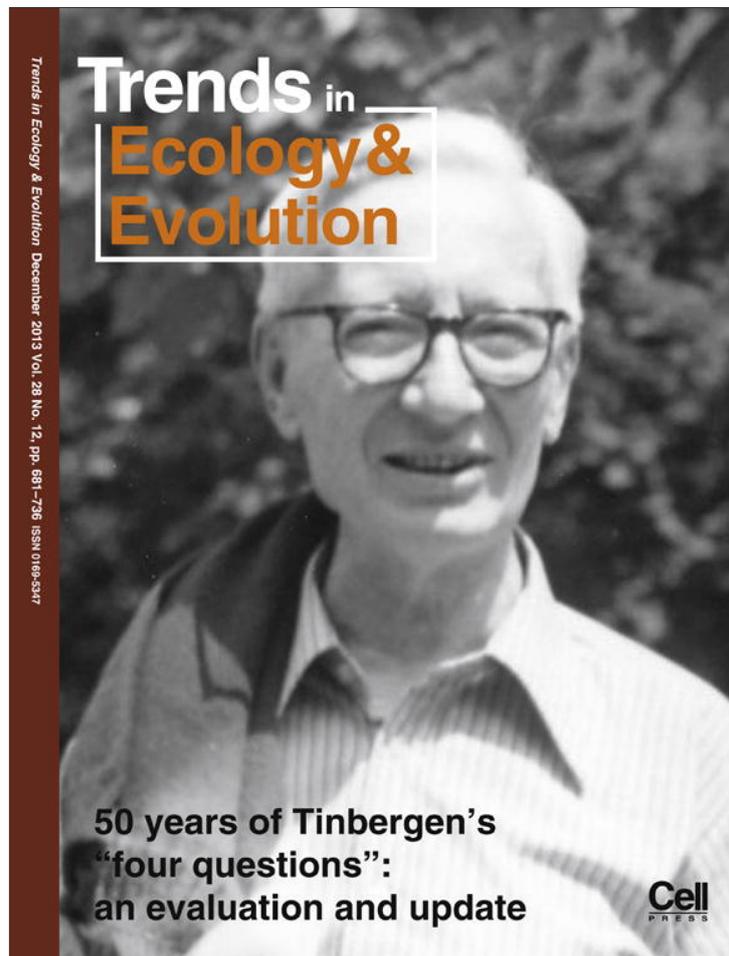


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tions, and two different objects of explanation. Two of the questions are about proximate mechanisms, and two are about evolution. Two of the objects of explanation are about the current trait, and two are about the sequences that result in the trait. This suggests a two-by-two table that illustrates how the questions are related (Table 1). When I started using a slide of this table in lectures at the turn of the millennium my discussions with the audience changed: instead of wanting answers to questions about Darwinian medicine they wanted only a copy of the slide.

The table has evolved in response to user suggestions. Tinbergen used 'evolution' to describe phylogeny, and 'survival value' to describe adaptive functions, but evolution now routinely refers to phylogeny and natural selection, and other evolutionary forces, and it is therefore the appropriate term for the overarching category. As noted by Bateson and Laland, 'survival value' is outmoded now that we recognize the centrality of reproductive success. 'Function' is a poor alternative because it encourages the incorrect assumption that each trait has one specific function, whereas some have none and others have several that may involve tradeoffs. The proposed term, 'current utility', seems likely to promote confusion. Current utility can, of course, be different from past utility, but as a recent article in this journal pointed out: 'it is impossible to differentiate exaptation from adaptation unless we interpret the term teleologically' [4]. Also, most students asked about the current utility of noses mention their usefulness in supporting eyeglasses. Tinbergen wanted evolutionary explanations of the form of a trait in terms of how its variations in previous generations interacted with past environments to help account for its current form. Yes, it can be hard to decide what selection forces help to explain the nature of a

trait, but that is no reason to give up on trying to answer what is often the most engaging question. As Tinbergen put it: 'I have always been amazed, and I must admit annoyed as well, when I met, among fellow-zoologists, with the implied or stated opinion that the study of survival value must necessarily be guesswork' ([5] p. 418).

Tinbergen's questions were framed for behavior, but they are equally useful for other traits. Skin tanning, the mechanisms that synthesize bilirubin from biliverdin, parietal cells in the stomach that secrete acid – these and a thousand other traits also need all four explanations. We need to know how they work, how they develop, their phylogeny, and how past variations have influenced fitness in ways that help to explain their current forms. Hopefully Tinbergen's Four Questions will, by their 100<sup>th</sup> anniversary, have been extended to the full range of biology.

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## On current utility and adaptive significance: a response to Nesse

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Randy Nesse agrees with us that Tinbergen's four questions were, and continue to be, an extremely valuable contribution to science, but disagrees over which term best replaces Tinbergen's now-dated term 'survival value'. Nesse favours 'adaptive significance' whereas we prefer 'current utility'. The problems with 'adaptive significance' are discussed in our main article [1]: it is ambiguous as to whether the term refers to original or current functionality (which frequently will not be the same) and misleadingly implies that all functionality must result from a biological evolutionary process (which is now known to be false). 'Current utility' suffers from neither of these drawbacks,

but we worry that Nesse's terminology, like his figure, will perpetuate these problems.

Nesse, by contrast, is concerned that 'current utility' seems likely to promote confusion, claiming that it will encourage 'noses function to support eyeglasses' reasoning. He asserts that it is only through teleological thinking that adaptations and exaptations can be distinguished. For us, this misses the point. Although we do not object to teleological interpretation, it clearly would be foolhardy to suggest that its utilization safeguards against the misdiagnosis of adaptation. Gould and Lewontin's [2] critique of the 'Panglossian paradigm' used Voltaire's satire to illustrate problems with a vulgar adaptationist stance in which 'noses function to support eyeglasses' reasoning is rife. They write (p. 581): 'We fault

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the adaptationist programme for its failure to distinguish current utility from reasons for origin' and for not considering how current utility 'may be an epiphenomenon of non-adaptive structures.' Likewise, Tinbergen's [3] annoyance with those who characterized the study of survival value as guesswork was precisely because he advocated the experimental investigation of how a character benefits its carrier in the present (i.e., its current utility) and not speculation about how it might have operated in the past. He describes in detail how survival value in the present can be investigated experimentally, drawing on his own pioneering research. It does not follow that researchers should ignore the origin and past functionality of the trait, but it is current utility that, for

Tinbergen, must be the primary, scientifically accessible question.

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## Inbreeding and asexuality: a response to Szulkin *et al.*

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Szulkin *et al.* [1] point out that inbreeding depression is not the only genetic factor relevant to the evolution of inbreeding strategies. Specifically, they discuss the inclusive fitness advantage of inbreeding that results from higher genetic relatedness of offspring to parents, which might favor inbreeding even in the face of inbreeding depression. However, they neglect the effects of the greater genetic recombination that results from outcrossing. Such effects are believed to overcome a twofold decrease in relatedness of offspring, thus accounting for the maintenance of meiotic sex in anisogamous species [2]. These effects are also relevant to the closely related question of avoidance of self-fertilization and other forms of inbreeding.

Szulkin *et al.* consider three factors: decreased offspring fitness due to inbreeding depression, increased relatedness of inbred offspring, and costs involved in avoiding inbreeding. In the absence of inbreeding depression, their reasoning would predict that self-fertilization will always be favored over outcrossing. However, obligate selfing is, in effect, a form of asexuality. So too is, for example, obligate brother-sister mating, which rapidly leads to homozygosity and hence an effective lack of recombination. In fact, complete dispensation of mating (i.e., non-meiotic production of offspring identical to the parent) would also be an optimal strategy under these simple assumptions. Thus, the very existence of sex suggests that this reasoning is incomplete. The myriad advantages that have been proposed for sex, most of which involve genetic recombination, should be included in the possible advantages of outcrossing.

This argument applies to milder forms of inbreeding as well. Just as obligate self-fertilization amounts to asexuality, partial self-fertilization is a partial retreat from sex. To the extent that inbreeding leads to homozygosity, it

decreases opportunities for meaningful recombination. There is, in effect, no genetic recombination among loci in the autozygous portion of an offspring's genome; the offspring's gametes preserve the associations that it has inherited.

Recombinational effects of inbreeding complicate the analysis of inbreeding strategies. These effects lack the immediacy of inbreeding depression – they are not manifest in the products of a mating, but only in subsequent generations – making them difficult to measure and model. Hypothesized advantages of recombination are numerous and varied, some involving deleterious mutation and some involving advantageous mutation [2]. Recombination can even be disfavored because it can break up coadapted combinations of alleles [2].

Despite these difficulties, the recombinational consequences of inbreeding must be taken into account. To neglect the effects of recombination when considering mating strategies is to ignore the reasons that mating arose in the first place.

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