

Vicious circles: positive feedback in major evolutionary and ecological transitions

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Evolutionary biologists and ecologists often focus on equilibrium states that are subject to forms of negative feedback, such as optima for phenotypic traits or regulation of population sizes. However, recent theoretical and empirical studies show how positive feedback can be instrumental in driving many of the most important and spectacular processes in evolutionary ecology, including the evolution of sex and genetic systems, mating systems, life histories, complex cooperation in insects and humans, ecological specialization, species diversity, species ranges, speciation and extinction. Taken together, this work suggests that positive feedback is more common than is generally appreciated, and that its self-reinforcing dynamics generate the conditions for changes that might otherwise be difficult or impossible for selection or other mechanisms to achieve. Testing for positive feedback requires analysing each causal link in feedback loops, tracking genetic, character and population-dynamic changes across generations, and elucidating the conditions that can result in self-reinforcing change.

The peacock's tail, the human brain, the extinction of passenger pigeons and the infestation of our genomes by repetitive elements are a few examples of the many remarkable phenomena in evolution and ecology that resist explication owing to the challenge of developing and testing hypotheses of their step-by-step evolution or occurrence. Indeed, since the Modern Synthesis, one of the most important tasks that any biologist has is to infer the processes that can generate large-scale changes in genetic systems, phenotypic traits, population sizes, species ranges and ecological communities [1,2]. Here, I suggest that a unique mechanism, positive feedback, has driven many of the most important changes in ecology and evolution, and that its influence is implicated in many of the transitions that appear most difficult to explain. I characterize the positive feedback process, provide examples from theory and empirical work, and present suggestions for recognizing further cases of self-reinforcing change.

Forms and dynamics of positive feedback

In conjunction with negative feedback loops, positive feedback cycles represent a common and efficient mechanism for the adaptive regulation of processes such as gene expression, endocrine pathways and self-organization of social insects [3–5], moving such systems rapidly between alternative adaptive modes. Intra-organismal or intra-colony feedback contrasts sharply with the dynamics of positive feedback in evolutionary and ecological situations. Here, positive feedback causes traits and populations to be driven from one state to another across generations, possibly resulting in increased adaptation.

Positive feedback loops can be categorized into one of two main forms (Table 1). First, positive feedback might entail across-generation evolutionary interactions between traits, such as the coevolution between male trait and female preference that typifies the fisherian runaway process. By this mechanism, changes in one trait drive the selection for changes in the other, and the traits are associated by the genes that underlie them [6]. Second, feedbacks might involve influences on and from population size, and thus result in ecological changes. For example, feedback between population density and density-mediated characters that influence individual survival and reproduction (so-called 'Allee effects') can lead to rapid population-dynamic change [7,8]; similarly, self-reinforcing loops between nutrient levels, microbial activity and primary producers can generate rapid recycling of nutrients in aquatic ecosystems [9], with profound effects on population sizes and community structure.

The positive feedback process begins with a change in aspects of traits, population sizes or environments that are either causally linked in a closed circular loop or that become linked as a result of the change. This perturbation initiates cycles of self-reinforcing change that continue over a certain time period or number of generations until the resultant changes, factors that are extrinsic to the feedback loop, or population extinction stop the cycling. The prevalence and efficacy of the positive feedback process should be higher with fewer links in each chain, because cycling is faster and there are fewer causal connections whose weakening or fracture would stop its course. Change by positive feedback can occur during arms races or coevolution [10], but arms races are usually restricted to situations involving conflict, and neither

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Table 1. Examples of positive feedback in major ecological and evolutionary transitions

Type of feedback	Research area	Main components of feedback loops	Potential results of feedback process	Refs
Feedback between traits	Mating systems	Male traits and female choice Sexual selection intensity, operational sex ratios and parental investment	Extreme male display traits Shifts between monogamy, polygamy and polyandry	[17,20] [23,26]
	Social systems	Colony size, worker reproductive potential and division of labour	Origin and evolution of eusociality	[33–35]
	Life history	Offspring versus adult survival rates, and nutrients for juveniles	Origin of semelparity (breeding once)	[27]
	Speciation	Fertility, lifespan and parental investment	Origin of menopause in humans	[32,61]
		Pre- and postzygotic isolation Ecological specialization and assortative mating	Rapid evolution of reproductive isolation Sympatric speciation	[46,47] [50]
Feedback involving population size	Ecological specialization	Gene flow and local adaptation in two habitat types	Specialization and increased adaptation	[38]
	Range sizes	Gene flow, local adaptation and range boundaries	Rapid shifts in ranges	[39]
	Species diversity	Ecological diversity and numbers of species	Rapid recovery of biota after mass extinctions	[41,42]
	Extinction	Group-mediated traits affecting fitness and population sizes	Loss of populations below a threshold size	[7,8,53]
		Frequency of deleterious alleles, effects of genetic drift and population size	Loss of populations below a threshold size	[54,55]

arms races nor coevolution necessarily involves the hallmark of positive feedback: the same causal loop repeating as the process occurs.

Positive feedback is a unique process in its dynamics and potential to cause change. However, perspectives based on negative feedback, equilibrated systems, mechanisms of population regulation and evolutionarily stable strategies appear to have hindered our appreciation of it [3]. Recent studies, combined with several classic cases, show that positive feedback might be more common than was previously recognized, and that it might be fundamentally important in driving some of the most spectacular transitions in ecology and evolution.

Arenas of positive feedback

I describe here a suite of evolutionary and ecological situations where empirical or theoretical studies implicate positive feedback in driving major changes. My aim is to present an appraisal of the scope of this process in evolutionary ecology, and to show that positive feedback has fundamental importance for a diverse set of disciplines, from the level of genes through to macroevolution.

Evolution of genetic and genomic systems

Recent evidence suggests that the evolution of three aspects of genetic systems (sexual reproduction, sex-determination mechanisms and the evolutionary dynamics of genomic elements, such as repetitive DNA) has been driven by positive feedback effects.

The origin of sex, and its paradoxical twofold cost, has long puzzled evolutionary biologists [1]. Bazinet [11] describes evidence that positive feedback between an increased capacity to transmit genes via parasitic or mutualistic endosymbiosis, and increased gene reception capability, favoured the evolutionary transformation of a rickettsia-like ancestor of mitochondria into the progenitors of sperm. This hypothesis is supported by data showing that bacterial endosymbionts related to

mitochondria can manipulate diverse aspects of gametogenesis in complex eukaryotes, and by other apparent vestiges of the origin of germline cells from endosymbionts. The self-reinforcing process here is directly analogous to fisherian runaway sexual selection, in that gene transmission corresponds to male display, and reception represents female choice. Moreover, as runaway sexual selection can lead to maladaptive male traits that decrease survival, so might a runaway origin of sex have led to the establishment of a maladaptive twofold cost of sex.

Werren *et al.* [12] present a two-locus model for the origin of sex-determination mechanisms, whereby maternal–offspring conflict can generate a positive feedback loop between the frequency of alleles that affect brood size and that are expressed in the mother, and the frequency of alleles expressed in the zygote affecting its own sex. Such loops can lead to either single-locus zygotic sex determination (e.g. XY males, or ZW females), or dominant maternal-effect alleles and the evolution of monogamy (single-sex broods). Similar feedback loops might have led to transitions from female to male heterogamy [13], and to the functional degeneration of Y chromosomes [14].

Nijman and Lenstra [15] describe a model for the evolution of repetitive DNA (e.g. mini- or microsatellites), whereby increasing repeat number above a critical threshold leads to accelerated rates of element multiplication. The self-accelerating expansion of repeats appears to be fundamental to several human diseases, such as fragile X syndrome, and might also help explain the large proportion of the human genome that comprises repeated DNA [16].

Mating-system and life-history evolution

Fisher's runaway process is a classic case of positive feedback, where functional phenotypic links between male traits and female preferences interact with the genetic correlation between them to generate bursts of

accelerating change. Challenges to the validity of this hypothesis have been dispelled by a new generation of models that incorporate costs, direct genetic benefits and spatial structure [6,17] and show that the runaway process can proceed unabated under a wide range of assumptions. Moreover, a recent model by Lorch *et al.* [18] shows that, when sexual selection is condition dependent (exhibiting positive covariance between male non-mating and mating fitness returns), self-reinforcing feedback between sexual and natural selection can be generated, which accelerates adaptation. Processes similar to fisherian runaway have also been proposed, involving the evolution of self-reinforcing genetic correlation between social signals and receiver systems [19,20], between propensity to altruism and mating within sibships [21], and between morphology and life history [22]. These studies further increase the generality of runaway processes and suggest that they occur in many contexts.

Sexual selection is only one component in the evolution of mating systems themselves, and here, positive feedback also appears to play a fundamental role. Andersson [23] proposed a quantitative-genetic model for the evolution of social polyandry from monogamy, driven by a positive feedback loop involving increased sexual selection on females, selection for reduced maternal investment (including smaller egg size) and increased variance in female mating success; his model is supported by a comparative analysis linking social polyandry to smaller eggs. Positive feedback has been implicated in the origin of leks by Sutherland [24], who suggested that females visit groups of males to enhance their prospects for adaptive mate choice, and such clumped males exhibit higher than average mating success; feedback between these two processes leads to implosion of territorial networks [25], whereby dispersed territories evolve into leks. Feedbacks between sexual selection and parental investment, coupled with effects from demography, behaviour and life-history traits, might be instrumental in causing other transitions between alternative mating systems (Figure 1) [23,26].

Positive-feedback processes have also been proposed in three life-historical contexts: the evolution of semelparity (breeding once), the evolution of neoteny (retention of juvenile traits into adulthood), and the evolution of senescence in social animals. Crespi and Teo [27] suggested that the origin of semelparity in Pacific salmon *Oncorhynchus* spp. was facilitated by the causal loop from increasing semelparity, to higher levels of local nutrients from spent carcasses, back to the higher offspring survival relative to adult survival that favours semelparous reproduction. This hypothesis can be generalized to other semelparous taxa, such as bamboos [28] in that local death of postreproductive adults might provide other benefits to juveniles. Horn proposed that positive feedback is also involved in evolution along an *r* versus *K* breeding strategy continuum (i.e. high fecundity–low survival–low investment, and vice versa), owing to links among body size, damping of environmental fluctuations, population demographics, parental investment levels and lifespan [29].

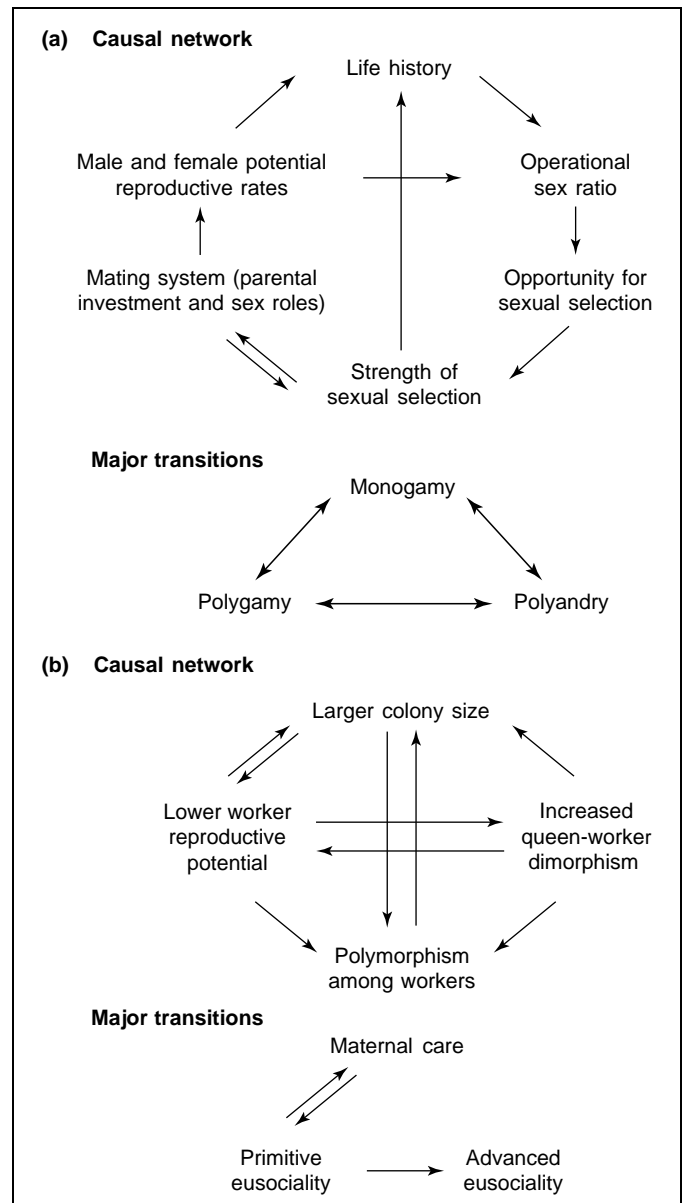


Figure 1. Two examples of causal networks exhibiting positive feedback loops, and the major transitions in evolution that they bring about. **(a)** Positive feedback in the evolution of mating systems, sexual selection and life history. Changes in any factor embedded in a closed loop can lead to a transition in mating system; for example, a more male-biased operational sex ratio might raise the intensity of sexual selection, leading to stronger male–male competition, less paternal care and a higher operational sex ratio; the outcome could be a transition from monogamy to polygamy. **(b)** Positive feedback in the evolution of eusociality. Larger colony size engenders reduced opportunities for workers to reproduce and stronger benefits from division of labour among workers. In turn, each of these changes increases colony productivity and leads to further colony size increases, as do enhanced adaptive differences in morphology between queens and workers. Such a self-reinforcing cycle might lead to a rapid transition from primitive eusocial forms, with small colonies, high levels of worker reproduction and no queen–worker dimorphism, to advanced eusociality, with large colonies, low levels of worker reproduction, and pronounced queen–worker dimorphism [33–35]. (a) and (b) reproduced, with permission, from [26] and [34], respectively.

Heterochronic changes, such as neoteny, have been proposed as being fundamental to diverse evolutionary transitions [30]. Martin and Gordon [31] present a case of apparent positive feedback involving increases in formerly adult-expressed duplicating ‘junk’ DNA of neotenic salamanders, whereby excess DNA has led to larger cell sizes, slower metabolism and developmental time, better adaptation to cool water and retention of the larval stage into

adulthood. These adaptations, and the mutational degeneration of adult-expressed genes, reinforce the evolution of neoteny.

Finally, Lee [32] describes a model for the role of resource transfer to descendants in shaping the senescence patterns of humans and other highly social animals, such as non-human primates, whereby a positive feedback loop becomes established between lower fertility, higher investment in offspring, and longer lifespan, leading in humans to postreproductive life. Several hypotheses involving positive feedback and arms races also seek to explain one of the other main features that distinguishes us from our primate relatives, our large brain and unique capacity for cognition (Box 1).

Social evolution

The origin of eusociality and the evolution of 'advanced eusocial' species represent two of the most remarkable transitions in evolutionary biology [1]. The origin of eusociality involves the seemingly paradoxical evolution of reduced reproduction in a permanent 'helper' caste, whereas the evolution of advanced eusocial species involves the evolution of large highly cooperative groups that, in many species, exhibit features of 'superorganisms'.

Alexander *et al.* [33] proposed a novel hypothesis based on positive feedback for the origin of eusociality. By their hypothesis, the first queen-worker differences were driven by a feedback loop from the initial increasing adoption of risky tasks by incipient workers, to increased extrinsic mortality, accelerated worker senescence, reduced importance of direct reproduction by workers and a consequent higher tendency to take work-related risks. The opposite considerations apply to queens, as the two castes rapidly differentiated in behaviour and lifespan.

'Primitively eusocial' forms of social animals, such as *Polistes* wasps, have small colonies, a lack of queen-worker dimorphism, and physical policing of worker reproduction by queens; by contrast, 'advanced eusocial' forms, such as honey bees *Apis mellifera*, are strikingly different, with large colonies, pronounced morphological caste differences, and worker reproduction regulated by worker policing and effects of queen pheromones or 'self-policing' by workers [33,34]. The transition between these two social attractors appears to be almost as problematic as the origin of eusociality itself: the forms differ fundamentally in key social traits, few if any 'transitional' forms exist and the shift appears to be evolutionarily irreversible. Bourke [34] proposed that positive feedback between increasing colony size, stronger queen-worker caste differentiation and increased colony productivity has driven this transition on multiple occasions in the evolution of social animals (Figure 1). His hypothesis has been supported by the reproductive skew model developed by Jeon and Choe [35], which demonstrates quantitatively the fundamental role of positive feedback between colony size and other social traits in the dynamics of cooperation and conflict among animals.

Box 1. Evolution of human cognitive capacity: driven by positive feedback?

The gulf between human cognitive abilities and those of even our closest relatives has resulted in diverse speculation regarding the selective pressures that led to this difference [1,57]. However, few theories predict the rapidity with which brain size has evolved along the human lineage or the abrupt emergence of diverse cultural innovations.

Alexander describes an 'autocatalytic' hypothesis of brain evolution, whereby, as humans become more ecologically dominant over other species, within-species competition for reproductive resources accelerates in intensity [57]. Most of this competition occurs between social groups of humans, which selects for enhanced within-group cooperation to succeed against other groups. Group-against-group competition leads to an accelerating social arms race involving imbalances of between-group power; the main object and focus of this strong selection within and between social groups is enhanced mental abilities, the unique human psyche. This social-competition hypotheses accords with the positive correlation between relative neocortex size and social group size across primates, the presence of primitive warfare in some chimpanzee populations, the omnipresent human adaptations related to within and between group interactions, and evidence from psychology that the functional design of the neocortex involves social scenario building and social-intellectual 'play' or 'practice' [57].

Alexander's hypothesis for the evolution of the human psyche focuses on humans as their own, primary, competitive 'hostile force of nature'. By contrast, Crews [58] proposed a cooperation-based hypothesis for the evolution of the human psyche centred on positive feedback between cognitive capacity, increased lifespan and inter-generational transfer of knowledge. By his hypothesis, increasing age led to more and better transfer of information to descendant kin, which enhanced their survivorship and reproduction; in turn, selection for improved knowledge acquisition and transfer drove the evolution of human cognitive capacity and function. This hypothesis accords well with three recent studies: (i) modelling and comparative evidence from Kaplan and Robson [59] on coevolution between intelligence, longevity and information transfer to descendants; (ii) archaeological evidence presented by Caspari and Lee [60] for coincident evolution of longer human life span and cultural innovation with population expansion during the Early Upper Palaeolithic; and (iii) data on strong inclusive fitness benefits of postreproductive female lifespan in two pre-modern human populations [61].

Evolution of specialization, species ranges and species diversity

Understanding the forces involved in transitions from ecological generalization to specialization is a classic problem in evolutionary biology, one that is closely allied to the evolution of species ranges and species diversity [36]. Positive feedback might drive these transitions via the causal links among adaptation, gene flow, population dynamics and spatial variation in habitat suitability.

Kawecki *et al.* [37] proposed a positive-feedback model for the evolution of ecological specialists, whereby mutations that are deleterious in marginal habitat favour increased specialization in the primary habitat, which cycles back to make marginal-habitat mutations relatively more deleterious. Maladaptation to marginal habitat also fosters specialization via the migrational meltdown model of Ronce and Kirkpatrick [38]. In this model, imbalances in population sizes between two habitat types connected by gene flow can lead to decreased local adaptation and reduced population sizes in one habitat type, which generates source-sink dynamics that lead, via positive

feedback, to specialization in the larger, better adapted population. Kirkpatrick and Barton [39] present a conceptually similar model of feedback among adaptation, gene flow and population dynamics, here in a continuously distributed rather than discrete-patch population. Their model predicts how species ranges can evolve, sometimes expanding or contracting dramatically as a result of small shifts in ecology or species traits being amplified by feedback effects. Such spatially based models are also important in understanding gene flow from crops to wild relatives, which might also give rise to migrational meltdown effects and drastic reductions in wild populations [40].

Local species diversity can change over an evolutionary timescale owing to increased or reduced specialization of community members, or over an ecological timescale via shifts in the ranges of species. Changes in diversity might also be driven by direct effects of ecological productivity, mediated by positive feedback, at various spatial and temporal scales. Thus, paleontological studies have inferred that biodiversity levels recover exponentially from disturbances such as mass extinction, via positive feedback between species diversity and ecological diversity [41,42]. Such processes are also supported by the ecological work on positive relationships among diversity, productivity and ecosystem functions in extant communities [43,44]. Finally, recent theoretical work by van Nes and Scheffer [45] shows that complex communities can shift radically in their composition as a result of small environmental or evolutionary changes, and that such drastic shifts between alternative community-composition attractors, or towards mass extinctions, are due, in part, to effects of positive feedback.

Speciation

Two recent theoretical studies have shown how positive feedback might drive speciation. By the first process, linkage between genes promoting prezygotic isolation and genes causing some degree of postzygotic isolation leads to increasing frequency of both sets of genes [46]. As mate choice evolves, linked genes for postzygotic isolation increase in frequency, leading to even stronger selection for prezygotic isolation, and the loop accelerates until populations become sexually isolated. Such a process might explain the 'snowball effect' of accelerating reproductive isolation between diverging populations of lepidopterans and of anurans [47]. Positive feedback between pre and postzygotic isolation is expected to be especially strong for sex-linked genes owing to hemizyosity (homozygosity due to haploidy) and reduced or absent recombination, and it might help to clarify the high incidence on sex chromosomes of genes related to sexual selection and reproductive isolation [48].

Second, positive feedback might develop between gene flow and local adaptation [49]. Selection for increased local adaptation would generate selection for reduced gene flow, which could further strengthen local adaptation. Such feedback might lead to sufficiently low levels of gene flow that reproductive isolation evolves more readily. The high prevalence of local adaptation suggests that this is an important general mechanism fostering speciation.

Caillard and Via [50] provide evidence for a similar process, positive feedback between ecological specialization and assortative mating of pea aphids *Acyrtosiphon pisum* on the alternative host plants pea *Trifolium pratense* and alfalfa *Medicago sativa*. This type of mechanism could have also helped to generate the striking species diversity of phytophagous insects. Such feedback might also drive the equivalent of speciation among microbes: Cohan [51] presents a model and empirical evidence that positive feedback between sequence divergence and decreasing recombination can generate ecological diversity among related strains of bacteria. Taken together, these models and examples demonstrate that positive feedback could greatly speed the evolution of reproductive isolation, even under sympatry.

Extinction

As positive feedback effects can help to create species, so might they also render them rapidly extinct. Allee effects, positive or negative influences of group sizes on population dynamics, are characterized by positive feedback among population sizes and traits affecting individual fitness, such as ability to find mates or social group members, or to satiate predators. An increase in recent theoretical and empirical work on Allee effects has demonstrated their efficacy, high prevalence, and role in the evolution of adaptation [7,8,52,53]. Most research has focused on the role of Allee effects, mediated by a wide range of behavioral and ecological mechanisms, in the extinction of populations that drop below some threshold size [7,53]. By contrast, Holt *et al.* [52] present models demonstrating how Allee effects can facilitate the evolution of local adaptation in populations that would otherwise serve as demographic sinks.

In contrast to Allee effect models, 'mutational meltdown' models focus on the role of population-genetic factors in cycling towards extinction. In these models, positive feedback proceeds from reduced population sizes, to stronger effects of drift, to increases in the frequency of deleterious alleles, and back to smaller populations [54,55]. Such models enable quantitative prediction of extinction vulnerability as a function of effective population sizes, and joint consideration of Allee effects with mutational meltdown thresholds should aid in managing species and populations at risk.

Finally, positive feedback effects might also be important in resource exploitation by humans, as when increased rarity of prey (e.g. fish or whale stocks) selects for more-efficient harvesting technology, which reduces populations further [56]. Indeed, interactions between such anthropogenic effects and Allee effects might have been responsible for extinction or massive population reductions of some formerly superabundant animals, such as American bison *Bison bison*, passenger pigeon *Ectopistes migratorius*, Pacific salmon *Oncorhynchus* spp. and Atlantic cod *Gadus morhua*.

Conclusions

Evolutionary ecologists often focus on equilibrium conditions, expressed in terms of evolutionarily stable strategies, ecosystem stability and homeostatic, negative

feedback-driven properties of natural systems. However, the diverse cases, contexts, models and conjectures described here indicate that positive feedback might be remarkably widespread in evolutionary and ecological processes, although its fleeting, episodic nature makes it difficult to observe directly. Detailed analyses of evolutionary changes where transitional forms are absent or rare, and empirical information about loops in the causal networks linking genes, phenotypes, population dynamics and communities, should lead to ever-increasing numbers of discoveries of positive feedback effects driving the major transitions in ecology and evolution.

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Forthcoming Conferences

Are you organizing a conference, workshop or meeting that would be of interest to *TREE* readers? If so, please e-mail the details to us at TREE@elsevier.com and we will feature it in our Forthcoming Conference filler.

30 March–1 April 2005

Annual BES Symposium, Ecological Consequences of Extreme Events, Manchester, UK.
<http://www.britishecologicalsociety.org/articles/meetings/current/annualsymposium2005/>

9–10 May 2005

Royal Society Discussion Meeting: Sexual Conflict: A New Paradigm? London, UK
<http://www.royalsoc.ac.uk/events/>

10–14 June 2005

Evolution 2005 (jointly sponsored conference of the Society for the Study of Evolution, the Society of Systematic Biologists, and the American Society of Naturalists) University of Alaska Fairbanks, AL, USA
<http://www.evolution05.uaf.edu/>

12–13 July 2005

BES/IEEM Conference on Ecological Impact Assessments: Science and Best Practice, Bath, UK
http://www.britishecologicalsociety.org/articles/groups/conservation/bes_ieem_conf/

15–19 July 2005

The 19th Annual Meeting of the Society for Conservation Biology, Brasília, Brazil.
<http://www.unb.br/ib/zoo/scb2005/>

19–21 July 2005

ASAB Summer Meeting, Behavioural Interactions: Visions for the Future, University of Lancaster, UK
<http://www.societies.ncl.ac.uk/asab/meetings.html>

6–10 August 2005

The Animal Behavior Society 2005 Annual Meeting, Snowbird, UT, USA
<http://www.animalbehavior.org/ABS/Program/>

7–12 August 2005

90th Annual Meeting of the Ecological Society of America, Montréal, Canada
<http://www.esa.org/montreal/>

15–20 August 2005

10th Congress of the European Society for Evolutionary Biology, Krakow, Poland
<http://www.eseb.org/index.html?http://www.eseb.org/congress.htm>

2–4 September 2005

Special BES Symposium, Body size and the organisation and function of aquatic ecosystems, University of Hertfordshire, UK
<http://www.britishecologicalsociety.org/articles/meetings/current/specialsymposium2005/>

26–27 September 2005

Royal Society Discussion Meeting: Major Steps in Cell Evolution: Evidence, Timing and Global Impact, London, UK
<http://www.royalsoc.ac.uk/events/>

17–18 October 2005

Royal Society Discussion Meeting: Evolution of the Antarctic Ice Sheet: New Understandings and Challenges, London, UK
<http://www.royalsoc.ac.uk/events/>