

Pacing polar bears and stoical sheep: testing ecological and evolutionary hypotheses about animal welfare

R Clubb and G Mason*

Department of Zoology, University of Oxford, South Parks Road, Oxford OX1 3PS, UK

* Contact for correspondence and requests for reprints: Georgia.Mason@zoo.ox.ac.uk

Abstract

Responses to potential threats to welfare vary greatly between species. Even closely related animals often differ in their fear of humans and/or novelty; their behavioural responses to pain; and when captive, their overall welfare and the form and frequency of their stereotypies. Such species differences stimulate hypotheses about 1) the way that responses to challenge co-vary with other biological traits; 2) the adaptive value of particular responses; and 3) the factors predicting responses to evolutionarily new scenarios, such as captivity. We illustrate how these ideas can be statistically tested with multi-species comparisons, and show how techniques such as the Comparative Analysis of Independent Contrasts can be used to control for any non-independence of data points caused by species' relatedness. For each of the three types of hypothesis, we then provide several welfare-relevant examples including one that has been fully tested (respectively, the relationships between sociality and anti-predator behaviour in antelopes; predation pressure, foraging niche and neophobia in parrots; and home range size and stereotypy in carnivores). Ultimate explanations such as these, based on species' ecology and evolutionary history, have great explanatory appeal. Species comparisons can also have great practical value, allowing the test of hypotheses that would be almost impossible to investigate experimentally, and generating principles that allow predictions about the welfare of similar unstudied species. Multi-species data, for example from the many taxa held in zoos, thus hold enormous potential for increasing the fundamental understanding of animal welfare.

Keywords: animal welfare, comparative methods, ecological niche, evolution, species differences, stereotypy

Introduction

Animal welfare research usually concentrates on proximate issues investigating the development and elicitation of responses reflecting stress and other problems. Yet, when trying to judge whether given responses could be adaptive in nature, or when trying to make sense of species differences, we need ultimate explanations based on ecology and evolutionary adaptation. Thus when asking "Why do sheep seem so stoical in the face of pain, while pigs are so vocal?" or "Why do caged carnivores tend to pace rather than perform other stereotypies?", we typically want to know the adaptive value of evolved traits, or the role of a species' ecological niche in determining reactions to captivity. Such ultimate explanations have enormous explanatory appeal, but their value is not just heuristic: they are uniquely placed to yield fundamental principles about welfare responses. Here, we show how to use species comparisons to test evolutionary and ecological hypotheses empirically. We provide several examples and also present many hypotheses that remain to be fully tested.

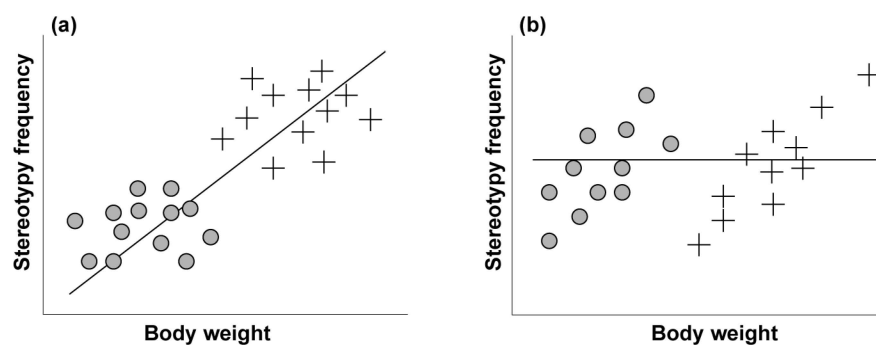
Species differences in response to potential threats to welfare

Humans have known for millennia that animals react differently to captive management. That some species domesticate readily, when even their close relatives may not, has long

been evidence of this (see eg Diamond 1997; Clutton-Brock 1999). More recently, data from farms and laboratories, and more importantly from zoos, have painted a more detailed picture of how species vary in their responses to potential threats to welfare.

Some species differences are in the 'style' with which animals respond to a given challenge, one example being fleeing versus freezing when frightened. When various rodent species are placed in a novel open arena, for instance, all show behavioural signs of stress, but guinea pigs (*Cavia porcellus*) tend to become immobile, while chinchillas (*Chinchilla laniger*) move actively around the arena, biting objects within it and defecating extensively (Glickman & Hartz 1964). Other species differences occur in the degree to which particular stimuli elicit responses, for example, how much fear is elicited by humans (eg foxes, *Vulpes vulpes* and *Alopex lagopus* [Pedersen & Jeppesen 1998]), or by novelty or changes to the environment. Even very closely related taxa may differ: crab-eating macaques (*Macaca fascicularis*) show greater corticosteroid responses to novelty or restraint, greater and more prolonged heart rate increases in response to a novel environment, and more alarm-calling when disturbed by humans, than do bonnet macaques (*Macaca radiata*), while these in turn respond far more than rhesus macaques (*Macaca mulatta*) (Clarke & Mason 1988;

Figure 1



Potential Type I error (a) and Type II error (b) caused by relationships between species. The two graphs (adapted from Gittleman & Luh 1992) show hypothetical cross-species analyses looking at the relationship between body weight and stereotypy frequency, using data from two groups of related species (represented by circles and crosses). Not controlling for relatedness could clearly lead to (a) an erroneous significant relationship where none exists (ie a Type I error), or to (b) a non-significant result when the correlation is actually strong (ie a Type II error).

Clarke *et al* 1994). Other aspects of captivity also affect species differently, with some species being very prone to developing abnormal behaviour, and others, much less so, even when housed almost identically (see van Hoek & ten Cate [1998] for species differences within parrots, for example).

In several instances more worrying signs of differential welfare exist. For example, while the ring-tailed lemur (*Lemur catta*) has minimal behavioural and veterinary problems in captivity and excellent breeding success, its relative the gentle lemur (*Haplemur griseus*) provides a striking contrast with its stereotypies and over-grooming, timidity, and high morbidity (Petter 1975). Similar unexplained variance in captive breeding success and/or morbidity occurs in other taxa, including monkeys (Portugal & Asa 1995; Mooney & Lee 1999; Savage *et al* 2002), canids (Ginsberg & Macdonald 1990), felids (Nowell & Jackson 1996; Mellen *et al* 2000) and artiodactyls (Primack 1998; Barnes *et al* 2002), and across different species of angelfish (S Fosså 2002, personal communication).

Species thus vary greatly in the nature and magnitude of their responses to captivity. This can be a practical problem when trying to understand and improve animal welfare, but also potentially provides an unparalleled insight into these responses.

Evolutionary and ecological explanations for species differences

Species differences are valuable because, first, they stimulate novel evolutionary or ecological hypotheses, and, second, they can be used to test such ideas statistically if data exist for enough species.

Species differences can generate and address three types of research question. The first is evolutionary, and asks how particular traits have co-evolved; do they co-occur, for example, or instead do they negatively correlate when a range of species is compared? For instance, we could ask “Does neophobia correlate with the volume of the amygdala, the brain region responsible for fear processing?” Such questions can reveal cross-species trends, such as relationships between particular behavioural patterns and specific

anatomical traits or physiological responses. The second type of question tackles issues of adaptation, using species comparisons to answer the question “What is the evolutionary function of trait X?” For example, if the function of freezing is to hide from predators, we might test this idea by predicting that it should then be most frequent in highly predated species, especially those whose predators hunt via visual and auditory cues. The final type of question investigates how responses to new scenarios are shaped by an animal’s prior traits or ecological niche. One example might be “Are oral stereotypies in captive ungulates predicted by natural foraging mode?” Unlike the previous two, this approach reveals patterns of pre-adaptation or vulnerability to new (potentially human-imposed) circumstances, rather than how natural selection has operated in the past.

We develop these approaches later in this paper, giving more examples of welfare-relevant hypotheses and demonstrating how some have been tested. But first, we discuss how data from multiple species should be handled, since species comparisons raise important methodological and statistical issues.

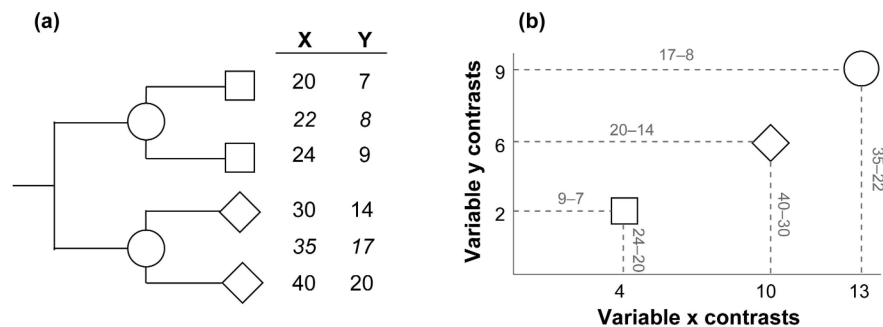
Testing hypotheses using species comparisons

In other fields of biology, species comparisons have long been used to test ideas about niche effects and evolution (eg Stearns 1983; Chaverud *et al* 1985; Harvey & Clutton-Brock 1985). In many ways, comparative studies proceed like any other statistical enquiry: requiring clear hypotheses, good quality data (ideally interval or ordinal), and as many independent replicates (eg species) as possible. Any likely confounds also need to be carefully considered when planning or interpreting analyses. However, two important additional features typify multi-species comparative analyses.

The first is that to achieve a good sample size, data are often collated from multiple sources (eg many separate papers on zoo animals). This necessitates careful thought as to how to ensure that only good quality data are used, for instance, by discarding reports that do not meet clear methodological criteria (see Gittleman 1989 for a detailed discussion of this important point).

Figure 2

The Comparative Analysis of Independent Contrasts (CAIC). On this hypothetical phylogeny (a), squares and diamonds represent living species, and circles represent their extinct ancestors. The values for the two variables of interest, x and y, are shown for each species (calculated, rather than measured directly, for ancestors). The differences between the most closely related species (eg the difference between x-variables for the squares) represent independent data points, or *contrasts*. These can then be plotted against each other (shown in [b], with calculations shown in grey along the dotted lines) to determine whether the two variables correlate, independent of phylogeny. Here, the greater the x contrast, the greater the y, suggesting that they positively correlate, although more contrasts are obviously needed for statistical testing. (Adapted from Purvis & Rambaut 1995.)



A second crucial consideration is that data points (eg species means) may not be statistically independent because of the relatedness between species. Sometimes known as 'phylogenetic signal' (Blomberg *et al* 2003), this is the danger that closely related species are inherently similar, leading to pseudo-replication (Harvey & Pagel 1991). For example, if investigating the correlates of ungulates' foraging modes, it might well be invalid to treat different species of equid as independent if they have all simply inherited the same grazing style from a common ancestor. Even non-inherited variables may be subject to this sort of problem. For example, we might well find that some aspects of captive husbandry (eg 'starve days' for some carnivores) are inherently similar for clusters of related species (see Freckleton *et al* 2002, p 723 for a discussion of the treatment of non-inherited characteristics). Such non-independence would violate the assumptions of most statistical tests, and, as illustrated in Figure 1, could result in Type I or Type II errors.

Controlling for the effects of relatedness between species

In order to control for the potential non-independence of species, we first need a phylogenetic tree that shows exactly how our subject species inter-relate. Luckily, several are readily available; for example, complete trees have been published for primates (Purvis 1995) and carnivores (Bininda-Emonds *et al* 1999), and partial trees for rodents (eg Degen *et al* 1998), ungulates (eg Pérez-Barbérica *et al* 2001), birds (eg Morrow *et al* 2003), and many other groups.

Next we need to select a method to deal with the problem. The most commonly used and well-understood methods investigate whether differences between related species in one variable are paralleled by similar differences in other variables of interest. This Independent Contrasts method, originally introduced by Felsenstein (1985), has been modified and built upon to form a range of other comparative methods (eg Grafen 1989; Pagel 1992).

The Comparative Analysis of Independent Contrasts (CAIC) (Purvis & Rambaut 1995) is derived from Felsenstein's (1985) method. A very basic outline of CAIC is provided in Figure 2. This method calculates weighted differences (ie contrasts) between related species (represented by similar symbols in Figure 2a), which can then be used as data points in normal statistical procedures. Its premise is that differences between related species are independent because they have evolved since the split from the common ancestor. X-variable contrasts are then plotted against the equivalent y-variable contrasts to see whether changes in the two variables correlate using standard statistical procedures. An advantage of CAIC is that it still works well even if there are imprecise areas of the tree (Garland & Diaz-Uriarte 1999), ie areas that have three or more species radiating from the same ancestor ('polytomies') (see Pagel 1992; Purvis & Rambaut 1995). It is possible to include a categorical variable in CAIC analyses, but given the loss of power this can lead to, other methods may need to be considered (see Grafen & Ridley 1996 for a review). The CAIC software is also freely available from the web (although currently for Macintosh computers only), with a comprehensive, user-friendly manual explaining how to use your tree and run the program (<http://www.bio.ic.ac.uk/evolve/software/caic>). For clear and more detailed descriptions of CAIC see Purvis and Rambaut (1995), and Purvis and Webster (1999), and for recent examples of its use, see Gittleman and Purvis (1998), Ruggiero and Lawton (1998) and Purvis *et al* (2000).

Another method, representing a more general application of Felsenstein's (1985) Independent Contrasts, is Generalised Least Squares (GLS) (Pagel 1992, 1994; Freckleton *et al* 2002). GLS involves the calculation of a parameter, lambda (0-1), which describes the degree to which variables are dependent on species' shared ancestry (based on the phylogenetic tree). This parameter is then incorporated into regression equation calculations so that the relationship

between the variables of interest is tested while controlling for the phylogenetic effect. Under specific conditions GLS returns exactly the same results as CAIC (Pagel 1999), but GLS has some additional advantages. It uses standard statistical methods, and so can easily be applied to a wide range of models (eg ANCOVA and MANOVA) as well as to normal regressions (Rohlf 2001). It also does not require extensive coding of tree data prior to analyses, as is necessary for CAIC. However, a slight drawback of GLS is that the phylogeny must be well resolved (ie without polytomies), although see Pagel (1992) for a way around this. (Alternatively, Grafen's [1989] multiple regression method can cope with incomplete trees.) GLS can be used to analyse data including categorical y-variables, but an alternative model is required for purely discrete data (see Pagel 1994; Grafen & Ridley 1996). The necessary computer program (called 'CONTINUOUS') is currently available only for Macintosh computers and can be obtained from the author (see Pagel 1997, 1999). Recent examples of the use of GLS can be found in Forbis *et al* (2002) and in Gage and Freckleton (2003).

An important point to remember before performing any of these tests is that not all variables are significantly affected by phylogeny (eg Gittleman & Luh 1992); this may be especially true for behavioural traits (eg Blomberg *et al* 2003), and so it may not always be necessary to take corrective measures (eg Björklund 1997; Price 1997). GLS actually incorporates a diagnostic test into its calculations, in the form of the lambda statistic, which tells you whether the data are significantly affected by phylogeny and by how much (rather than the simple 'yes/no' response provided by other tests [see Freckleton *et al* 2002]). Other comparative methods, including CAIC, require a separate test to be run prior to analyses. Blomberg *et al* (2003) provide a good overview of the methods currently available, and also present a new method that is compatible with CAIC and GLS. For more general information about comparative methods, see Gittleman (1989), and Harvey and Pagel (1991); for reviews of some of the different methods available, see Gittleman and Luh (1992), and Martins and Hansen (1996).

Overall, comparative tests thus use many species, do their utmost to ensure good quality data, and check, and if necessary control, for relatedness between species, which can lead to statistical pseudo-replication. Now let us consider the role of such methods in animal welfare.

Using comparative approaches in animal welfare research

Using species differences to investigate how traits have co-evolved

There are many examples of species comparisons being used to test hypotheses about co-evolution. For instance, Nunn and colleagues investigated the correlates of circulating leucocyte level by comparing the white blood cell counts of 41 primate species with various aspects of their behavioural biology (Nunn *et al* 2000). Both in simple cross-species regressions and in analyses correcting for

phylogeny, leucocyte levels correlated with promiscuous mating systems.

Several authors have suggested similar, but more welfare-relevant ideas that could be investigated with comparative techniques. Mendoza and Mason (1997), for example, propose from a study of two monkey species that low sympathetic responses to stress are associated with high parasympathetic tone. Anti-predator behaviour may also co-vary with particular traits. Hedenstrom and Rosen (2001) hypothesise a relationship between wing-loading and patterns of escape-flight in birds fleeing from avian predators; Leal (2000), based on a study of two *Anolis* species, suggests that lizards that signal to predators that they have been spotted also show good endurance running; and Brashares *et al* (2000) hypothesise that antelope anti-predator behaviour co-varies with group size. Unlike the other examples here, this last idea was properly tested. In a phylogenetically controlled study of 75 species, solitary and pair-living antelopes were found to typically seek cover and hide, while gregarious species were found to take flight or stand at bay. Thus, comparative methods potentially have great value for revealing how welfare-related traits (eg the tendency to seek cover when frightened) may be predicted from other aspects of an animal's biology.

Using species differences to investigate adaptive hypotheses

Comparative techniques are one of the few ways of testing evolutionary hypotheses about fitness. For example, two studies (on birds and rodents) have used this approach to investigate the idea that group-living functions to reduce individual predation risk by testing the prediction that group-size co-varies with predation pressure (Ebensperger & Cofré 2001; Beauchamp 2002). Here we present two further, welfare-related ideas from other authors.

The first concerns the function of pain responses. Species differ markedly in their reactions to tissue damage: some display clear signs of distress (eg pigs), while others (eg sheep) show little, if any, overt behavioural response, even after surgical procedures that other evidence shows to be painful and aversive (eg Rushen & Congdon 1987; Broom 1998). Such observations have inspired two adaptive hypotheses: that distress vocalisations function to solicit help from conspecifics; and that hiding injury, by moving and behaving normally, functions to avoid attracting predator attention (Bateson 1991; Broom 1998, 2001). These ideas generate clear and testable predictions. If the former is correct, distress vocalisations should be most common in naturally group-living species, especially ones in which conspecifics protect or provision each other. If the latter is correct, we should expect behavioural signs of pain (eg limping) to be most common in non-predated species, and least common in species whose predators use visual cues to pre-select their targets. However, comparative techniques have not yet been used to test either of these interesting ideas.

Our second example concerns responses to novelty. Several authors have suggested that neophilia assists dietary generalists to explore and thus exploit novel foodstuffs, while neophobia functions to reduce exposure to predation risk

(eg Glickman & Sroges 1966). Evidence for these hypotheses has been accumulated for several species of bird (eg Greenberg 1990) and primate (Vitale *et al* 1991; Clarke & Lindburg 1993; Clarke *et al* 1995; Day *et al* 2003), but neither was properly tested until recently. Mettke-Hofmann and co-workers (2002) collected data on exploration and neophobia for 61 species of parrot, and compared these with ecological variables using both cross-species and phylogenetically controlled statistics. As predicted, island-living species (subject to low predation) were neophilic, showing short latencies to explore and exploring for long durations, although they were unexpectedly no less neophobic than other species, being equally deterred from eating when a novel object was near their food. Species from complex ecological niches, for example, forest margins, were also neophilic, although only when phylogeny was corrected for. This study could perhaps have used more direct measures of dietary generalism and predation pressure, but still illustrates the potential power of testing functional hypotheses with multi-species data.

Using species differences to investigate responses to evolutionarily new circumstances

Probably most relevant to welfare are questions about how biological traits predict animals' reactions to new scenarios, including ones imposed by humans. Conservation biology provides some excellent examples, with comparative methods being used to identify traits that increase vulnerability to extinction in the wild (Purvis *et al* 2000) and in reserves (Woodroffe & Ginsberg 1998) and that increase the likelihood of thriving when introduced to new locations (eg Wolf *et al* 1998; Sol *et al* 2002). Many traits have been hypothesised to predict responses to human management, although only a few have been tested. These include ideas about the factors predisposing certain species to domestication (see Diamond 1997; Clutton-Brock 1999), as well as more welfare-focused hypotheses about stress and stereotypic behaviour in captivity.

Several traits have been suggested to predispose species to poor captive welfare, including fear of humans (Hediger 1950), an endangered conservation status in the wild (Ginsberg & Macdonald 1990), being a dietary generalist (Morris 1964; Ormrod 1987), and having a naturally large home range size (Prescott & Buchanan-Smith 2004). These ideas largely remain untested, although recent work on carnivores provides support for the last hypothesis, as we discuss below.

Stereotypies, which show great taxonomic variation in form and frequency (see eg Mason 1993a), have attracted particular attention. For example, the propensity of deprivation-reared primates to self-clasp when rocking has been suggested to relate to their high degree of maternal contact in the wild (Berkson 1967, cited in Mason 1993b), while the common performance of oral stereotypies by herbivores (eg Dittrich 1976) and pacing by carnivores (eg Mason 1993b) has been suggested to reflect natural foraging movements (Terlouw *et al* 1991; Mason & Mendl 1997). Even within herbivores, species-typical oral stereotypies vary in form in a way

suggested to mirror the biting of naturally foraging sheep and goats, for example, versus the tongue-prehension of giraffes, okapis and cattle (Sambraus 1985).

Yet more ideas have been stimulated by variance in stereotypy frequency, with highly stereotypic species suggested to be naturally more active (eg Meyer-Holzappel 1968); territorial (Morris 1964); wide-ranging (Forthman-Quick 1984); generalist in their diet (eg Morris 1964); or to be more active foragers, for example, relying on extensive prey search and pursuit (eg Terlouw *et al* 1991; Mason & Mendl 1997). These hypotheses were recently tested for the Carnivora (Clubb 2001; Clubb & Mason 2003). Data were collected from 35 species on stereotypy and also on husbandry, to check that any differences stemmed from species biology rather than from differential housing. Cross-species and phylogenetically corrected comparisons with various aspects of wild behaviour revealed that only natural home range size and distances travelled daily in the wild predicted stereotypy levels in captivity. The success of this approach in distinguishing between competing hypotheses suggests it would be fruitful in the future to run similar analyses for other taxa.

Conclusions and animal welfare implications

Most animal welfare problems are experienced by a handful of species (poultry, pigs, laboratory mice, etc), and these rightly attract the most research, usually with species-specific and proximate objectives. However, for more fundamental insights it can be inspiring and useful to take an ultimate approach and to look at the 'bigger picture'. After all, how animals react to humans, the lack of opportunity to forage, and restricted space, is at least partly influenced by their evolved characteristics.

As we have seen, species differences allow the statistical testing of three types of evolutionary or ecological hypothesis. We can thus use them to address welfare-relevant questions about the adaptive value of different responses to challenge; patterns of co-evolution; and relationships between particular biological variables and responses to aspects of captive management. Testing these sorts of ideas is of heuristic value, providing fundamental, interesting explanations likely to appeal to students, the public, and researchers in 'purer' areas of biology. Comparative approaches also have a practical value. They can yield general principles, for example to predict likely responses and problems in little-studied species. They can be used to investigate hypotheses that would be difficult, unethical or simply impossible to tackle experimentally (such as the relative importance of predation compared to natural ranging in carnivores). They can also yield novel insights with direct implications for improving housing. For instance, considering the ecological correlates of carnivore stereotypies potentially leads to new ideas about husbandry, shifting the focus towards incorporating aspects of large home ranges into enclosures (eg more space, den sites, viewpoints, and complexity) and away from the foraging-based changes currently favoured (eg Shepherdson *et al* 1998).

In conclusion, species comparisons have enormous potential value, especially considering how currently under-utilised data gathered in zoos are. As well as allowing the

thorough testing of the many hypotheses presented here, ideas about species' reproductive performance, morbidity and mortality could readily be investigated using data already collated in the *International Zoo Yearbooks* and International Species Information System (ISIS). The huge number of individual studies on behavioural abnormalities, time budgets and responses to environmental enrichments (eg as published in volumes of *Zoo Biology* and *Environmental Enrichment Conference Proceedings*) could also be capitalised upon. Looking to the future, we hope that an increasing number of species will also generate additional data on other responses, such as motivations to perform natural activities (cf eg Mason *et al* 2001), general aspects of behavioural control (cf eg Garner *et al* 2003) and hypothalamic-pituitary-adrenal (HPA) axis functioning (cf eg Wingfield *et al* 1992, 1995; O'Reilly & Wingfield 2001). With such information, we can envisage comparative approaches giving us, in the future, new and fundamental insights into species variation in the prioritisation of different behaviour patterns, abnormal behaviour development in captivity, and endocrine stress-responsiveness — all important issues that are currently far from understood.

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References

- Barnes R, Greene K, Holland J and Lamm M** 2002 Management and husbandry of duikers at the Los Angeles Zoo. *Zoo Biology* 21: 107-121
- Bateson P** 1991 Assessment of pain in animals. *Animal Behaviour* 42: 827-839
- Beauchamp G** 2002 Higher-level evolution of intraspecific flock-feeding in birds. *Behavioral Ecology and Sociobiology* 51: 480-487
- Bininda-Emonds O R P, Gittleman J L and Purvis A** 1999 Building large phylogenies by combining phylogenetic information: a complete phylogeny of the extant Carnivora (Mammalia). *Biological Sciences* 74: 143-175
- Björklund M** 1997 Are 'comparative methods' always necessary? *Oikos* 80: 607-612
- Blomberg S P, Garland T and Ives A R** 2003 Testing for phylogenetic signal in comparative data: behavioral traits are more labile. *Evolution* 57: 717-745
- Brashares J S, Garland T and Arcese P** 2000 Phylogenetic analysis of coadaptation in behavior, diet, and body size in the African antelope. *Behavioral Ecology* 11: 452-463
- Broom D M** 1998 Welfare, stress, and the evolution of feelings. *Advances in the Study of Behavior* 27: 371-403
- Broom D M** 2001 Evolution of pain. In: Lord Soulsby and Morton D (eds) *International Congress and Symposium Series* 246 pp 17-25. Royal Society of Medicine Press: London, UK
- Cheverud J M, Dow M M and Leutenegger W** 1985 The quantitative assessment of phylogenetic constraints in comparative analyses: sexual dimorphism in body weight among primates. *Evolution* 39: 1335-1351
- Clarke A S and Lindburg D G** 1993 Behavioral contrasts between male cynomolgus and lion-tailed macaques. *American Journal of Primatology* 29: 49-59
- Clarke A S and Mason W A** 1988 Differences among three macaque species in responsiveness to an observer. *International Journal of Primatology* 9: 347-364
- Clarke A S, Czekala N M and Lindburg D G** 1995 Behavioural and adrenocortical responses of male cynomolgus and lion-tailed macaques to social stimulation and group formation. *Primates* 36: 41-56
- Clarke A S, Mason W A and Mendoza S P** 1994 Heart rate patterns under stress in three species of macaques. *American Journal of Primatology* 33: 133-148
- Clubb R E** 2001 *The roles of foraging niche, rearing conditions and current husbandry on the development of stereotypes in carnivores*. PhD Thesis, University of Oxford, UK
- Clubb R and Mason G** 2003 Captivity effects on wide-ranging carnivores. *Nature* 425: 473-474
- Clutton-Brock J** 1999 *A Natural History of Domesticated Mammals*. Cambridge University Press: Cambridge, UK
- Day R L, Coe R L, Kendal J R and Laland K N** 2003 Neophilia, innovation and social learning: a study of intergenerational differences in callitrichid monkeys. *Animal Behaviour* 65: 559-571
- Degen A A, Kam M, Khokhlova I S, Krasnov B R and Barraclough T G** 1998 Average daily metabolic rate of rodents: habitat and dietary comparisons. *Functional Ecology* 12: 63-73
- Diamond J** 1997 *Guns, Germs, and Steel: the Fates of Human Societies*. W W Norton and Company: London, UK
- Dittrich L** 1976 Food presentation in relation to behaviour in ungulates. *International Zoo Yearbook* 16: 48-54
- Ebensperger L A and Cofré H** 2001 On the evolution of group-living in the New World cursorial hystricognath rodents. *Behavioral Ecology* 12: 227-236
- Felsenstein J** 1985 Phylogenies and the comparative method. *American Naturalist* 125: 1-15
- Forbis T A, Floyd S K and de Queiroz A** 2002 The evolution of embryo size in angiosperms and other seed plants: implications for the evolution of seed dormancy. *Evolution* 56: 2112-2125
- Forthman-Quick D L** 1984 An integrative approach to environmental enrichment. *Zoo Biology* 3: 65-77
- Freckleton R P, Harvey P H and Pagel M** 2002 Phylogenetic analysis and comparative data: a test and review of evidence. *American Naturalist* 160: 712-726
- Gage M J G and Freckleton R P** 2003 Relative testis size and sperm morphometry across mammals: no evidence for an association between sperm competition and sperm length. *Proceedings of the Royal Society of London, Series B, Biological Sciences* 270: 625-632
- Garland T and Diaz-Uriarte R** 1999 Polytomies and phylogenetically independent contrasts: examination of the bounded degrees of freedom approach. *Systematic Biology* 48: 547-558
- Garner J P, Mason G J and Smith R** 2003 Stereotypic route-tracing in experimentally caged songbirds correlates with general behaviour disinhibition. *Animal Behaviour* 66: 711-727
- Ginsberg J R and Macdonald D W** 1990 *Foxes, Wolves, Jackals and Dogs: an Action Plan for the Conservation of Canids*. International Union for the Conservation of Nature and Natural Resources (IUCN): Gland, Switzerland
- Gittleman J L** 1989 The comparative approach in ethology: aims and limitations. In: Bateson P P G and Klopfer P H (eds) *Perspectives in Ethology* 8 pp 55-76. Plenum Press: New York, USA
- Gittleman J L and Luh H-K** 1992 On comparing comparative methods. *Annual Review of Ecology and Systematics* 23: 383-404
- Gittleman J L and Purvis A** 1998 Body size and species-richness in carnivores and primates. *Proceedings of the Royal Society of London, Series B, Biological Sciences* 265: 113-119

- Glickman S E and Hartz K E** 1964 Exploratory behavior in several species of rodents. *Journal of Comparative and Physiological Psychology* 58: 101-104
- Glickman S E and Sroges R W** 1966 Curiosity in zoo animals. *Behaviour* 26: 151-188
- Grafen A** 1989 The phylogenetic regression. *Philosophical Transactions of the Royal Society of London* 326: 119-156
- Grafen A and Ridley M** 1996 Statistical tests for discrete cross-species data. *Journal of Theoretical Biology* 183: 255-267
- Greenberg R** 1990 Novelty responses: the bridge between psychology, behavioral ecology and community ecology. *Trends in Ecology and Evolution* 10: 165-166
- Harvey P H and Clutton-Brock T H** 1985 Life history variation in primates. *Evolution* 39: 559-581
- Harvey P H and Pagel M D** 1991 *The Comparative Method in Evolutionary Biology*. Oxford University Press: Oxford, UK
- Hedenstrom A and Rosen M** 2001 Predator versus prey: on aerial hunting and escape strategies in birds. *Behavioral Ecology* 12: 150-156
- Hediger H** 1950 *Wild Animals in Captivity*. Butterworths: London, UK
- Leal M** 2000. Avoiding versus confronting the predator: endurance capacity influences escape tactics in *Anolis* lizards. *Proceedings of the 37th Annual Meeting of the Animal Behaviour Society, August 5-9, Morehouse College and Zoo Atlanta, Atlanta, Georgia, USA*. Abstract available at: http://www.animalbehavior.org/ABS/Program/Past/Morehouse_00/absAL.html
- Martins E P and Hansen T F** 1996 The statistical analysis of interspecific data: a review and evaluation of phylogenetic comparative methods. In: Martins E P (ed) *Phylogenies and the Comparative Method in Animal Behavior* pp 22-75. Oxford University Press: Oxford, UK
- Mason G, Cooper J and Clarebrough C** 2001 Frustrations of fur-farmed mink. *Nature* 410: 35-36
- Mason G J** 1993a Age and context affect the stereotypes of caged mink. *Behaviour* 127: 191-229
- Mason G J** 1993b Forms of stereotypic behaviour. In: Lawrence A B and Rushen J (eds) *Stereotypic Animal Behaviour: Fundamentals and Applications to Welfare* pp 7-40. CAB International: Wallingford, UK
- Mason G J and Mendl M** 1997 Do the stereotypes of pigs, chickens and mink reflect adaptive species differences in the control of foraging? *Applied Animal Behaviour Science* 53: 45-58
- Mellen J D, Wildt D E and Shoemaker A** 2000 *AAZPA Felid Taxon Advisory Group Regional Collection Plan 2000-2002*. Disney's Animal Kingdom: Lake Buena Vista, Florida, USA
- Mendoza S P and Mason W A** 1997 Autonomic balance in *Saimiri sciureus* and *Callicebus moloch*: relation to life-style. *Folia Primatologica* 68: 307-318
- Mettke-Hofmann C, Winkler H and Leisler B** 2002 The significance of ecological factors for exploration and neophobia in parrots. *Ethology* 108: 249-272
- Meyer-Holzappel M** 1968 Abnormal behaviour in zoo animals. In: Fox M W (ed) *Abnormal Behaviour in Animals* pp 476-503. W B Saunders: London, UK
- Mooney J C and Lee P C** 1999 Reproductive parameters in captive woolly monkeys (*Lagothrix lagotricha*). *Zoo Biology* 18: 421-427
- Morris D** 1964 The response of animals to a restricted environment. In: Edholm O G (ed) *The Biology of Survival: Symposia of the Zoological Society of London No. 13* pp 99-120. Zoological Society of London: London, UK
- Morrow E H, Pitcher T E and Arnqvist G** 2003 No evidence that sexual selection is an 'engine of speciation' in birds. *Ecology Letters* 6: 228-234
- Nowell K and Jackson P** 1996 *Wild Cats: Status Survey and Conservation Action Plan*. International Union for the Conservation of Nature and Natural Resources (IUCN): Cambridge, UK
- Nunn C L, Gittleman J L and Antonovics J** 2000 Promiscuity and the primate immune system. *Science* 290: 1168-1170
- O'Reilly K M and Wingfield J C** 2001 Ecological factors underlying the adrenocortical response to capture stress in Arctic-breeding shorebirds. *General and Comparative Endocrinology* 124: 1-11
- Ormrod S A** 1987 The welfare of animals in captivity. In: Gibson T E (ed) *Proceedings of the Animal Welfare Foundation's 4th Symposium* pp 22-27. British Veterinary Association Animal Welfare Foundation: London, UK
- Pagel M** 1994 Detecting correlated evolution on phylogenies — a general method for the comparative analysis of discrete characters. *Proceedings of the Royal Society of London, Series B, Biological Sciences* 255: 37-45
- Pagel M** 1997 Inferring evolutionary processes from phylogenies. *Zoologica Scripta* 26: 331-348
- Pagel M** 1999 Inferring the historical pattern of biological evolution. *Nature* 401: 877-884
- Pagel M D** 1992 A method for the analysis of comparative data. *Journal of Theoretical Biology* 156: 431-442
- Pedersen V and Jeppesen L L** 1998 Different cage sizes and effects of behaviour and physiology in farmed and blue foxes. *Scientific* 22: 13-21
- Pérez-Barbéria F J, Gordon I J and Illius A W** 2001 Phylogenetic analysis of stomach adaptation in digestive strategies in African ruminants. *Oecologia* 129: 498-508
- Petter J J** 1975 Breeding of Malagasy lemurs in captivity. In: Martin R D (ed) *Breeding Endangered Species in Captivity* pp 187-202. Academic Press: London, UK
- Portugal M M and Asa C S** 1995 Effects of chronic melengestrol acetate contraceptive treatment on perineal tumescence, body weight, and sociosexual behavior on hamadryas baboons (*Papio hamadryas*). *Zoo Biology* 14: 251-259
- Prescott M J and Buchanan-Smith H M** 2004 Cage sizes for tamarins in the laboratory. *Animal Welfare* 13: in press
- Price T** 1997 Correlated evolution and independent contrasts. *Philosophical Transactions of the Royal Society of London* 352: 519-529
- Purmack R B** 1998 *Essentials of Conservation Biology*. Sinauer Associates: Sunderland, Massachusetts, USA
- Purvis A** 1995 A composite estimate of primate phylogeny. *Philosophical Transactions of the Royal Society of London* 348: 405-421
- Purvis A and Rambaut A** 1995 Comparative analysis of independent contrasts (CAIC): an Apple Macintosh application for analysing comparative data. *Computer Applications in the Biosciences* 11: 247-251
- Purvis A and Webster A J** 1999 Phylogenetically independent comparisons and primate phylogeny. In: Lee P (ed) *Comparative Primate Socioecology* pp 44-68. Cambridge University Press: Cambridge, UK
- Purvis A, Gittleman J L, Cowlshaw G and Mace G M** 2000 Predicting extinction risk in declining species. *Proceedings of the Royal Society of London, Series B, Biological Sciences* 267: 1947-1952
- Rohlf F J** 2001 Comparative methods for the analysis of continuous variables: geometric interpretations. *Evolution* 55: 2143-2160
- Ruggiero A and Lawton J H** 1998 Are there latitudinal and altitudinal Rapoport effects in the geographic ranges of Andean passerine birds. *Biological Journal of the Linnean Society* 63: 283-304

- Rushen J and Congdon P** 1987 Electro-immobilization of sheep may not reduce aversiveness of a painful treatment. *Veterinary Record* 120: 37-38
- Samraus H H** 1985 Mouth-based anomalous syndromes. In: Fraser A F (ed) *Ethology in Farm Animals* pp 391-422. Elsevier: Amsterdam, The Netherlands
- Savage A, Zirowsky D S, Shideler S E, Smith T E and Lasley B L** 2002 Use of levonorgestrel as an effective means of contraception in the white-faced saki (*Pithecia pithecia*). *Zoo Biology* 21: 49-57
- Shepherdson D J, Mellen J D and Hutchins M** 1998 *Second Nature: Environmental Enrichment for Captive Animals*. Zoo and Aquarium Biology and Conservation Series. Smithsonian Institution Press: Washington, USA
- Sol D, Timmermans S and Lefebvre L** 2002 Behavioural flexibility and invasion success in birds. *Animal Behaviour* 63: 495-502
- Stearns S C** 1983 The influence of size and phylogeny on patterns of covariation among life-history traits in mammals. *Oikos* 41: 173-187
- Terlouw E M C, Lawrence A B and Illius A W** 1991 Influences of feeding level and physical restriction on development of stereotypies in sows. *Animal Behaviour* 42: 981-991
- van Hoek C S and ten Cate C** 1998 Abnormal behavior in caged birds kept as pets. *Journal of Applied Animal Welfare Science* 1: 51-64
- Vitale A F, Visaberghi E and De Lilli C** 1991 Responses to a snake model in captive crab-eating macaques (*Macaca fascicularis*) and captive tufted capuchins (*Cenusa apella*). *International Journal of Primatology* 12: 277-286
- Wingfield J C, O'Reilly K M and Astheimer A B** 1995 Modulation of the adrenocortical response to acute stress in Arctic birds — a possible ecological basis. *American Zoologist* 35: 285-294
- Wingfield J C, Vleck C M and Moore M C** 1992 Seasonal changes of the adrenocortical response to stress in birds of the Sonoran desert. *The Journal of Experimental Zoology* 264: 419-428
- Wolf M C, Garland T and Griffith B** 1998 Predictors of avian and mammalian translocation success: reanalysis with phylogenetic independent contrasts. *Biological Conservation* 86: 243-255
- Woodroffe R and Ginsberg J R** 1998 Edge effects and the extinction of populations inside protected areas. *Science* 280: 2126-2128