The 'species alias' problem

SIR — May and Nee[1] correctly raise the issue of synonymy — multiple names for single biological entities — as an important one for biodiversity studies. As Solow et al.[2] showed, roughly 20% of names for thrips proposed during this century are now regarded as synonyms. Using the time needed to detect the synonymy to model asymptotic levels, true relation between synonymy rate and mass (using order-of-magnitude values for each order) is $r_s = 0.755$ $(P<0.05)$. Rate estimates range from a low of 17% for the inconspicuous and poorly known shrew opossums (Paucituberculata) to 78% for tapirs (Perissodactyla; other groups, edentates 64%, opossums 64%, primates 59%, carnivorans 56%, ungulates 56%, monitos

Mammalian orders	(a)* Species both in 1982 and currently	(b) Synonyms newly sunk	(c) Synonyms newly elevated	(d) Names newly proposed
Didelphimorphia	52	21	9	3
Paucituberculata	5	2	0	1
Microbiotheria	1	0	0	0
Xenarthra	29	0	0	1
Lipotyphla	13	0	1	2
Chiroptera	236	6	23	11
Primates	46	1	29	7
Carnivora	54	0	4	0
Perissodactyla	3	0	0	0
Artiodactyla	17	0	2	0
Rodentia	479	32	105	35
Lagomorpha	2	0	0	0
Faunal totals	**937**	**62**	**173**	**60**

NOMENCLATUREL CHANGES FOR SPECIES OF NEOTROPICAL MAMMALS SINCE 1980[7]

*Current species diversity estimate is the sum of columns (a) + (c) + (d)

synonymy rates may actually be closer to 40%. In discussing the general implications of this argument for biodiversity, May and Nee stated that rates of synonymy are lower among the more charismatic vertebrate groups, and that global estimates of diversity need to be correspondingly reduced to correct for these lacunae of misunderstanding.

Both of these important conclusions are debateable. Using an ongoing database for Neotropical mammals[3], it is possible to consider these points for roughly 25% of the world's mammal species. Across 12 terrestrial mammal orders, 1,173 species and 1,439 subspecies are currently recognized as valid, with another 2,143 names treated as synonyms. So defined, synonyms comprise 45% of all mammalian names, about twice the fraction demonstrated for thrips (this number actually climbs to 75% if subspecies are discounted). Synonymy rates for mammalian orders are not correlated with ordinal diversity ($r_s = 0.06$), but are positively (not negatively) correlated with body size and presumed conspicuousness. The rank cor-

50%, shrews 43%, bats 39%, rodents 36%, rabbits, 26%).

Species concepts play central and underappreciated roles in all biodiversity matters[4], especially those involving species diversity and synonymy. Widespread acceptance of the biological species concept[5] led many taxonomists in the mid-twentieth century to treat earlier names as synonyms of large polytypic species. Modern workers, perhaps increasingly motivated by phylogenetic interests, place more emphasis on diagnosis of taxa and less on establishing their reproductive limits[6]. A result of this trend has been the resurrection of names that were earlier treated as synonyms. This tendency is documented for Neotropical mammals in the table : three-quarters of the names for all species recognized since 1980 had earlier been regarded as synonyms. Over this same time period, three times as many names were resurrected from synonymy as were newly sunk or newly proposed. Nearly 15% of the names for all valid species today were considered synonyms as recently as 1982[7]. (See also last week's issue[8])

Granted, lower resurrection rates might be expected among the invertebrate groups highlighted by May and Nee. Synonymies among less intensively studied groups are more likely to be a consequence of unwitting duplication of effort than of conceptual disagreement or revision. Nevertheless, synonyms are not purely errors in applying systematic classifications, but are also by products of the

systematic concepts used. Although future investigations will assuredly reveal many current names to be synonyms of others now in circulation, changing systematic concepts and improved technologies for detecting and defining species will continue to breathe new life into yesterday's entombed synonyms.

B. D. Patterson
Department of Zoology
The Field Museum
Chicago, Illinois 60605-2496, USA

In the red zone

SIR — The problem of whether temporal fluctuations in natural populations are composed mainly of low- or high-frequency variation is of theoretical as well as practical interest for ecological and evolutionary questions. Cohen[1] examined eight population models given by difference equations of the form $P_{t+1} = P_t \cdot f(P_t)$, where P_t is the population density at time t, and $f(P_t)$ is a density-dependent fitness function. He argued that high frequencies dominate in the power spectra of chaotic time series obtained from these models. This casts doubt on the usefulness of one-dimensional difference equations for modelling fluctuating population dynamics, because low frequencies are expected to dominate the spectra of natural time series[2,3].

It may, however, be too early for general conclusions. Cohen[1] reports results for a limited choice of parameters in each model, yet these models exhibit chaos for a broad
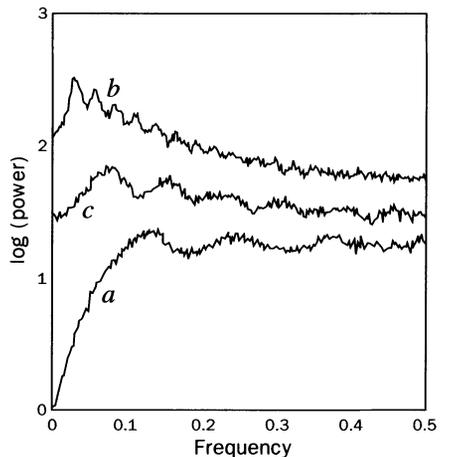

FIG. 1 Averaged power spectra for three one-dimensional models obtained using exactly the same method as Cohen[1]. Curve *a* results from the Ricker equation, with $r = 4.7$. With increasing r, the initial slope and the similarity with white noise increase, although the fluctuations in the corresponding time series become very large. Curve *b* results from the Maynard Smith model, with $a = 0.02$, $r = 1.5$ and $b = 50.0$, and curve *c* from Bellows' equation with $a = 0.1$, $r = 3.0$ and $b = 4.8$. Both spectra are reddened.

1. May, R. M. & Nee, S. *Nature* **378**, 447–448 (1995).
2. Solow, A. R., Mound, L. A., & Gaston, K. J. *Syst. Biol.* **44**, 93–96 (1995).
3. Patterson, B. D. *Biodiversity Let.* **2**, 79–86 (1994).
4. Mallet, J. *Trends Ecol. Evol.* **10**, 294–299 (1995).
5. Mayr, E. *Systematics and the origin of species*, (Columbia Univ. Press, New York (1942).
6. Cracraft, J. in *Speciation and its consequences* (eds Otte, D. & Endler, J. A.) 28–59 (Sinauer , Sunderland, Massachusetts, 1989).
7. Honacki, J. H., Kinman, K. E. & Koeppl, J. W. (Eds) *Mammal species of the World* (Allen Lawrence, Kansas, 1982).
8. Altaba, C. R., *Nature* **380**, 488–489 (1996).

589

range of parameters. Even in the simple Ricker model, with only one parameter in the fitness function (model 1 in ref. 1), the spectrum changes for different parameter values: increasing the growth rate r flattens the spectrum (Fig. 1, curve a), and it becomes reminiscent of white noise, where all frequencies have equal power.

More sophisticated models, with more parameters, are more flexible, and the changes can be more dramatic. For example, in the Maynard Smith model $f(P_t) = r \cdot [1+(aP_t)^b]^{-1}$ (model 5 in ref. 1), the dynamics are determined by the parameter b, describing the type and strength of competition, and by the intrinsic growth rate r, whereas a scales the carrying capacity. In this model, large values of b (severe density dependence) and small values of r typically yield reddened spectra with more power at low frequencies (Fig. 1, curve b).

A very general model for density dependence, not analysed by Cohen[1], is Bellows'[4] fitness function $f(P_t) = r \cdot \exp[-(aP_t)^b]$. (The Maynard Smith model is a simplified version obtained by truncating a Taylor series expansion of the denominator.) In this model, reddened power spectra (Fig. 1, curve c) are common. An index for the colour of a spectrum is the ratio between the area under the spectrum ranging from 0 to 0.25 and
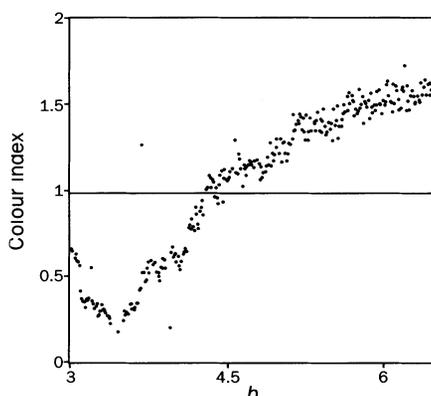

FIG. 2 Colour index for spectra from the Bellows model (see text). White noise has an index of 1 (horizontal line). Indices larger than 1 indicate reddened spectra and those smaller than 1 blue spectra. Outliers in the figure correspond to spectra with discrete peaks in the sense of Cohen[1].

the area ranging from 0.25 to 0.5: the ratios of blue spectra with more power at high frequencies are smaller than 1, while those of red spectra are larger than 1.

Figure 2 shows the colour index for the spectra corresponding to 300 values of parameter b in the interval [3, 6.5]. The other parameters were fixed at $r = 2.5$ and $a = 0.005$. Only b values leading to chaotic time series were considered. The lower

limit of the b interval was chosen to ensure that chaotic time series are possible, the upper limit to prevent unrealistically large fluctuations in these trajectories. Red spectra occur for a broad range of b values describing intermediate to strong competition.

We conclude from our calculations that blue spectra are indeed easy to observe in the models considered by Cohen. For each model, however, there is a range of parameters where fluctuations are chaotic but the corresponding spectra are reddened, or at least very similar to white noise. For the equations of Bellows and Maynard Smith, which are the most general one-dimensional ecological models[4,5], reddened spectra are common, especially when competition is intense. The open question posed by these results and by Cohen's is to understand when and why some parameter values give blue spectra and others red spectra.

Albert Blarer
Michael Doebeli
Zoology Institute, University of Basel,
Rheinsprung 9,
CH-4051 Basel, Switzerland

1. Cohen, J. E. Nature **378**, 610–612 (1995).
2. Sugihara, G. Nature **378**, 559–560 (1995).
3. Halley, J. M. Trends Ecol. Evol. **11**, 33–37 (1996).
4. Bellows, T. S. Jr J. anim. Ecol. **50**, 139–156 (1981).
5. Doebeli, M. Theor. Populat. Biol. **47**, 82–106 (1995).

Why squid can breathe easy

SIR — Cephalopods are all predators and typically have high metabolic rates. Nevertheless, a huge biomass of squid apparently live in the deep oceans, often in severely hypoxic waters[1]. This prompted us to examine the gills of various deep-sea cephalopods. Compared with their shallow-water relatives, squid from the cold deep oceans tend to have large gill areas and very thin blood–water barrier thicknesses[2] (see table). Among fish, only the warm-blooded tuna[3,4] have similar weight-specific gill areas and comparable barrier thicknesses. The limited data available on the morphometrics of deep-water fish gills suggest that these gill areas are actually reduced in comparison

with shallow-water species[5].

Estimates of the gill diffusion capacities of deep-water squid indicate that these animals could remain active, swimming about rapidly even in the oxygen-minimal layers of the open ocean. The price is very fragile gills. Cephalopods can tolerate these conditions where fish cannot because the gills do not form part of the buccal apparatus; there is no danger of damage from sharp fragments of cuticle, scales and bones penetrating the gills when the animal feeds. Deep-water squid are living in an environment where only very clear, grit-free water enters the mantle — even the anus is downstream of the gills. We suspect that very high oxygen

diffusion capacities of these fragile gills give squid like *Bathyteuthis* or *Brachioteuthis* a much-needed edge in their competition with fish and are perhaps in part responsible for the huge numbers of cephalopods to be found in the deep oceans.

J. J. Madan
M. J. Wells
Department of Zoology,
University of Cambridge,
Cambridge CB2 3EJ, UK

1. Clarke, M. R. in Cephalopod Life Cycles Vol. 2 (ed. Boyle, P. R.) 221–237 (Academic, London, 1987).
2. Madan, J. J. thesis (Univ. Cambridge, 1995).
3. Perry, S. F. in Oxygen Transport in Biological Systems (eds Eggington, S. & Ross, H. F.) 57–77 (Cambridge Univ. Press, 1992).
4. Hughes, G. M. Respir. Physiol. **14**, 1–25 (1972).
5. Hughes, G. M. J. Linn. Soc. Zool. **59**, 195–208 (1976).
6. Eno, N. C. J. Mar. Biol. ass. U.K. **74**, 687–706 (1994).

CEPHALOPOD GILL DATA					
Cephalopod species	Weight	Ambient seawater oxygen content	Gill area	Blood–water diffusion barrier	Gill diffusion capacity
	(g)	(ml per l)	(cm^2 per g)	(μm)	(ml O_2 per kg per mmHg per min)
Deep-water species					
Bathyteuthis abyssicola [2]	4.27	2.59	21.88	1.10	2.999
Brachioteuthis riisei [2]	8.26	3.23	45.14	1.01	3.160
Cranchia scabra [2]	11.51	3.73	27.04	3.10	0.755
Liocranchia reinhardti [2]	5.49	2.59	13.33	1.58	0.882
Histioteuthis reversa [2]	37.09	4.44	11.87	2.52	0.435
Octopoteuthis danae [2]	26.53	3.43	8.96	1.63	0.492
Vampyroteuthis infernalis [2]	18.81	3.62	4.74	3.34	0.311
Shallow-water species					
Octopus vulgaris [6]	40.00	5.15	5.40	8.58	0.058
Eledone moschata [2]	334.00	5.15	2.91	14.98	0.025
Alloteuthis subulata [6]	8.98	5.15	11.76	6.19	0.274
Lolliguncula brevis [2]	10.58	5.15	7.03	1.34	0.512