



Trends in animal behaviour research (1968–2002): ethoinformatics and the mining of library databases

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We applied modern bioinformatic tools to titles and keywords of animal behaviour publications contained in an electronic library database to examine trends in animal behaviour research. We provide the first quantitative overview of animal behaviour research covering 42 836 documents published in the last three decades, across 25 journals. Our study confirms several patterns noted by previous reviews, and offers several novel insights into the history of our field. Profound historical distinctions between early ethology and comparative psychology have been recently bridged by shared interest in communication and social behaviour, and research from physiology and applied areas. Although we reiterate the rise of sexual selection and mating behaviour as prominent areas of research, we also show that interest in mechanism and development has proven particularly resilient over the years. Currently, researchers at hundreds of institutions worldwide are studying animal behaviour. Domesticated animals, foraging/dispersal and learning/memory are topics that appear most frequently in publications from regions that have little history of animal behaviour research, suggesting that these subjects are central to the early development of the discipline. Overall, the study of animal behaviour is healthy, growing, and becoming progressively more integrative over time.

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The study of animal behaviour has a long and illustrious history (Durant 1986; Dewsbury 1989) featuring many of the great names in science (e.g. Darwin 1872; Tinbergen 1951; Thorpe 1956; Lorenz 1965). Our discipline has undergone remarkable change, particularly over the last few decades. Recent reviews note the rise in popularity of behavioural ecology (Alcock 2003; Bateson 2003), and debate the potential consequences of this apparent skew on other areas of animal behaviour research (e.g. the study of mechanism and development: Bateson & Klopfer 1989; Stamps 2003; West et al. 2003). There are many practical and social factors that may influence the types of questions addressed by behavioural researchers (e.g. modern advances in life sciences technology, global information exchange over the internet). Until recently, however, these factors were exceedingly difficult to consider in any comprehensive way. Here, we make use of modern informatics techniques and electronic library databases to

study the recent history of published animal behaviour literature. We first validate our approach by documenting patterns noted by previous reviewers (e.g. the rise of behavioural ecology), and then apply our methods to explore the relative importance of disciplinary and geographical factors.

In the late 19th century, the study of animal behaviour was largely restricted to amateur naturalists (Durant 1986). The discipline emerged formally with the appearance of *Zeitschrift für Tierpsychologie* (1937; now *Ethology*), *Behaviour* (1948) and the *British Journal of Animal Behaviour* (1953; now *Animal Behaviour*). By 1973 the Nobel Prize committee had recognized the pioneering work of Niko Tinbergen, Konrad Lorenz and Carl von Frisch (1953, 1967), and the study of animal behaviour had become well established. We now have sophisticated methods for examining the genetic and physiological underpinnings of behaviour (e.g. Landgraf et al. 2003; Phelps & Young 2003; Cooper & Goller 2004). Technological advances have facilitated the study of function (e.g. acoustic and video playbacks: McGregor 1992; Ord & Evans 2002) and evolution (e.g. the comparative method: Gittleman 1989; Martins 1996), as well as improving techniques for

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studying behaviour in the field (Altmann & Altmann 2003). Mathematical and computer modelling have become invaluable tools for predicting how animals will interact with other individuals (e.g. game theory: Maynard Smith & Price 1973) and the environment (e.g. foraging theory: Stephens & Krebs 1986).

The 50-year anniversary of *Animal Behaviour* prompted several recent reflections on the current status and future of the field (Alcock 2003; Altmann & Altmann 2003; Bateson 2003; Slater 2003; Stamps 2003; West et al. 2003). These reviews note the prominence of behavioural ecology (Alcock 2003; Bateson 2003), but also a renaissance of studies on mechanism and development (Stamps 2003; West et al. 2003). However, these commentaries are necessarily based on subjective overviews of only a small proportion of the published literature. Even limiting a survey to only those studies appearing in the last three decades, there are literally hundreds of academic journals that have collectively published tens of thousands of papers (e.g. Table 1). Previous reviews therefore rely on a small subset of material (e.g. Dewsbury 1992; Klopfer &

Polemics 2002; Alcock 2003; Huntingford 2003; Salvador et al. 2003) and/or personal reflections (e.g. Bateson & Klopfer 1989; Bateson 2003). In this study, we take a different approach, using specialized computer software to mine library information databases for important historical and contemporary trends. Innovations in information science have spurred the development of a plethora of software to exploit the huge quantities of information offered by new online databases. Although these methods are necessarily limited by the availability of electronic information, they offer scholars a potentially more objective view of the available literature, and a comprehensive way to explore the current focus and historical content of research.

There are numerous articles providing excellent discussion on the potential social and political issues underlying apparent direction shifts in animal behaviour research (Durant 1986; Sherman 1988; Barlow 1989; Dawkins 1989; Dewsbury 1989, 1992, 1994; Armstrong 1991; Alcock & Sherman 1994; Alcock 2003; Bateson 2003; Slater 2003; Stamps 2003; West et al. 2003). To begin our

Table 1. Number of article records available for each journal in this study

	Start of coverage	Incomplete or no coverage	Total documents	1971–1972	1981–1982	1991–1992	2001–2002
Core ABA journals							
<i>Animal Behaviour</i>	1968		5887	154	226	382	491
<i>Behavioral Ecology and Sociobiology</i>	1976	1977–1982, 1985–1991	2011			208	262
<i>Applied Animal Behaviour Science</i>	1986		1700			174	235
<i>Behavioral Ecology</i>	1990		928			81	206
<i>Behaviour</i>	1968		2000	61	81	131	160
<i>Ethology</i>	1991		870			97	158
<i>Behavioural Processes</i>	1976	1977	1244		52	103	131
<i>Journal of Insect Behavior</i>	1988		850			104	118
<i>Animal Learning & Behavior</i>	1973	1978–1980	1500		146	96	64
<i>Journal of Experimental Psychology: Animal Behavior Processes</i>	1975		780		24	74	64
<i>Learning & Motivation</i>	1971		888	52	53	37	53
<i>Journal of Ethology</i>	1986		302			36	40
<i>Bird Behavior</i>	1981	1982–1983, 1988, 1992–1995	112		4	16	8
		Subtotal	19 072	267	586	1539	1990
Supplement journals							
<i>Hormones and Behavior</i>	1971		1496	53	69	83	564
<i>Physiology & Behavior</i>	1968		11 120		639	744	539
<i>Behavioural Brain Research</i>	1980		3257		137	239	502
<i>Behavioral Neuroscience</i>	1984		1931			195	228
<i>Journal of Comparative Psychology</i>	1984	1986–1990	628			88	102
<i>Behavior Genetics</i>	1970	1970–1972, 1977	1178		76	208	86
<i>Learning & Memory</i>	1998		219				85
<i>Aggressive Behavior</i>	1974	1975–1978	652		22	55	70
<i>Journal of the Experimental Analysis of Behavior</i>	1968		2186	178	126	120	70
<i>Ethology Ecology & Evolution</i>	1989		433			68	59
<i>Behavior Research Methods</i>	1984		524			48	50
<i>Behavioral and Brain Sciences</i>	1981	1981–1991, 2002	140		2	15	24
		Subtotal	23 764	231	1071	1863	2379
		Total	42 836	498	1657	3402	4369

'Core ABA journals' are those chosen by Animal Behavior Abstracts (CSA, Inc. 2002), not including *The Birds of North America* or *Etologia*. 'Supplement journals' refer to additional journals included in our analyses despite not being listed as core serials by ABA list (see text for details).

own study, we first confirm the validity of our approach by documenting some of the patterns shown by earlier authors (e.g. distinctions between classical ethology and comparative psychology (Dewsbury 1989, 1992), and the expansion of behavioural ecology (Bateson & Klopfer 1989; Dawkins 1989; Alcock 2003; Bateson 2003)). We then consider several entirely new questions, for example, measuring the extent to which initial differences between ethology and comparative psychology have been bridged, questioning the decline and/or resurgence of 'mechanism' studies, and exploring the role of specific journals in changing our field. We also offer a contemporary snapshot of our discipline in terms of the research being done, where it is being published, and who is producing it.

To conduct our quantitative overview of animal behaviour research, we applied data-mining and knowledge visualization tools to citation records available online in the Biological Abstracts database (BioSciences Information Service, BIOSIS, Inc. Philadelphia, Pennsylvania, U.S.A.). Of the 25 journals that exhibited a primary focus on the study of behaviour, we found 42 836 records for documents published from 1968 to 2002. First, we adopted a historical perspective and mapped major trends in research interest over the last three decades. We used similarities in title vocabulary to identify research topics that linked individual studies into clusters and explored how these clusters have changed over time. We also conducted a 'burst' analysis to identify dramatic increases and/or sustained usage of particular terms and to track changes in popular title-words over time. Second, we shifted our focus to keywords and explored patterns in contemporary behavioural research (2001–2002) explained by journal, geographical and institutional factors.

METHODS

Data Collection and Extraction

To identify journals covering animal behaviour research, we began with the serials source list used by the Animal Behavior Abstracts (ABA) database (Cambridge Scientific Abstracts, CSA, Inc., Bethesda, Maryland, U.S.A. 2002). This list covers 235 journals categorized by relevance, including 15 'core' journals in which all material appearing in the journal is pertinent to animal behaviour (e.g. *Animal Behaviour*). Focusing on these core journals, we removed two: there were no publication records available for *Etologia*, and *The Birds of North America* (a natural/life history reference) seemed too general in scope to be included in our analyses. There were several conspicuous absences from the ABA core list, most notably the *Journal of Comparative Psychology* (not appearing anywhere on the ABA list) and physiology-oriented journals, such as *Hormones and Behavior* (usually listed by ABA as 'priority', reflecting that these serials sometimes publish research that could not be strictly considered 'animal behaviour'). We therefore supplemented the reduced ABA list with 12 additional journals: the *Journal of Comparative Psychology* and those that include 'behaviour', 'ethology' or 'learning' in the journal

title (Table 1). Although we conducted separate analyses on the 13 core ABA journals and the complete listing of 25 journals, we report results only for the latter unless otherwise specified.

There are many biological journals that publish animal behaviour research not included in our study (e.g. *Nature*, *Science*, *Proceedings of the Royal Society of London, Series B*). However, such journals also produce a massive number of nonbehaviour-related publications, which would bias the results of our analyses and compromise the objectives of our study. Although papers appearing in high-impact journals such as *Nature* or *Science* are important contributions to our field, the value of including these articles in our analyses is negated by technological limitations of having to also incorporate the entirety of the journal's contents. Doing so would obscure most of the interesting patterns related to animal behaviour research and expand the focus of our study from trends in behavioural research to those more relevant to the life sciences as a whole (e.g. see Mane & Börner 2004). The *Proceedings of the National Academy of Sciences* alone published more research articles in the last 20 years of our sample than did the 25 journals included in our study combined (Boyack 2004). A preliminary run of our analyses that included *The Birds of North America* identified 'geographic distribution' as the most common keyword in animal behaviour publications, simply because the large number of publications in this serial, and its consistent use of a particular keyword, swamped patterns from other animal behaviour journals. We struck a balance by supplementing our 'core' animal behaviour journals with ABA 'priority' serials that clearly emphasize behavioural research, despite publishing also more general scientific research. A comparison between these two types of journals gives us some insight into differences between publications in core and peripheral journals, leaving for future studies the task of developing reliable methods for identifying 'behaviour' papers in more general scientific journals (e.g. Griffiths & Steyvers 2004).

Using International Standard Serial Numbers (ISSN) to identify journals, we downloaded all available citation records as ASCII text files from the Biological Abstracts database (BIOSIS, Inc. 2002). The standard library web interface prevents data streaming by restricting the number of records that can be downloaded at a time, which can result in a large number of network time-outs and failures. Instead, we used access client software SilverPlatter WinSPIRS v4.01 (Ovid Technologies, Inc., New York, New York, U.S.A.) to download records directly from the server of Indiana University's main library.

We wrote several parsers to extract relevant data from downloaded files. Parsers are algorithms that identify and break data into smaller elements according to their structure or syntax within a data file. For example, a parser was written to use commas to break up an address string (e.g. T. J. Ord, Department of Biology, Indiana University, Bloomington, Indiana 47405, U.S.A.) into separate sections identifying author, department, university, city, state and country, allowing the extraction of information associated with a specific field (e.g. country). Other parsers resemble the 'find and replace' option available in word-processing software. All parser code and software used in

this study are available through the Information Visualization Software Repository (Börner & Zhou 2001; Börner 2004). Using parsers, we converted downloaded files to delimited text files and removed duplicate documents (identified by the string 'title#year#author#keywords'). To verify that our data set was complete, we noted the number of documents listed by Biological Abstracts during each ISSN search and later crosschecked this number with those files actually downloaded. Finally, we calculated summary information on the number of unique records for each journal in each year. Publication records for several journals were incomplete, ranging from approximately 1 year (e.g. *Behavioural Processes*: 1977) to 13 years (e.g. *Behavioral Ecology and Sociobiology*: 1977–1982, 1985–1991; Table 1). Before proceeding with our analyses, we confirmed these records were missing from Biological Abstracts (E. Ten Have, BIOSIS, personal communication) and not the consequence of errors accumulated during data acquisition. Our final data set covered 25 journals from 1968 to 2002 totalling 42 836 records of published material (Table 1, Fig. 1).

Our analysis focuses on the vocabulary chosen for titles and keywords of animal behaviour publications. Keywords and title vocabulary in the animal behaviour literature provide complementary rather than duplicate information. Titles tend to focus on the primary subject of a paper and are more useful in identifying broad themes in animal behaviour research. We used title-words to explore major changes in topics and study organisms of interest across the three decades included in our data set. Keywords contain more detailed information and have the advantage of retaining compound terms, such as 'sexual selection' and 'parental care'. We used keywords for more detailed analysis of journal and geographical trends.

In our analysis of title-words, we began by using parsers to remove uninformative words such as 'of' and 'the', identified from stop-word lists (available from Börner & Zhou 2001; Börner 2004). Keyword information is presented in Biological Abstracts as a string of compound

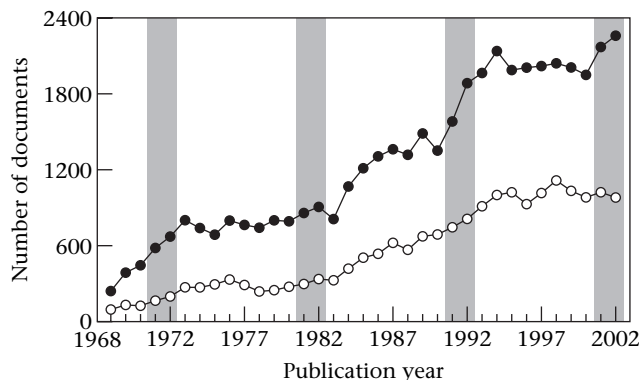


Figure 1. The number of documents covered in the Biological Abstracts database that appear in journals publishing animal behaviour research. Open circles indicate document counts for journals considered to be core contributors to Animal Behavior Abstracts, while closed circles represent counts for all journals included in this review (see Table 1). Shaded areas represent 2-year 'snapshots' used in some document analyses.

words separated by semicolons (e.g. 'anthophilous insects; breeding systems; climate severity; disturbance; evolution; habitat') and are found in two separate fields: DE or 'descriptors', and MI or 'misc. indicators'. We combined keywords from DE and MI fields before conducting further analysis. For both title and keyword analyses, we also removed 'behavio/ur' and 'behavio/ural', which occurred often enough that they might obscure more subtle document associations.

Knowledge Domain Visualizations

Relationships among prominent topic areas through time

To identify broad themes in animal behaviour, and to monitor their changes over time, we entered title-words into a latent semantic analysis (LSA; Landauer et al. 1998). LSA produces a large matrix of documents by title-words and applies a singular value decomposition (using LSA SVDPACKC; Berry 1993) to highlight important latent dimensions in the matrix. Put simply, the analysis isolates each word in a title and searches for the same term in other document titles. When the program finds common vocabulary, it creates a link between the documents. The more links shared between records, the greater the assumed overlap in topic area (see below).

There were 24 850 unique title-words in our data set, a sample size too large to be effectively manipulated by visualization software. To explore changes in prominent research themes and topic relationships through time, we isolated publications appearing in 1971–1972, 1981–1982, 1991–1992 and 2001–2002 for all 25 journals (Fig. 1, Table 1), conducting separate analyses for each pair of years. These 'snapshots' reduced the data set to a manageable size, while still providing a broad sample to illustrate research trends reliably.

In essence, LSA produces a similarity score for each comparison of two publication titles based on the number and context of common words. The strength of LSA lies in its ability to resolve the potentially confounding problem of synonymy (similar meaning words) and polysemy (words with multiple meaning) by comparing, not only the similarity in vocabulary, but also the context in which words appear. Hence, document titles with common words used in similar contexts will be judged to be more closely related than if they simply share identical terms. Text similarity judgements obtained using LSA are consistent with human word sorting and category judgements (Landauer et al. 1998).

We used Pajek visualization software (Batagelj & Mrvar 1997, 2003) to identify clusters of related documents and links among them based on the most important latent dimensions. Implementing the 'Kamada–Kawai' algorithm (Kamada & Kawai 1989) with circular start position, this program was used to draw two-dimensional images of the document similarity matrices, effectively highlighting groups or clusters of documents with similar title vocabulary. The program begins by placing documents (represented by a node or dot) along an outer circle. It then sifts through the similarity matrix produced by the LSA and connects publications with a line according to their

similarity values. As links are created, documents are drawn together. By providing a visual representation of matrices (hence ‘visualization’), we can easily identify how documents are related to each other.

To reduce clutter in plots caused by superfluous links between documents, only similarity scores greater than 70% were traced. The success of particular thresholds to draw out salient document associations is dependent on the number of documents analysed: the larger the pool of samples, the greater the chance an individual record has of sharing semantic similarity with another document. Because the number of articles published in each 2-year snapshot varied (Table 1), we tailored similarity cutoffs for each cohort to optimize the visibility of clusters. Final cutoffs were 0.70, 0.70, 0.74 and 0.755 for 1971–1972, 1981–1982, 1991–1992 and 2001–2002, respectively. Last, we labelled each observed cluster by manually isolating individual documents that occurred unambiguously within a cluster, extracting the title-words for these documents and identifying which shared words were the most common (and hence predominantly responsible for the aggregation). While the overall two-dimensional projection of documents holds no inherent meaning (e.g. the circular start position of nodes at the beginning of the plot-rendering process), the spatial layout of clusters relative to each other does allow the identification of links between document groups and a way to quantify relationships between prominent research areas.

Emergence and longevity of new topic areas

Next we applied a ‘burst’ detection algorithm (Kleinberg 2002) to explore how major themes in animal behaviour research have changed across time. Kleinberg’s (2002) model was originally designed to sort email automatically into meaningful folders by identifying important topics as they appear, grow in popularity for a period of time and then fade away. As applied here, the burst detection algorithm focuses on the temporal intervals between repeated appearances of the same term. When a term is popular, it will be used frequently and the time intervals between repeated appearances will be short. The two-state form of the burst detection algorithm finds the model that best describes the data as a collection of temporal strings of high (i.e. bursts) and low episodes of popularity for each of the terms studied. ‘Weights’ are also calculated to allow for direct comparison among bursts for the same and different words in terms of their relative prominence.

Returning to the complete set of 42 836 publications appearing over 35 years, we excluded words such as ‘the’ and ‘an’ to obtain a total of 24 850 unique title-words. We further focused our attention on the 739 title-words that appeared at least 100 times in the data set. To these, we applied the burst detection algorithm, looking across the full 35 years of publications, to identify rapid increases and decreases in popularity (bursts) for each term through time.

Journal, geographical area, and institutional patterns

For more detailed consideration of current journal, geographical and institution coverage, we shifted our

focus to keywords, considering only terms reported for the most recent publications (2001–2002; 4369 records). First, to assess journal coverage, we identified and compared the most common keywords used by each of the 25 journals of interest. Second, for examining differences in research trends across the world, we used the institutional address of the first author to identify the country of origin. We excluded all records with ambiguous affiliations resulting from missing words or country abbreviations and grouped the subsequent 57 identifiable countries into eight geographical regions to facilitate interpretation. Finally, the five-digit zip code of the U.S. is also unusually informative as it allows the identification of specific institutions (each institution is typically given a unique zip code). Using the address of the first author, we extracted documents published by scholars in the U.S. Zip codes were then examined to reveal those institutions that produced the most animal behaviour publications over the 2001 and 2002 period. Unfortunately, we were unable to conduct a similar analysis on a global scale, in part, as zip (or post) codes in many countries are less likely to be specific to particular institutions. Institutional names proved even more difficult to isolate reliably because of variation in how the names were abbreviated and where they were placed within address strings.

RESULTS

The number of documents published in 25 animal behaviour journals has increased steadily from 1968 to 2002 (229 to 2254 documents in each year, respectively; Fig. 1). *Animal Behaviour* is by far the largest recent contributor of the 13 core journals covered by Animal Behavior Abstracts (11.2%; Table 1), followed by *Behavioral Ecology and Sociobiology*, *Applied Animal Behaviour Science*, *Behavioral Neuroscience* and *Behavioral Ecology*, which contribute 5–6% each. Note that roughly half of the publications included in our study appeared in journals not listed by ABA as ‘core’ sources, irrespective of time frame considered (Table 1).

Topic Area Associations Identified by Title-words

The vocabulary used in publication titles has become dramatically diverse over the last three decades, in part because of a huge increase in the number of publications. The occurrence of unique title-words in our data set increased from 1540 title-words in the 1971–1972 snapshot to 2238 title-words in the 2001–2002 snapshot. As a consequence, identifiable clusters in our visualizations also increased from approximately nine in 1971–1972 to over 20 in 2001–2002 (Fig. 2).

The language relationships appearing in publication titles for 1971–1972 and 1981–1982 reflects a profound separation between early ethology and comparative psychology. In 1971–1972, there is one cluster focused on function (e.g. ‘feeding’, ‘sexual’, ‘aggression’: cluster 1), two clusters concentrating on animal learning (e.g. ‘stimulation’, ‘schedule’, ‘reinforcement’, ‘conditioned’:

(a) 1971–1972

1
Feeding
Sexual
Aggression
Primates

2
Electroshock
Convulsive
Stimulation
Amnesia
Brain

3
Schedule(s)
Reinforcement
Fixed-interval
Avoidance

4
Song
Calls

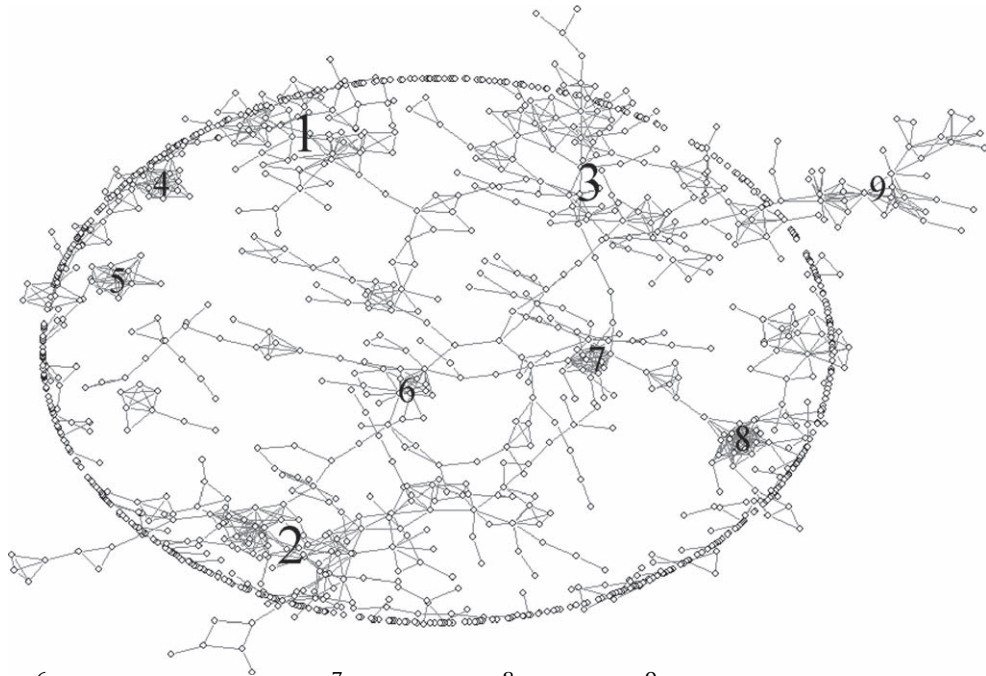
5
Pattern
Rodent
Grasshoppers
Walk, gaits
Communication

6
Rats
Nonnutritive
Ulceration
Stomach

7
Morphine
Tolerance
Anorexigenic
Amphetamine

8
Rat
Motivated
Sniffing

9
Stimulus
Conditioned
Suppression
Transfer



(b) 1981–1982

1
Social
Macaca
Aggression
Foraging
Spacing patterns

2
Rats
Scent
Attractivity
Receptivity
Pregnant

3
Rat
Pheromonal emission
Pups, weaning
Problem solving
Deficiency

4
Informational
Communication
Ant

5
Detection
Prey
Chemical
Genetic

6
Memory
Pigeon

7
Feeding
Sheep
Maternal

8
Matching
Detection
Pigeon
Dolphin

9
Reinforcement
Schedule(s)

10
Response
Man
Punishment

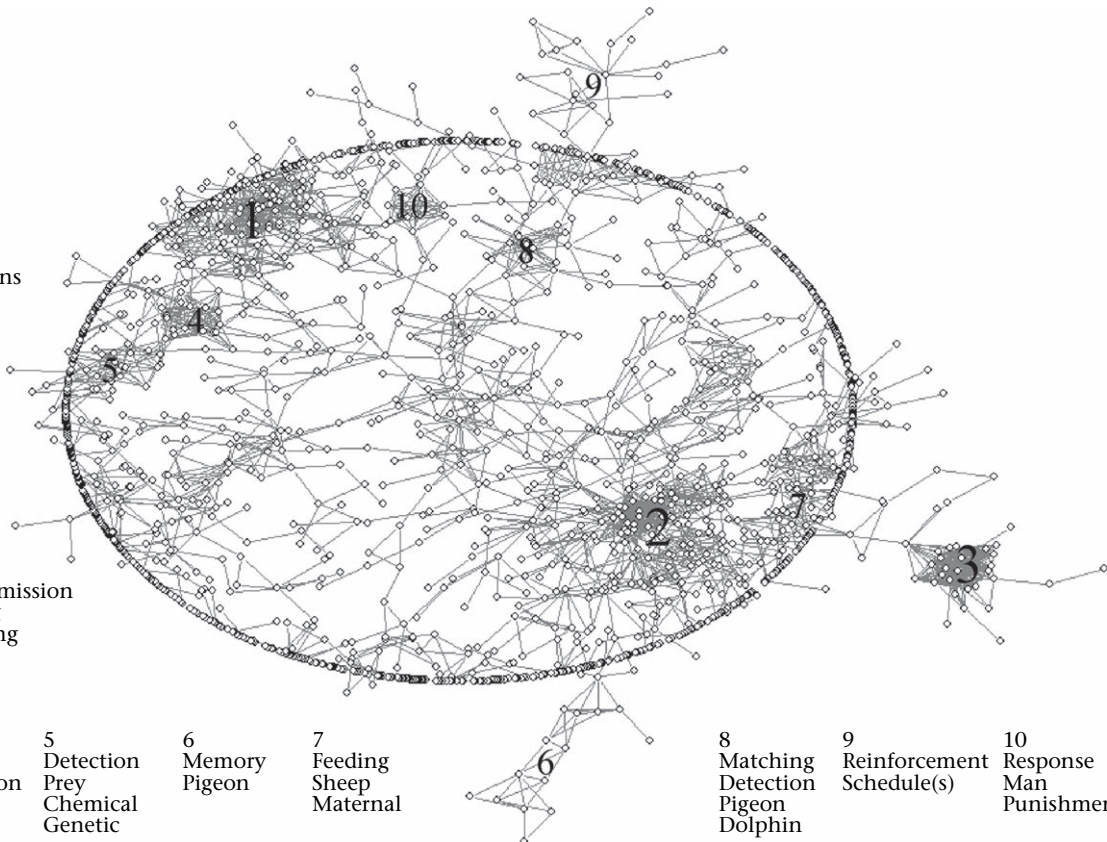


Figure 2. Visualization plots of latent semantic analyses for documents published in all 25 behaviour journals for (a) 1971–1972, (b) 1981–1982, (c) 1991–1992 and (d) 2001–2002. Nodes represent individual papers, with connecting lines indicating similarity in title vocabulary. Common areas of research form clusters. Salient terminology producing prominent clusters are given. Those nodes left on the periphery are generally unrelated to records within the document space. See text for details.

(c) 1991–1992

1
Genetic analysis
Reproductive
Sperm competition
Comparative
Environmental

2
Rats
Food
Stress
Behavioural patterns
Intake

3
Foraging

4
Priming
Marmota
Calling

5
Song
Syllable
Organization
Sparrow, starlings

6
Recognition
Parent
Vocal
7
Song
Macaca
Conflict
Repertoires

8
Social
Insects

9
Pigeons
Preference
Homing

10
Grazing
Sows
Nursing

11
Growth
Sows, piglets

12
Associations
Habituation
Sensitization

13
Rat
Modulation
Peripheral

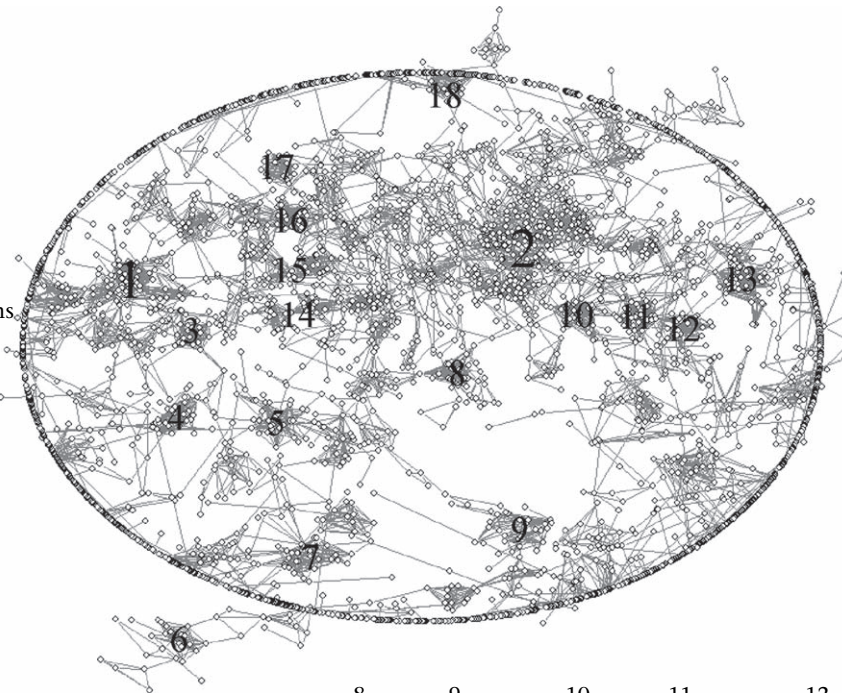
18
Reinforcement
Schedule(s)

17
Learning

16
Mate guarding

15
Mice
Female choice
Infanticidal

14
Mating success
Lek



(d) 2001–2002

1
Mating
Parental care
Mate choice
Competition
Reproductive success

2
Foraging
Selection
Long term
Movement
Habitat

3
Memory
Activity
Cues
Hippocampus
Pigeons

4
Rats
Food
Response
Information
Activation
5
Maternal
Brain
Control
Suckling
Induction

6
Macaca
Hymenoptera
Detection
Communication

7
Ant

8
Development
Vocal

9
Feeding
Dominance

10
Psychiatric
disorders

11
Honeybee

20
Rat
Momentum
Odour

19
Mice
Anxiety

18
Rats
Social

17
Social
Status
Communication

16
Aggression

15
Dairy
Growth
Motor properties

14
Dairy calves
Handling
Training

13
Discrimination
Perception

12
Learning

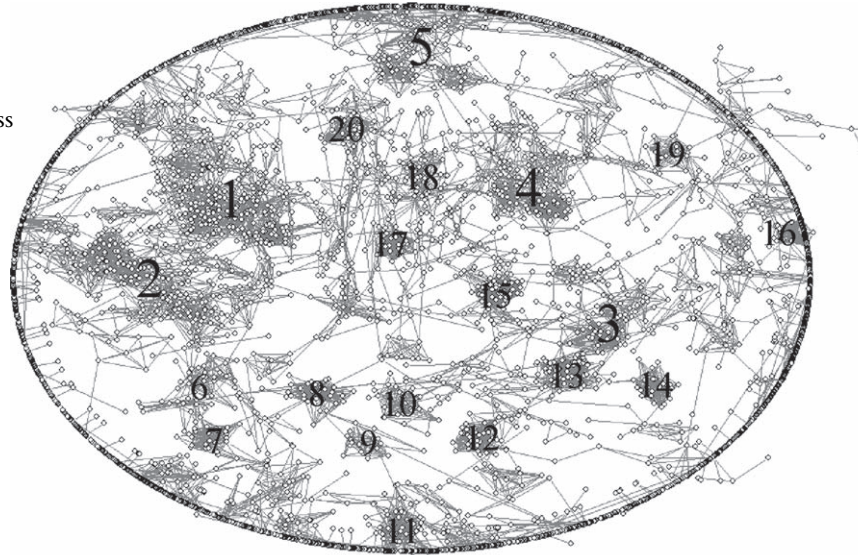


Figure 2. (continued)

clusters 3 and 9), and several other groups centred on specific experimental techniques (e.g. ‘electroshock’, ‘ulceration’, ‘amphetamine’; Fig. 2a). In 1981–1982 (Fig. 2b), there was prominent clustering around ‘social’, ‘aggression’ and ‘foraging’ (cluster 1), with smaller connected

clusters featuring ‘communication’ and ‘prey’. Interestingly, ‘genetic’ and ‘chemical’ also appeared to be associated with these groups. Animal learning is now loosely united across clusters 8 (‘matching’, ‘detection’) and 9 (‘reinforcement’), and comparative psychologists have

identified a preferred model organism with two large clusters (clusters 2 and 3) joining documents describing research on 'rat/s'. Both animal learning and 'rat/s' groups are only distantly connected to ethologically oriented publications (cluster 1), emphasizing the continuing distinction between ethology and comparative psychology into the 1980s.

Between 1991 and 1992 there was a considerable increase in heterogeneity of title vocabulary (Fig. 2c), with 18 clearly identifiable clusters reflecting diversification across a multitude of topic areas. There was still a large, linked cluster describing ethological studies of animal behaviour (cluster 1), although with a greater emphasis on genetics and reproduction, in addition to 'sperm competition' (a previously unseen topic area). As in earlier years, a second large cluster focused on 'rats' (cluster 2). However, these clusters are now linked through several smaller groupings focusing on reproductive behaviour and mate choice (clusters 14–16). Appearing in four clusters, sexual selection has emerged as a fashionable topic area. Acoustic communication has also grown, featuring heavily in several clusters (clusters 4–7). Other clusters indicate a new interest in applied animal behaviour research (e.g. clusters 10 and 11: 'sows', 'growth' and 'nursing').

Continued diversification is evident in 2001–2002. The emphasis on reproductive behaviour and sexual selection seems to have expanded to other areas such as 'parental care' (cluster 1). A second large and related cluster describes greater interest in 'foraging', 'movement' and 'habitat' (cluster 2). The large 'rats' cluster has now become subdivided into separate groups describing specific types of behaviour, including: 'memory' (cluster 3); 'food' and 'response' (cluster 4); 'maternal', 'brain', and 'control' (cluster 5); and 'learning' (cluster 12). Several new groups indicate a concentration of research on specific model and domesticated organisms (e.g. 'bees', 'ants', 'mice', 'dairy calves'). Interestingly, the remnants of the division between ethology (e.g. clusters 1 and 2) and comparative psychology (e.g. clusters 3 and 4) are now bridged primarily by clusters relating to communication and social behaviour (clusters 17 and 18), and a growing cluster referring to rat and odour (cluster 20). Applied animal behaviour (clusters 14 and 15) also remains well represented and offers new links to the comparative psychology clusters.

Bursts in Popularity of Title-words

Focusing our attention on the 739 title-words that appeared at least 100 times in our data set, the burst detection algorithm identified 506 bursts of popular title-words across 35 years. Bursts were regularly spaced, lasting a median of 4 years (mean \pm SE = 5.6 ± 0.19). There were 470 title-words such as 'effect', 'role' or 'difference' that are difficult to interpret further. If we focus on the remaining 269 terms, there appear to be three vocabulary periods: pre-1985, 1985–1995, and post-1995 (Fig. 3). Terms that burst in popularity during the 1985–1995 'transition' period tended not to burst before or afterwards.

Of the 269 potentially meaningful terms, 200 reflect topics of interest in animal behaviour research (e.g.

'operant', 'evolution', 'predation'). The words occurring within each of the three time periods cross disciplinary boundaries, indicating the continuing diversity of animal behaviour research throughout the history of our field. The early periods, for example, show bursts from 'shock', 'reinforcement', 'natal' and 'testosterone'. 'Guarding', 'genetic', 'anxiety' and 'opioid' all burst during the transition time period (1985–1995). 'Receptor', 'anxiety', 'paternity' and 'mate' all burst in the most recent time interval.

The 69 remaining terms refer to a type of animal (e.g. 'rats' appeared 5550 times; Fig. 3b), and also reflect some meaningful shifts over the years. Before 1985, virtually all animal terms undergoing bursts of popularity were model organisms, including cats, monkeys, squirrels (which could also be 'squirrel monkeys') and chickens (Fig. 3b). In the 1985–1995 transition period, there were several bursts referring to insects (especially hymenoptera (e.g. bees, wasps and ants) and orthoptera (e.g. crickets, grasshoppers and katydids)) that were not abundant earlier. In the mid-1990s, there was a sudden surge of interest in a more diverse group of domesticated animals (e.g. dogs) and those of economic importance (e.g. cows, deer).

Journal Focus

Listing the 10 most frequently reported keywords for each of the 25 journals in 2001–2002, we found a total of 143 different terms and only a moderate degree of overlap across journals. Learning, memory, reinforcement and related terms appeared consistently in the top-10 keyword lists of all but a few journals, emphasizing the continuing importance and broad impact of these themes to animal behaviour research. Mate choice, reproductive success and sexual selection also appeared frequently, indicating the popularity of evolutionary questions. When the most common keywords for all journals were pooled and ranked, terms referring to aggression, learning/memory, foraging and sexual selection were at the top of the list (Fig. 4a).

Keywords also showed the existence of a continuum between journals that emphasize evolutionary ethology and those that publish comparative psychology. On one extreme, *Behavioral Ecology* and *Behavioral Ecology and Sociobiology* place an unusually strong emphasis on 'sexual selection', and other terms related to reproduction and mating (Fig. 4b). *Animal Behaviour*, *Behaviour* and *Ethology* also publish articles on sexual selection, but add social behaviour, predation, foraging, communication (usually 'vocalization') and evolution. At the other extreme, nearly all popular keywords reported by *Behavioural Processes* and *Animal Learning & Behavior* address learning and memory (Fig. 4c).

Interestingly, *Applied Animal Behaviour Science* lies somewhere in between; including 'aggression' and 'vocalization' as prominent keywords, but also 'stress' and 'motivation'. Most of the journals that appeared on our supplemented list of 25, but not in the core list from ABA, also appeared somewhere in the middle. For example, physiology journals like *Hormones and Behavior* frequently publish studies about 'sexual behaviour' and 'aggression',

in addition to 'stress', 'learning' and 'photoperiod'. The *Journal of Comparative Psychology* showed an unusually high peak with 'animal communication' appearing alongside research relating to 'habituation', 'development' and 'imitative learning'. These journals therefore form an important bridge between the academic descendants of early ethologists and comparative psychologists. They also tend to be more specialized than journals at the extremes, leading to a more highly skewed distribution of keywords and/or a larger proportion of unique terms (Fig. 4d). For example, the focus of *Applied Animal Behaviour Science* is on 'animal welfare', whereas *Hormones and Behaviour* publishes more papers described by 'neuro/endocrinology'.

Global and Institutional Trends

In 2001–2002, animal behaviour publications were produced by researchers affiliated with institutions in every region of the world (Fig. 5a), with North America and Western Europe being the primary producers of animal behaviour research. Keywords used by North America, Western Europe and Australia/New Zealand were remarkably similar, reflecting global agreement on popular topic areas in animal behaviour (Fig. 5b). The relatively few contributions from remaining regions (South America, Eastern Europe, Asia and Africa) shared an emphasis on animal learning and domesticated animals, indicating

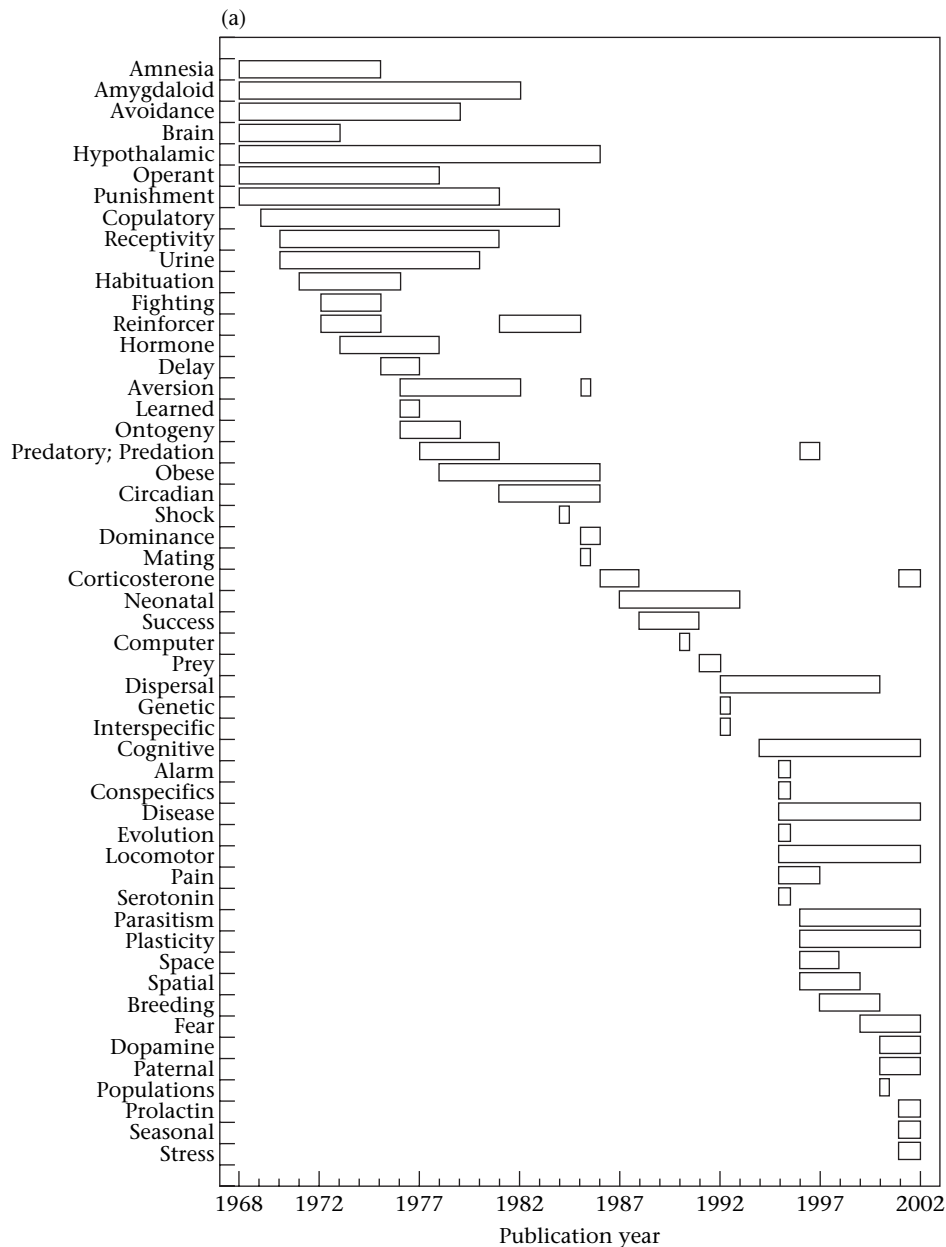


Figure 3. Bursts in popular title-words for documents published in 25 behaviour journals from 1968 to 2002. Vocabulary surges have occurred regularly throughout the last 35 years. (a) However, a subset of the 200 meaningful terms show divisions of vocabulary across three periods: pre-1985, 1985–1995 and post-1995. (b) Popular study organisms also vary over time.

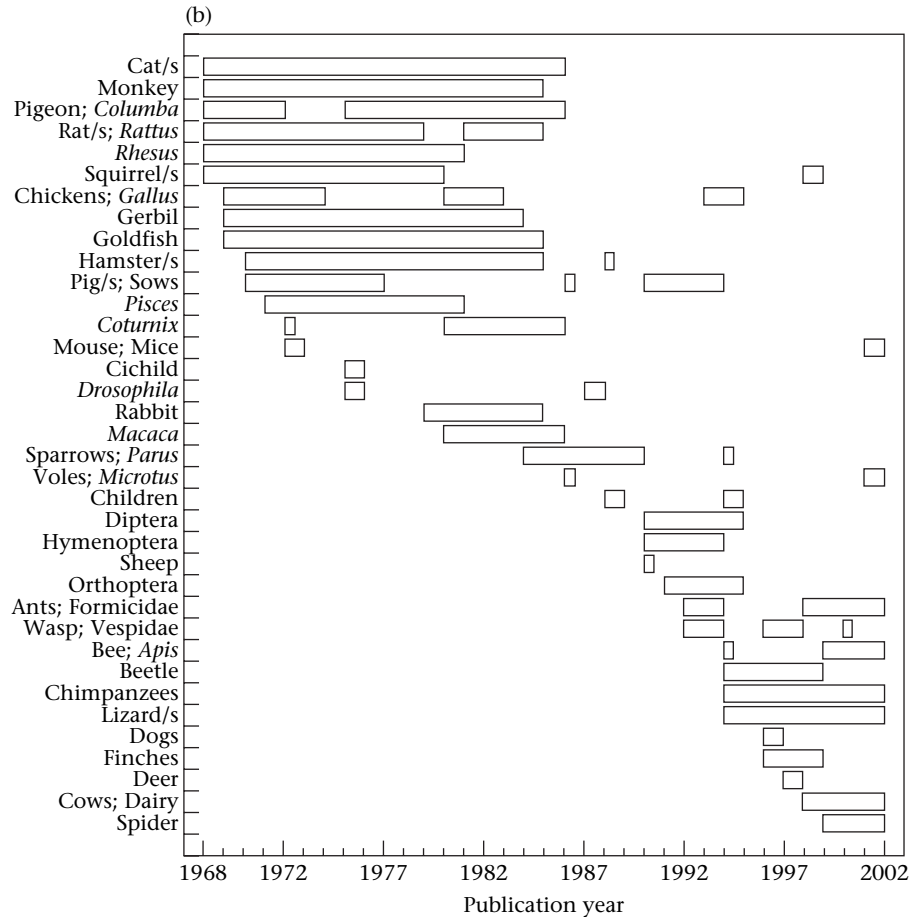


Figure 3. (continued)

strong interest in applied animal behaviour research. Relative representation by South America and Asia was larger when considering all 25 journals, whereas Africa, Middle East and Eastern Europe were better represented when only core ABA serials were considered.

In the United States alone, we counted 1806 publications from first authors located at more than 487 different zip codes during the 2001–2002 period. Over 100 zip codes tallied five or more animal behaviour publications, although it is possible that some zip codes do not identify unique institutions (e.g. some could be personal residences). Also, the major representation of some institutions may result from an unusually large number of contributions by single investigators in this 2-year period. The number of documents associated with each zip code also varied between the two lists (13 ABA core journals and complete list of 25). Nevertheless, several institutions known to have larger graduate programmes or a greater number of animal behaviour researchers account for a disproportionate share of publications by geographical location within the U.S. (Table 2).

DISCUSSION

Despite our analyses being necessarily limited by the scope of our study (e.g. the choice of journals, availability

of electronic data, interpretations of zip codes), our approach succeeds in documenting many of the patterns mentioned by earlier reviews using very different methods (e.g. Durant 1986; Sherman 1988; Barlow 1989; Dawkins 1989; Dewsbury 1989, 1992, 1994; Armstrong 1991; Alcock & Sherman 1994; Alcock 2003; Bateson 2003; Slater 2003; Stamps 2003; West et al. 2003), while also offering several new insights that have gone previously undetected by traditional review methods. Our findings confirm the historical divisions between biological and psychological branches of animal behaviour research (Dewsbury 1989, 1992). However, the gap between ethology and comparative psychology has diminished over time, with frequent present-day interaction across disciplines occurring through a shared interest in communication and social behaviour. We also document the rise in popularity of behavioural ecology (Bateson & Klopfer 1989; Alcock 2003; Bateson 2003), but find a healthy, continued interest in mechanism, learning and development. Finally, our results offer several tantalizing glimpses into the roles of core and peripheral journals, as well as geographical trends in the study of behaviour.

Tinbergen (1963) described the study of animal behaviour as encompassing four main areas of investigation: mechanism, function, development and evolution/phylogeny. Subsequent authors have grouped these topics into

'proximate' and 'ultimate' questions (mechanism/development and function/evolution, respectively). Commentaries on the development of our field typically herald or lament a shift in interest between adaptive and mechanistic/developmental questions (Wilson 1975; Barlow 1989; Dawkins 1989; Bateson 2003; Stamps 2003; West et al. 2003). However, the relevance of this dichotomy has also been debated (Sherman 1988; Armstrong 1991; Dewsbury 1992, 1994; Alcock & Sherman 1994). Our analysis of the vocabulary used by authors to describe their own research shows that, although the popularity of studies addressing evolutionary function (especially sexual selection) has increased in recent years, interest in mechanistic/developmental research has remained strong throughout the history of animal behaviour research. Instead of one research area dominating the field at the expense of

another, a more accurate description is that our field has collectively expanded and become integrated across multiple topic areas. Hence, contemporary research still reflects the diversity and comprehensive approach advocated by Tinbergen (1963) and Huxley (1942).

We found a major difference between 'core' and 'priority' animal behaviour journals (those that publish behavioural research frequently, but also other types of research). The physiology and applied journals included in our study appear to play a pivotal role, not only producing a large number of animal behaviour publications (about half of those reviewed in our study), but offering an important intellectual link between disparate arms of our discipline. In contrast, newer journals that emphasize animal behaviour research appear to be more specialized than their older counterparts, emphasizing

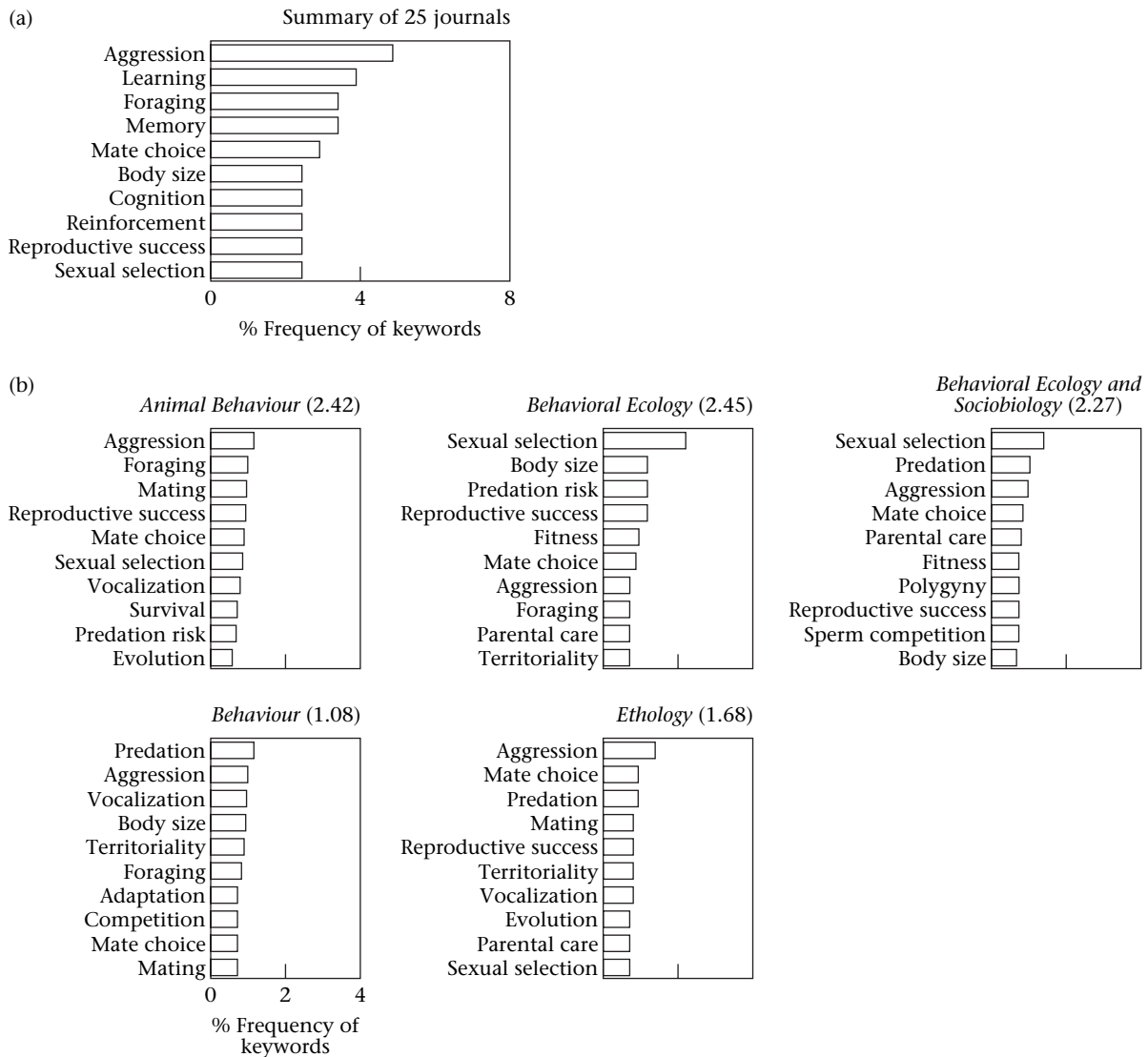


Figure 4. Keyword frequency distribution plots summarizing the content of journals publishing animal behaviour research for 2001–2002: (a) the 10 most frequently used keywords for all journals ranked collectively; (b) journals emphasizing 'evolutionary ethology'; (c) journals largely covering animal learning and memory; and (d) journals that are relatively intermediate in their document coverage. Values in parentheses are journal impact scores calculated by ISI Web of Science for 2002 (Thomson Scientific, Philadelphia, Pennsylvania, U.S.A.; <http://www.isinet.com/>).

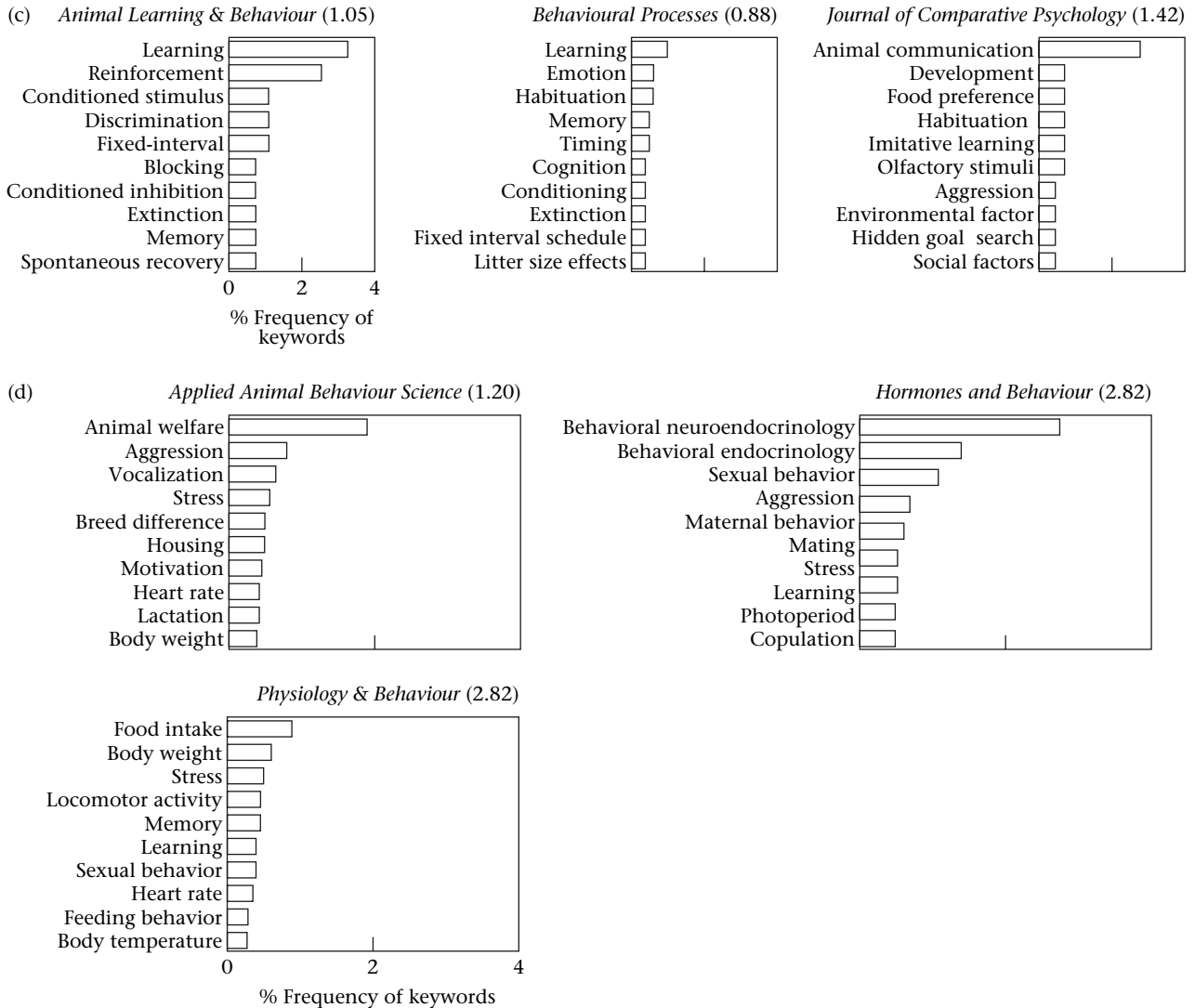


Figure 4. (continued)

distinctions between subdisciplines rather than building bridges across them. For example, *Behavioral Ecology* (founded in 1990) and *Behavioral Ecology and Sociobiology* (1976) have a stronger focus on sexual selection and mating than do the older *Ethology* (1937), *Behaviour* (1948) and *Animal Behaviour* (1953). Further analyses exploring the role of the other 200 odd journals that occasionally publish animal behaviour research may provide valuable insight into this phenomenon.

Our results also highlight several intriguing patterns driven by geographical distributions, the impact of particular institutions, and the timing of cultural shifts. We found little evidence for disciplinary differences across geographical regions. North America and Western Europe are very similar in research focus despite the unique historical events in the development of animal behaviour research in these regions (Durant 1986; Dewsbury 1989). Research in countries with little history in the study of behaviour also tend to encompass the breadth of animal behaviour research (i.e. both ethology and comparative

psychology), but some geographical regions (Africa, Middle East, Eastern Europe) are better represented in core journals, whereas others (South America, Asia) publish more frequently in journals that do not specialize as much in animal behaviour. Our zip code analysis showed that behavioural research, in the U.S. at least, is widely distributed, with more than 100 institutions contributing five or more animal behaviour publications in a 2-year period. Finally, our results show the rise and fall in popularity of research terms and study organisms in roughly 10-year cycles. As a consequence, the vocabulary and animals examined in the 1970s and 1980s are noticeably different from those studied today.

This study confirms that the study of animal behaviour is active, healthy, and growing. It is being studied by researchers representing hundreds of institutions around the world, including geographical regions with little history of life science research. Sexual selection is clearly an important topic in modern research, but interest in animal learning, aggression, foraging, and other reproductive and

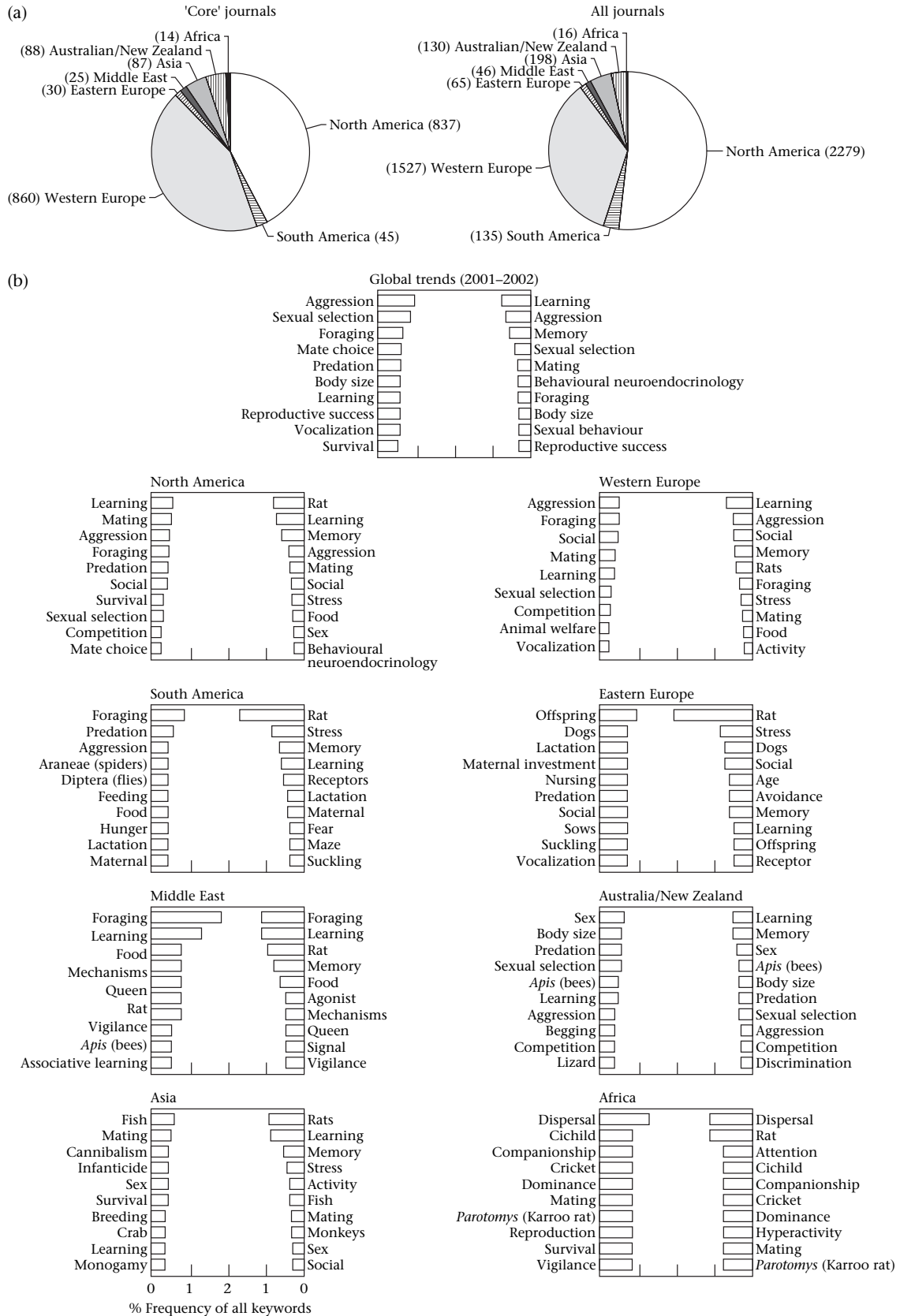


Figure 5. Publication trends in 2001–2002 across the world for both core ABA and supplemented journal listings. (a) The proportion of total documents by region, with values in parentheses representing absolute numbers of documents. (b) Keyword profiles for core (left) and all behaviour journals (right) across the globe and eight separate geographical regions differentiated by principal author address. Histograms are frequency distributions of document keywords.

Table 2. Number of articles published in animal behaviour journals by the first 25 U.S. institutions on our lists for 2001–2002

Core ABA journals (670 total publications)	Document count	All journals (1806 total publications)	Document count
Univ. California, Davis (95616)	20	Univ. California, Davis (95616)	44
Cornell Univ. (14853)	18	Cornell Univ. (14853)	36
Indiana Univ., Bloomington (47405)	14	Indiana Univ., Bloomington (47405)	27
Univ. Memphis (38152)	13	Univ. Michigan (48109)	27
Univ. Kentucky (40506)	13	Univ. Washington (98195)	26
Univ. Washington (98195)	13	Univ. Pennsylvania (19104)	25
Purdue Univ. (47907)	12	Univ. California, Los Angeles (90095)	25
Univ. Michigan (48109)	11	Michigan State Univ. (48824)	24
Univ. Wisconsin- Madison (53706)	11	Purdue Univ. (47907)	23
Arizona State Univ. (85287)	11	Univ. Massachusetts (01003)	22
Univ. California, Los Angeles (90095)	11	Univ. Texas, Austin (78712)	22
Washington State Univ. (99164)	11	Emory Univ. (30322)	21
SUNY, Binghamton (13902)	10	Ohio State Univ. (43210)	21
Brown Univ. (02912)	9	Univ. Pittsburgh (15260)	20
Michigan State Univ. (48824)	9	Florida State Univ. (32306)	20
Univ. Pennsylvania (19104)	8	Univ. Wisconsin-Madison (53706)	20
Univ. Georgia (30602)	8	Arizona State Univ. (85287)	19
Texas A & M Univ. (77843)	8	Boston Univ. (02215)	17
Univ. California, San Diego (92093)	8	SUNY, Binghamton (13902)	16
Univ. California, Berkeley (94720)	8	Univ. Maryland (20742)	16
Univ. Massachusetts (01003)	7	Univ. Georgia (30602)	16
Univ. Maryland (20742)	7	Univ. California, San Diego (92093)	16
Colorado State Univ. (80523)	7	Univ. Kentucky (40506)	15
Harvard Univ. (02138)	6	Univ. California, Berkeley (94720)	15
Princeton Univ. (08544)	6	John Hopkins Univ. (21218)	14

Institutions were identified by the zip code appearing in first author addresses. Counts may include some publications by geographically similar, but unaffiliated researchers (see text for details).

social behaviour remain strong. Animal behaviour research also continues to draw new attention from areas such as domesticated animal science and animal welfare. Moreover, the approach adopted in our study leads to many appealing avenues for future research. Detailed analysis can go beyond titles and keywords to explore the complex web of relationships formed by citation (e.g. White et al. 2004) and collaboration, to investigate how 'schools of thought' develop. Records of awards given by funding bodies could be examined to determine the importance of external grants in directing trends in mainstream research (e.g. Boyack & Börner 2003; Boyack 2004). Similar bioinformatic tools can be applied to organized collections of behavioural measurements, such as those envisioned by EthoSource (a new global initiative to facilitate the sharing and combining of behavioural data; Martins & Clark 2002), and highlight the opportunities for a new field of 'ethoinformatics'.

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