance. However, by restricting analysis to a 'sliding' time window of 15 years, in which the starting year is moved forward one year at a time, it was found that cross-correlations between sites could change considerably through time, often drifting from being highly positive to strongly negative over only a few years. Similarly variable temporal dynamics have been found in the spatial structure in acorn production by individual oak trees within a single site in central coastal

California using a sliding time window of 10 years (W.D. Koenig *et al.*, unpublished). These latter results suggest that significant changes through time in geographical synchrony could be widespread among ecological phenomena, even when dispersal is not an issue.

A second example of how higher-order patterns in ecological phenomena can be suggested by spatial analyses is a study of vole damage to young forests in Finland[32], which documented that damage is geographically asynchronous and that the epicenter of damage moves north with increasing severity. One interpretation of these results is that these patterns are caused by 'travelling waves' or pulses of vole outbreaks spreading from south to north, increasing in severity as they go. Analysis of vole plagues in France suggests an analogous pattern, except that the wave of damage moved from north to south.

More widespread application of statistical techniques designed to deal specifically with spatial autocorrelation in ecological phenomena that vary with time (Box 1) should promote innovative investigations into the spatial dimension of population fluctuations. Analyses need not be restricted to the same species (autocorrelations) but can be applied to populations of different species or even to completely independent, but potentially related, ecological phenomena (cross-correlations). For example, cross-correlational analyses could help to reveal the cause of a variety of potentially interconnected ecological phenomena, including the following: the 'eruptions' of boreal seed-eating birds into southern latitudes, which are apparently related to seed-crop failure of trees within their normal range[33]; tradeoffs between growth and reproduction in masting trees[25,34]; and the apparent link between acorn crops, rodent populations, gypsy moth outbreaks and Lyme disease[35].

With sufficient data, such analyses could contribute substantially towards resolving controversies over population regulation and the causes of spatial synchrony within populations. For example, the geographical patterns of synchrony in UK butterfly populations found by Pollard[36] prompted him to conclude that large-scale external factors, rather than community-specific local interactions, such as competitors, predators or parasitoids, play a dominant role in determining patterns of population fluctuation. Lack of significant cross-correlations between population densities of appropriate species (parasitoids, predators and competitors) with the butterfly data, even when sympatric or at least in close geographical proximity, would provide critical evidence to test this conclusion.

Conclusions

Population ecology is about understanding fluctuations in numbers over time and space. Despite decades of intensive work devoted towards understanding the factors affecting the demography of individual populations, we are only beginning to investigate geographical patterns of population fluctuations rigorously. Progress in detecting these patterns has been slow for several reasons, including the paucity of coordinated sets of long-term data on population abundance, problems in manipulating large amounts of data, and a general lack of well-developed statistical techniques to detect and analyse such patterns. These difficulties are rapidly being overcome: standard spatial statistical techniques have been modified to address the issue of spatial synchrony; various long-term, large-scale datasets have become more accessible; and modern technology has made powerful computational facilities readily available to everyone. Future progress in this ecological frontier promises to yield exciting insights into a broad spectrum of ecological questions.

References

1 Horn, H.S. (1968) **The adaptive significance of colonial nesting in the Brewer's blackbird (*Euphagus cyanocephalus*)**, *Ecology* 49, 682–694
2 Verner, J. and Willson, M.F. (1966) **The influence of habitats on mating systems of North American passerine birds**, *Ecology* 47, 143–147
3 Koenig, W.D. *et al.* (1992) **The evolution of delayed dispersal in cooperative breeders**, *Q. Rev. Biol.* 67, 111–150
4 Bradbury, J. (1981) **The evolution of leks**, in *Natural Selection and Social Behavior: Recent Research and New Theory* (Alexander, R.D. and Tinkle, D.W., eds), pp. 138–169, Chiron Press
5 Harrison, S. and Quinn, J.F. (1989) **Correlated environments and the persistence of metapopulations**, *Oikos* 56, 293–298
6 Gilpin, M. (1996) **Metapopulations and wildlife conservation: approaches to modeling spatial structure**, in *Metapopulations and Wildlife Conservation* (McCullough, D.R., ed.), pp. 11–27, Island Press
7 Koenig, W.D. (1998) **Spatial autocorrelation in California land birds**, *Conserv. Biol.* 12, 612–620
8 Thomson, J.D. *et al.* (1996) **Untangling multiple factors in spatial distributions: lilies, gophers, and rocks**, *Ecology* 77, 1698–1715
9 Hanski, I. and Woiwod, I.P. (1993) **Spatial synchrony in the dynamics of moth and aphid populations**, *J. Anim. Ecol.* 62, 656–668
10 Fortin, M-J. and Gurevitch, J. (1993) **Mantel tests: spatial structure in field experiments**, in *Design and Analysis of Ecological Experiments* (Sheiner, S.M. and Gurevitch, J., eds), pp. 342–359, Chapman & Hall
11 Hatch, S.A. (1996) **Concordance of seabird population parameters: analytical methods and interpretation**, in *Studies of High-latitude Seabirds. 4. Trophic Relationships and Energetics of Endotherms in Cold Ocean Systems* (Montevecchi, W.A., ed.), pp. 37–48, Canadian Wildlife Service
12 Reams, G.A. and Van Deusen, P.C. (1993) **Synchronic large-scale disturbances and red spruce growth decline**, *Can. J. For. Res.* 23, 1361–1374
13 Lindén, H. (1988) **Latitudinal gradients in predator–prey interactions, cyclicity and synchronism in voles and small game populations in Finland**, *Oikos* 52, 341–349
14 Koenig, W.D. and Knops, J.M.H. (1998) **Testing for spatial autocorrelation in ecological studies**, *Ecography* 21, 423–429
15 Ranta, E., Lindström, J. and Linden, H. (1995) **Synchrony in tetraonic population dynamics**, *J. Anim. Ecol.* 64, 767–776
16 Clifford, P., Richardson, S. and Hémon, D. (1989) **Assessing the significance of the correlation between two spatial processes**, *Biometrics* 45, 123–145
17 Sinclair, A.R.E. *et al.* (1993) **Can the solar cycle and climate synchronize the snowshoe hare cycle in Canada? Evidence from tree rings and ice cores**, *Am. Nat.* 141, 173–198
18 Ranta, E. *et al.* (1997) **Solar activity and hare dynamics: a cross-continental comparison**, *Am. Nat.* 149, 765–775
19 Haydon, D. and Steen, H. (1997) **The effects of large- and small-scale random events on the synchrony of metapopulation dynamics: a theoretical analysis**, *Proc. R. Soc. London Ser. B* 264, 1375–1381
20 Ydenberg, R.C. (1987) **Nomadic predators and geographical synchrony in microtine population cycles**, *Oikos* 50, 270–272
21 Ims, R.A. and Steen, H. (1990) **Geographical synchrony in microtine population cycles: a theoretical evaluation of the role of nomadic avian predators**, *Oikos* 57, 381–387
22 Krebs, C.J. *et al.* (1995) **Impact of food and predation on the snowshoe hare cycle**, *Science* 269, 1112–1115
23 Ranta, E. *et al.* (1995) **Synchrony in population dynamics**, *Proc. R. Soc. London Ser. B* 262, 113–118
24 Grenfell, B.T. *et al.* (1998) **Noise and determinism in synchronized sheep dynamics**, *Nature* 394, 674–677
25 Koenig, W.D. and Knops, J.M.H. (1998) **Scale of mast-seeding and tree-ring growth**, *Nature* 396, 225–226
26 Ranta, E. *et al.* (1997) **The Moran effect and synchrony in population dynamics**, *Oikos* 78, 136–142

27 Sutcliffe, O.L., Thomas, C.D. and Moss, D. (1996) **Spatial synchrony and asynchrony in butterfly population dynamics,** *J. Anim. Ecol.* 65, 85–95

28 Lindström, J., Ranta, E. and Lindén, H. (1996) **Large-scale synchrony in the dynamics of capercaillie, black grouse and hazel grouse populations in Finland,** *Oikos* 76, 221–227

29 Heino, R. (1994) *Climate in Finland during the Period of Meteorological Observations,* Finnish Meteorological Institute (Contribution No. 12)

30 Goodridge, J.D. (1991) **One hundred years of rainfall trends in California,** in *Proceedings of the Seventh Annual Pacific Climate Workshop* (Interagency Ecological Studies Program Technical Report 26) (Betancourt, J.L. and Tharp, V.L., eds), pp. 109–114, California Department of Water Resources

31 Ranta, E., Kaitala, V. and Lundberg, P. (1997) **The spatial dimension in population fluctuations,** *Science* 278, 1621–1623

32 Ranta, E. and Kaitala, V. (1997) **Travelling waves in vole population dynamics,** *Nature* 390, 456

33 Bock, C.E. and Lepthien, L.W. (1976) **Synchronous eruptions of boreal seed-eating birds,** *Am. Nat.* 110, 559–571

34 Kelly, D. (1994) **The evolutionary ecology of mast seeding,** *Trends Ecol. Evol.* 9, 465–470

35 Jones, C.G. *et al.* (1998) **Chain reactions linking acorns to gypsy moth outbreaks and lyme disease risk,** *Science* 279, 1023–1026

36 Pollard, E. (1991) **Synchrony of population fluctuations: the dominant influence of widespread factors on local butterfly populations,** *Oikos* 60, 7–10

Beauty is in the eye of the beholder: causes and consequences of variation in mating preferences

Fredrik Widemo and Stein Are Sæther

Mate choice (any behaviour that restricts the set of potential mates, Box 1) may evolve whenever access to mates of a certain quality, or resources provided by mates, limits the reproductive success of individuals[1,2]. This is often the case for females, whereas males tend to be limited by the number of available mates. The latter situation favours the evolution of adaptations that expand rather than restrict the set of potential mates. The outcome of mate choice depends on the individual mating preferences and the extent to which they can be expressed. Thus, it can be difficult to determine mating preferences from the outcome of mate choice[3,4] (Box 1). Contest competition can often influence the mating pattern. However, the distinction between contest competition and mate choice is not always obvious. Females might set the stage for male–male contest competition, thereby exerting a form of indirect mate choice without necessarily comparing males directly[1,2]. Here, we focus on mating preferences under direct mate choice expressed before copulation (Box 1).

In a recent and comprehensive review, Jennions and Petrie[3] examined empirical and theoretical studies of variation in mating preferences and concluded that individual variation in preferences is common and can have major consequences for models of sexual selection. We have adopted the terminology used by Jennions and Petrie, whereby mating preferences are determined by preference functions and degree of choosiness. In Box 1, we have

To a large extent, the success of evolutionary ecology stems from its focus on individual variation and acknowledging that individuals vary in predictable ways. Sexual selection is probably the branch of evolutionary ecology that has received most interest in the past two decades. Paradoxically, progress has been hampered by not taking individual mating preferences into account. Now, researchers are starting to pay more attention to individual variation in preferences. This change in focus holds great promise for future advances in the study of sexual selection.

Fredrik Widemo is at the Section of Animal Ecology, Dept of Zoology, Villav. 9, SE-752 36 Uppsala, Sweden (fredrik.widemo@zoologi.uu.se); Stein Are Sæther is at the Dept of Zoology, Norwegian University of Science and Technology, N-7034 Trondheim, Norway (sas@alfa.itea.ntnu.no).

extended their concepts to provide a framework for thinking about factors affecting the outcome of mate choice and the potential sources of variation in preferences.

Variation in mating preferences

Previously, there has been a strong tendency to view mating preferences typologically as species-specific and uniform[3,5]. Variation in mate choice is often claimed to stem from errors in mate assessment or limited availablility of partners. Alternatively, poor observational or experimental methods have been blamed.

Geographical variation in mating preferences is, however, well documented; examples come from insects, amphibians, fish and birds[3]. Choosiness might be expected to vary geographically depending on ecological conditions, but preference functions can also vary[6]. For example, geographical variation in mating preferences might be expected in hybrid zones. Here, a high degree of choosiness and strong preference for traits that differentiate between species would be expected in order to avoid hybridization. Indeed, female *Ficedula* flycatchers were recently found to reverse their allopatric preferences for elaborate traits in areas of sympatry, to facilitate species recognition and hybrid avoidance[7].

Variation in mating preferences within populations has received less attention, but evidence for such variation is now accumulating[3,8–13]. How then can variation in mating preferences be generated?