There are some important differences between copying individual decisions and cultural inheritance of mating preferences, which mean that this result should be interpreted cautiously. I have taken care to distinguish mate copying and cultural transmission, because whilst copying may result in cultural inheritance, it need not necessarily do so. Cultural inheritance requires that females not only imitate individual behaviours (in this case the mating decisions of other females), but that they also tend to repeat this *type* of behaviour (ie. make similar mating decisions) subsequently[15]. For example, if a female guppy observes another female choosing the duller of two males (guppies usually prefer to mate with brighter males), and then proceeds to mate with the same male, that is evidence of copying. However, only if she then tends to mate consistently with duller males can she be said to have inherited (at least one aspect of) the mating preference of the model female.

Earlier theoretical work[7,8] modelled copying, rather than cultural transmission, showing how it can cause an increase in the opportunity for sexual selection. Recent models have moved on to address cultural preference transmission[16,17], in which the female's preference is lastingly altered in response to the types of males that she observes mating. However, none of the empirical evidence for copying (in any species)[1–3,12–14] has shown that females' tendency to copy has any long-term effects on the expression of their mating preferences. One obvious priority for future research, therefore, should be to test whether copying can result in the shaping of individual female's preferences, and meaningful population-level change (*sensu* Boyd and Richerson[15]) in mate choice.

Acknowledgements
Many thanks to Graham Alexander, Mark Blows, John Endler and Mike Jennions for helpful comments and discussion, and to JCU and the FRD (South Africa) for postdoctoral support.

Robert Brooks

Dept of Zoology & Tropical Ecology, School of Biological Sciences, James Cook University of North Queensland, Townsville, Qld 4811, Australia

References

1 Dugatkin, L.A. (1992) **Sexual selection and imitation: females copy the mate choice of others,** *Am. Nat.* 139, 1384–1389
2 Dugatkin, L.A. and Godin, J-G. (1992) **Reversal of female mate choice by copying,** *Proc. R. Soc. London Ser. B* 249, 179–184
3 Dugatkin, L.A. (1996) **The interface between culturally based preferences and genetic preferences: female mate choice in *Poecilia reticulata*,** *Proc. Natl. Acad. Sci. U. S. A.* 93, 2770–2773
4 Lafleur, D.L., Lozano, G.A. and Sclafani, M. (1997) **Female mate-choice copying in guppies, *Poecilia reticulata*: a re-evaluation,** *Anim. Behav.* 54, 579–586
5 Clutton-Brock, T.H., Hiraiwa-Hasegawa, M. and Robertson, A. (1989) **Mate choice on fallow deer leks,** *Nature* 340, 463–465
6 Clutton-Brock, T.H. and McComb, K. (1993) **Experimental tests of copying and mate choice in fallow deer (*Dama dama*),** *Behav. Ecol.* 4, 191–193
7 Pruett-Jones, S. (1992) **Independent versus nonindependent mate choice: do females copy each other?** *Am. Nat.* 140, 1000–1009
8 Wade, M.J. and Pruett-Jones, S.G. (1990) **Female copying increases the variance in male mating success,** *Proc. Natl. Acad. Sci. U. S. A.* 87, 5749–5753
9 Brooks, R. (1996) **Copying and the repeatability of mate choice,** *Behav. Ecol. Sociobiol.* 39, 323–329
10 Endler, J.A. (1995) **Multiple-trait coevolution and environmental gradients in guppies,** *Trends Ecol. Evol.* 10, 22–29
11 Briggs, S.E., Godin, J-G. and Dugatkin, L.A. (1996) **Mate-choice copying under predation risk in the Trinidadian guppy (*Poecilia reticulata*),** *Behav. Ecol.* 7, 151–157
12 Grant, J.W.A. and Green, L.D. (1996) **Mate copying versus preference for actively courting males by female Japanese medaka (*Oryzias latipes*),** *Behav. Ecol.* 7, 165–167
13 Schlupp, I. and Ryan, M.J. (1994) **Benefit to male sailfin mollies of mating with heterospecific females,** *Science* 263, 373–374
14 Schlupp, I. and Ryan, M.J. (1997) **Male sailfin mollies (*Poecilia latipinna*) copy the mate choice of other males,** *Behav. Ecol.* 8, 104–107
15 Boyd, R. and Richerson, P.J. (1985) *Culture and the Evolutionary Process*, University of Chicago Press
16 Kirkpatrick, M. and Dugatkin, L.A. (1994) **Sexual selection and the evolutionary effects of copying mate choice,** *Behav. Ecol. Sociobiol.* 34, 443–449
17 Laland, K. (1994) **Sexual selection with a culturally transmitted mating preference,** *Theor. Popul. Biol.* 45, 1–15

Scaling up the value of bioindicators

Species whose presence or abundance readily reflect some measure of the character of the habitat within which they are found are often identified as bioindicators[1], most frequently to monitor changes within a particular habitat. In spite of the intuitive appeal of bioindication, largely as a consequence of its cost-effectiveness in the face of urgent conservation issues, indicator studies frequently fall short of providing spatially explicit and objectively determined indicator species or species subsets. This is particularly true of studies involving invertebrates. A recent paper by Dufrêne and Legendre[2] outlines and applies a straightforward and efficient method for addressing this shortcoming.

Although previously-developed and commonly-used techniques seek to identify bioindicators within groups of taxa (e.g. I-tests, correspondence analysis, two-way indicator species analysis), many of these suffer from methodological problems[3,4]. For example, one is frequently constrained in the choice of site clusters for the identification of indicator sets by the site classification procedure used. Also, many of these methods use relative species abundance measures that are easily biased by sampling methods with differential sampling efficiency for different taxa. This use of compositional data can also severely bias the patterns that are generated by classification procedures[5]. Furthermore, many techniques have a tendency to select rare species as being distinctive of particular habitats or sample units[3]. The risks associated with such choices include the possibility of selecting vagrant species, or individuals from non-viable or sink populations[6].

The value of bioindicators would thus be highest if species whose indicator values were calculated independently of other species in the assemblage were truly representative of a group of sites, by being unique to that site group (high specificity), as well as by being abundant and widespread within it (high fidelity). Such species would not only have a high information content, but also a high probability of being sampled during monitoring and assessment. If, at the same time, one had the freedom to combine sites in as many meaningful ways as required, the optimum group of sites necessary for the conservation of the indicator species could be established. This approach is of particular value when dealing with taxa, such as invertebrates, where there is a paucity of information on the distribution and biology of the majority of species sampled.

This is the essence of the approach and method advocated by Dufrêne and Legendre[2]. The indicator value (IndVal) of a species is expressed as the degree (%) to which it fulfills the criteria of specificity and fidelity within any particular group of sites. The method derives indicators from any, *a priori* or *a posteriori*, hierarchical or non-hierarchical site classification. The association between each species and site group may be determined independently both of the clustering procedure and of

  0169-5347/98/$19.00 PII: S0169-5347(97)01279-2

other species, and, importantly, the significance of each indicator species is subsequently established using a site randomization procedure. The indicator value of a species (see Box 1), defined as the most characteristic species of each group, is thus highest when the individuals of the species are present in all sites of only one site group. Because the indicator value of a species can also be calculated for any combination of sites (or for any level of a hierarchical classification), the maximum indicator value (see Box 1) not only identifies the species with the highest indicator value, but also the site grouping (or level) for which it is most representative. Thus, for example, if a beetle species is equally abundant both in woodland and pasture its indicator value will by necessity be highest for the two habitats combined, rather than for either of these.

This flexibility with regard to the site categorization on which the IndVal measures (Box 1) are based is one of the most significant advantages of the method. For example, it can be used for the identification of bioindicators for existing conservation areas or habitat types (which may have been arbitrarily selected); for groups of sites based on the outcome of the classification of any set of non-target taxa (e.g. insect bioindicators of plant community classifications), as well as for site clusters determined using the target taxa themselves (i.e. groups of sites clustered using the target taxa, and bioindicator species selected from within these clusters). There are a number of other methodological and practical advantages associated with the method that Dufrêne and Legendre advocate. Because each IndVal measure is absolute (expressed as a percentage), and is calculated independently of other species in the assemblage, direct comparisons of indicator value can be made between taxonomically unrelated taxa, taxa in different functional groups, or those in different communities. In addition, and importantly, if taxa show very similar specificity and fidelity trends, but differ in abundance (e.g. mites versus carabid beetles), their IndVal remains the same, hence making comparisons across taxa robust to differences in abundance.

When the sites within a group are spatially contiguous, the method can also be used to delimit the core of the distribution range of the focal species for the sites concerned. This group of sites will thus have the highest probability of encompassing viable populations of those species with the highest indicator values, and can therefore be used to identify core conservation areas for particular species where little to no distributional or biological information is available.

The IndVal of a species *absence*, which can be calculated using a rationale similar to the one underlying the species presence IndVal, also has advantages. This absence IndVal, which unlike most previous absence values is not symmetric to the presence IndVal, identifies species that occur less frequently and in very much lower abundances in a particular group of sites than in any other of the site groups. As such, it provides one method for improving the objectivity with which species transient to an assemblage in a particular group of sites can be identified, a problem that has traditionally beset analyses involving species abundances of little known taxa[7].

Dufrêne and Legendre's approach is in principle rather similar to the Braun–Blanquet system[8,9] used extensively by phytosociologists. Nonetheless, their method considerably advances the field of bioindication, especially where terrestrial invertebrates are concerned. It provides a simple method for identifying the value of indicator species that is robust to differences in the numbers of sites between site groups, to differences in abundance between sites within a particular group, and to differences in the absolute abundances of very different taxa which may show similar trends. Furthermore, by using a permutation test to assess the significance of individual indicator species, Dufrêne and Legendre complement Clarke's methods for assessing the significance of differences between clusters[3] in a hierarchical classification, using the randomization procedures that are becoming so indispensable to ecologists[10].

Taxa proposed as bioindicators have often been accused of being merely the favourite taxa of their proponents[1,11]. Ornithologists prefer birds, lepidopterists butterflies, and coleopterists beetles. Dufrêne and Legendre have provided an objective method for assessing the merits of rather different taxa for a given range of sites. The species that do emerge from this procedure as the most useful indicators of a group of sites are also likely to be robust to small differences in sampling procedures that could alter species relative abundances. Thus these species, which show both high site specificity and fidelity, can confidently be used in practical conservation for monitoring site changes. As a consequence, Dufrêne and Legendre have increased the value to conservation practitioners of a concept that has long appealed to conservation biologists, but until now has fallen somewhat short of its practical goals.

Box 1. The indicator species value[2]

Specificity measure

$A_{ij} = \text{Nindividuals}_{ij}/\text{Nindividuals}_{i.}$

where Nindividuals_{ij} is the mean number of species *i* across sites of group *j*, and $\text{Nindividuals}_{i.}$ is the sum of the mean numbers of individuals of species *i* over all groups.

Fidelity measure

$B_{ij} = \text{Nsites}_{ij}/\text{Nsites}_{.j}$

where Nsites_{ij} is the number of sites in cluster *j* where species *i* is present, and $\text{Nsites}_{.j}$ is the total number of sites in that cluster.

Indicator Value

$A_{ij} \times B_{ij} \times 100 = \text{IndVal}_{ij}$
$\max[\text{IndVal}_{ij}] = \text{IndVal}_{i}$

Acknowledgements

We thank Niek Gremmen (Bureau Data Analyse Ecologie, Netherlands) for helpful comments on phytosociological approaches, and both he and Clarke Scholtz (University of Pretoria) for commenting on an earlier draft of this manuscript.

Melodie A. McGeoch
Steven L. Chown

Dept of Zoology and Entomology, University of Pretoria, Pretoria, 0002, South Africa

References

1 Stork, N.E. and Samways, M.J. (1995) **Inventorying and monitoring of biodiversity,** in *Global Biodiversity Assessment* (Heywood, V.H., ed.), pp. 453–543, Cambridge University Press
2 Dufrêne, M. and Legendre, P. (1997) **Species assemblages and indicator species: the need for a flexible asymmetrical approach,** *Ecol. Monogr.* 67, 345–366
3 Clarke, K.R. (1993) **Non-parametric multivariate analyses of changes in community structure**, *Aust. J. Ecol.* 18, 117–143
4 Belbin, L. and McDonald, C. (1993) **Comparing three classification strategies for use in ecology,** *Veg. Sci.* 4, 341–348
5 Jackson, D.A. (1997) **Compositional data in community ecology: the paradigm or peril of proportions?** *Ecology* 78, 929–940
6 Vane-Wright, R.I. (1996) **Identifying priorities for the conservation of biodiversity: systematic biological criteria within a socio-political framework,** in *Biodiversity. A Biology of Numbers and Difference* (Gaston, K.J., ed.), pp. 309–444, Blackwell
7 Gaston, K.J. *et al.* (1993) **Relationships between abundance and body size: where do tourists fit?** *Ecol. Entomol.* 18, 310–314
8 Goodall, D.W. (1953) **Objective methods for the classification of vegetation. II. Fidelity and indicator species,** *Aust. J. Bot.* 1, 434–456
9 Jongman, R.H.G., Ter Braak, C.J.F. and Van Tongeren, O.F.R., eds (1995) *Data Analysis in Community and Landscape Ecology*, Cambridge University Press
10 Crowley, P.H. (1992) **Resampling methods for computation-intensive data analysis in ecology and evolution,** *Annu. Rev. Ecol. Syst.* 23, 405–447
11 Williams, P.H. and Gaston, K.J. (1994) **Measuring more of biodiversity: can higher taxon richness predict wholesale species richness?** *Biol. Conserv.* 67, 211–217