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Commentary

Where have all the trees gone? The declining use of phylogenies in animal behaviour journals

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Phylogenetic comparative methods have a rich history in the study of animal behaviour (Brooks & McLennan 1991; Martins 1996; Owens 2006). For early ethologists, comparative studies of multiple species were an essential technique for reconstructing the processes and patterns of behavioural evolution (Lorenz 1941, 1958; Tinbergen 1951, 1959, 1963; McKinney 1965; van Tets 1965; also see Darwin 1872). Indeed, this approach was one of Niko Tinbergen's four 'levels of analysis', the others being the functional significance, ontogenetic development and proximate mechanisms underlying such traits (Tinbergen 1963; Sherman 1988). To these researchers, phylogenetic relationships among species provided a fundamental framework upon which our understanding of the other processes responsible for animal behaviour may be derived (Brooks & McLennan 1991).

Despite its early importance, however, the historical component of behaviour subsequently received relatively little attention in comparison to other research interests in the field (Brooks & McLennan 1991; Wenzel 1992; Ryan 1996; Owens 2006). This reduced attention was due in part to early scepticism that behavioural similarities between species due to homology could be distinguished from similarities due to convergent evolution (Atz 1970). Behavioural traits were often considered far too labile and homoplasious to be useful as characters in phylogenetic analyses (reviewed by Wenzel 1992). But this change in focus also coincided with a variety of exciting new approaches for understanding behavioural traits (e.g. Hamilton 1964; Maynard Smith 1974) and a general shift in interest towards current adaptive function (Ryan 1996; Owens 2006). Wenzel (1992, page 361) put it bluntly in his assessment that 'ethology has made almost no advance with respect to a phylogenetic understanding of behavior since the late 1950s'.

Yet, during this same time period, another science was flourishing. Hennig's (1966) cladistic methods inspired a progression of new techniques for estimating phylogenetic relationships and comparing traits across taxa, which together revolutionized our abilities to reconstruct character evolution (Brooks & McLennan 1991; Harvey & Pagel 1991; Avise 2004; Freckleton 2009). For example, from a statistical perspective, accurate phylogenies are necessary to transform comparative data so that they do not violate the assumptions of statistical independence (Felsenstein 1985; Garland et al. 1992; Martins & Hansen 1997). Studies also

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revealed that behavioural traits are not necessarily any more homoplasious than are other phenotypic traits (Wenzel 1992; de Quiroz & Wimberger 1993; Gittleman et al. 1996) and, indeed, that even complex behaviours can be studied using rigorous phylogenetic methods (Irwin 1996; Slikas 1998; Price & Lanyon 2002). Following the publication of two widely influential books on these methodologies by Brooks & McLennan (1991) and Harvey & Pagel (1991), the field of animal behaviour showed renewed enthusiasm for using a phylogenetic comparative approach to address behavioural questions (Martins 1996; Owens 2006).

Without question, this is an exciting time for researchers interested in studying the historical component of animal behaviour. With a variety of recent advances, including the increasing availability of DNA-based phylogenies, the development of increasingly sophisticated phylogenetic comparative techniques, and the advent of large-scale behavioural databases, our abilities to reconstruct behavioural evolution have never been greater. Yet the actual impact of these new methodologies on the study of animal behaviour is unclear. To track this developing field, we investigated the use of phylogenetic information in behaviour papers during the past 25 years.

METHODS

We surveyed papers published from 1985 to 2009 in five behaviour journals: *Animal Behaviour*, *Behaviour*, *Behavioral Ecology*, *Behavioral Ecology and Sociobiology* and *Ethology*. For each journal, we used the ISI Web of Science™ database to search for papers containing the search terms 'phylogen* or comparative' in their titles, abstracts and keywords, with the rationale that such terms indicate the use of phylogenetic information or phylogenetic comparative techniques (Owens 2006). Each of the resulting articles from these searches was then examined by eye to determine whether they contained a phylogenetic tree in figure form.

For comparison, we conducted similar word searches in a variety of other science journals over the same time period. For these analyses we selected widely read journals that cover general scientific and biological findings (*Nature*, *Proceedings of the National Academy of Sciences, U.S.A.*, *Proceedings of the Royal Society, Series B*, and *Science*) as well as more specialized journals from disciplines closely related to the study of behaviour (e.g. evolutionary biology: *Evolution, Journal of Evolutionary Biology, Trends in Ecology & Evolution*; ornithology: *Auk, Condor, Journal of Avian Biology*; ecology: *American Naturalist, Ecology, Functional Ecology, Oecologia, Oikos*; physiology: *Journal of Applied Physiology, Journal of Comparative Physiology A and B, Journal of Experimental Biology, Physiological and Biochemical Zoology*). For all, the appearance of phylogenetic information in papers was measured as a proportion of total papers published each year. Such annual values are not necessarily independent due to temporal autocorrelation; therefore, we did not test any apparent increases or decreases in publication frequency within journals for statistical significance. Rather, we compared the slopes of these trends using analyses of covariance (ANCOVA), with either journal type or publication period (before or after 2000; see below) as a fixed factor. All statistical analyses were performed using SPSS v.18.0.2 (IBM Corporation, Somers, NY, U.S.A.).

RESULTS

Of the 16 672 papers published in behaviour journals during the past 25 years, overall, only 2.7% (455) referred to phylogenetic information, as indicated by word searches for 'phylogen* or comparative', and fewer than 1% (129) included figures of phylogenies. These frequencies are similar to the overall proportions of papers using phylogenetic or comparative terminology in general science journals (1.8% of articles), but they are lower than the proportions measured in several other disciplines closely related to the study of behaviour, such as journals in evolutionary biology (15.0%), ornithology (6.4%) and ecology (4.6%).

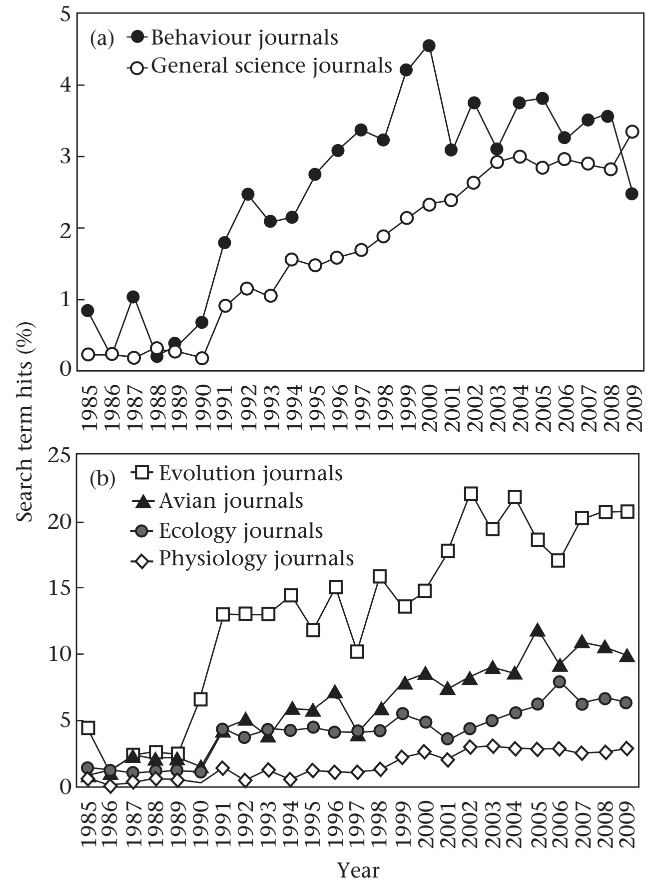

Figure 1. Total percentage of papers over the last 25 years (1985–2009) that referred to phylogenetic information, as indicated by hits in 'phylogen* or comparative' word searches on ISI Web of Science™, in (a) behaviour journals (*Animal Behaviour*, *Behaviour*, *Behavioral Ecology*, *Behavioral Ecology and Sociobiology* and *Ethology*; $N = 16\,672$) and general science journals (*Nature*, *Proceedings of the National Academy of Sciences, U.S.A.*, *Proceedings of the Royal Society, Series B*, and *Science*; $N = 218\,319$) and in (b) evolution journals (*Evolution*, *Journal of Evolutionary Biology*, *Trends in Ecology & Evolution*; $N = 10\,978$), avian journals (*Auk*, *Condor*, *Journal of Avian Biology*; $N = 7160$), ecology journals (*American Naturalist*, *Ecology*, *Functional Ecology*, *Oecologia*, *Oikos*; $N = 25\,492$) and physiology journals (*Journal of Applied Physiology*, *Journal of Comparative Physiology A and B*, *Journal of Experimental Biology*, *Physiological and Biochemical Zoology*; $N = 32\,782$).

All journals surveyed showed a general increase in the appearance of phylogenetic information from 1985 to 2000, especially following publication of the books by Brooks & McLennan (1991) and Harvey & Pagel (1991) (Fig. 1a, b). After the year 2000, however, the appearance of such information in behaviour journals generally declined, in contrast to the continued increase seen in all other journals surveyed. For example, before the year 2000, the phylogenetic content in both behaviour journals and general science journals increased steadily with very similar slopes (ANCOVA: $F_{2,141} = 2.61$, $P = 0.11$; Fig. 1a), but trends in these two groups of journals differed significantly after that year ($F_{2,87} = 4.34$, $P = 0.04$). Trends in behaviour journals also differed significantly before and after 2000 (ANCOVA: $F_{2,122} = 7.27$, $P = 0.008$), whereas trends in general science journals during these same time periods did not ($F_{2,97} = 0.381$, $P = 0.54$). Indeed, in all of the other

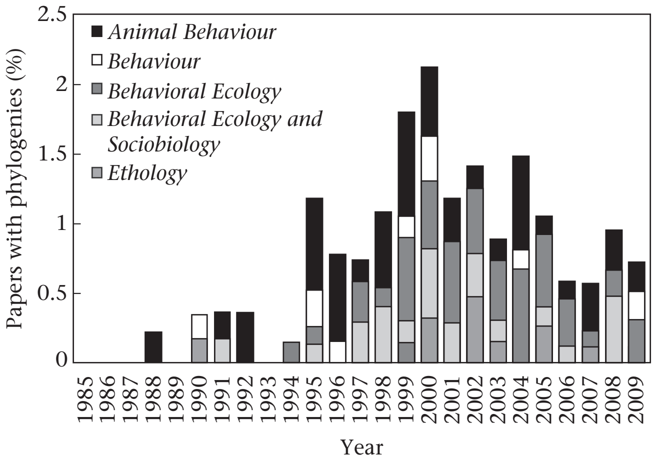

Figure 2. Percentage of papers in five animal behaviour journals that included figures of phylogenies (*Animal Behaviour*: $N = 7270$; *Behaviour*: $N = 1851$; *Behavioral Ecology*: $N = 2021$; *Behavioral Ecology and Sociobiology*: $N = 3208$; *Ethology*: $N = 2322$).

disciplines surveyed, increases in phylogenetic content did not differ in slope before and after 2000 (evolution: $F_{2,69} = 0.50$, $P = 0.48$; avian: $F_{2,63} = 0.004$, $P = 0.95$; ecology: $F_{2,118} = 2.13$, $P = 0.15$; physiology: $F_{2,83} = 1.92$, $P = 0.17$; Fig. 1b), and such consistent increases were also seen in additional 25-year surveys across a range of other biological disciplines (e.g. *Journal of Mammalogy*, *American Journal of Botany*, *Journal of Parasitology*). Thus, the decreasing appearance of phylogenetic information in behaviour journals appears to be unique to this discipline.

The appearance of figures of phylogenies in the five surveyed behaviour journals showed an equally striking pattern (Fig. 2), increasing in frequency from 1985 to 2000 and then deceasing steadily over the subsequent decade. Regression coefficients before and after the year 2000 differed significantly (ANCOVA: $F_{2,122} = 5.43$, $P = 0.021$) and were almost perfectly inversely related (before 2000: 0.024; after 2000: −0.024).

DISCUSSION

In a previous survey of behaviour literature, Owens (2006) noted that fewer than 5% of papers published from 2001 to 2005 used a phylogenetic approach (using search terms 'phylog* or comparative'). But he also anticipated that new comparative techniques and information, especially molecular phylogenies and large-scale behavioural databases, were generating renewed interest among behavioural ecologists in employing such methods. Similar levels of enthusiasm are evident in recent editions of several textbooks (e.g. Alcock 2009; Dugatkin 2009), in which the comparative analysis of behaviour remains an important focus. Clearly, the historical component of animal behaviour is viewed by many as a topic worth investigating.

Yet, despite this apparent interest, our evidence suggests that the use of phylogenetic and comparative methods in animal behaviour studies has not increased during the past decade. In fact, such approaches appear to have declined in behaviour journals while at the same time increasing in many other scientific publications (Fig. 1). This decline is especially evident in the decreasing appearance of phylogenetic trees in papers, a trend that does not appear to be the result of changes in any single journal (Fig. 2). The decline in phylogenies is also not easily explained by authors increasingly referring to trees published previously or in other journals; if this were the case, references to phylogenetic information (Fig. 1a) would presumably not have declined in concert with the decline in trees (Fig. 2). Word searches using the terms 'phylogen* or comparative' produced overall trends that were remarkably similar in shape to searches using 'phylogen*' alone, suggesting that these recent declines are not simply due to changes in the terminology used in describing comparative data.

It could be that this apparent decline is simply a random fluctuation. The appearance of phylogenies is relatively rare in behaviour journals (never more than 4% of articles in any journal during any year) and thus should be expected to exhibit notable variation in frequency from year to year. But the overall trend in behaviour journals, a consistent increase followed by a general decade-long decline, does not match publication trends in any other discipline surveyed that had similar proportions of hits in our word searches. Moreover, even if the use of phylogenies has simply levelled off in behaviour journals rather than declined, this difference from other disciplines should still generate concern among those who study animal behaviour, as they may be overlooking some important and increasingly useful approaches for understanding behavioural evolution. Assuming we can reject the null hypothesis that these patterns are due to chance, what might explain the trends shown in behaviour journals?

An interesting but perhaps unlikely possibility is that the most readily studied systems for addressing broad historical questions have already been investigated, such as the evolution of various life history traits (Brooks & McLennan 1991; Gittleman et al. 1996; Alcock 2009), leaving fewer opportunities for further research. Some groups of organisms are certainly better suited than others for studying the evolution of particular traits. However, this explanation that we have 'plucked the low-hanging fruit' seems unlikely given the increasing availability of information on a wide variety of behaviours (e.g. vocalizations, visual displays, breeding systems), especially through online databases. Furthermore, our abilities to estimate phylogenetic relationships have increased dramatically in recent years and phylogenies have been revised accordingly, so many earlier comparative studies are now in need of re-evaluation.

Alternatively, it may be that such repeated revisions to phylogenetic hypotheses have themselves been a problem. That is, some animal behaviour researchers may have turned away from phylogenetic comparative methods in part because the phylogenies used in these studies have been revised so frequently (Ryan 1996). The 1990s saw a dramatic increase in the use of phylogenetic methods in general following books by Brooks & McLennan (1991) and Harvey & Pagel (1991) at the beginning of that decade, including a renewed interest in using such methods in studies of behaviour (e.g. Martins 1996). But this early excitement led to critical reappraisals later on (Gittleman et al. 1996; Ricklefs & Starck 1996; Martins & Hansen 1997; Cunningham et al. 1998; Losos 1999; Omland 1999; Freckleton et al. 2002; Freckleton 2009). Furthermore, as often happens in science, a number of exciting new findings about behavioural mechanisms (e.g. Searcy 1992) were later discounted as new phylogenetic information became available (Gray & Hagelin 1996). Historical interpretations of behaviour are only as good as the phylogenies upon which they are based, and many of the early phylogenetic trees used in comparative studies were much less certain than many researchers may have presumed. In addition, phylogenetic comparative methods have become increasingly sophisticated in recent years, as have the software packages used to perform them (Freckleton 2009). Thus, the updating of phylogenetic hypotheses during these last two decades as well as the increasing sophistication of comparative techniques may have caused some to abandon this promising new field.

A final possibility is that the use of phylogenetic information by behavioural researchers actually has increased during the previous decade, as in other disciplines, but these researchers are publishing their studies in other journals, such as those specializing in evolutionary or general biology. This is a difficult idea to test, but it certainly rings true for those of us who have published many of our phylogenetic behavioural studies in nonbehaviour journals. If this is indeed the case, we contend that these trends should still be a significant cause for concern within the field of animal behaviour, because a key component in our understanding of behaviour, indeed one of Tinbergen's (1963) 'four questions' for behavioural analysis (Sherman 1988; Alcock 2009), may be increasingly appearing in journals outside of the discipline. At the very least, those who publish these behaviour journals should consider the missed opportunities represented by such a shift.

Regardless of the underlying factors, our evidence that phylogenetic information is being used less often in behaviour journals should caution researchers in this field to avoid turning away once again from a historical perspective on behaviour, which previously had been such an important and useful component of the discipline. Declines in phylogenetic behavioural studies may be occurring just as a variety of exciting new methodologies are proving themselves so useful in other fields. Indeed, phylogenetic hypotheses have become increasingly reliable in recent years, in large part due to dramatic increases in the availability of molecular data (Haussler et al. 2009), so revisions to phylogenies may be occurring less and less often. There has never been a better time for animal behaviour researchers to revisit the use of phylogenetic information and thus revive interest in Tinbergen's important fourth question.

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