

## A review of the global conservation status of bats

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**Abstract** There are 1,001 species of bats, almost a quarter of which are globally threatened. The Chiroptera Specialist Group of IUCN's Species Survival Commission has produced two Action Plans examining conservation issues for all species and detailing recommendations for action to conserve the most threatened species and habitats. These Plans are aimed principally at key decision makers as well as organisations and individuals who are promoting bat conservation issues. The underlying threat to bats is pressure on resources from increasing human populations that leads to the loss or modification of foraging habitats and roosts. Bats frequently have a negative public image that influences the response to the problems of rabies and vampire bats in Latin America and conflicts between bats and commercial fruit growers in other areas of the world. In some areas bats are

persecuted because people are ignorant of the life history of bats and their role in ecosystems, while in other areas bats are overexploited for food. There is also a general lack of information about the distribution, status, biology and ecology of many species. This review examines some of the more general issues relating to bat conservation. It provides information on bat faunas of all countries worldwide, and on the most threatened species. It highlights the priority areas where action is needed immediately at a global, regional or national level. It highlights in particular the global importance of islands and caves for bats.

**Keywords** Action Plan, bats, caves, Chiroptera, conservation priorities, islands.

### Introduction

Bats belong to the Order Chiroptera, with 1,001 species divided into two suborders – the Megachiroptera (often known as Old World fruit bats) with 167 species and the Microchiroptera with 834 species (Mickleburgh *et al.*, 1992; Hutson *et al.*, 2001). Bats are recorded from all areas of the world except the Arctic and Antarctic and a few isolated oceanic islands. More than 20% of all mammal species are bats. In many countries bats are major contributors to mammalian biodiversity, while in some, particularly small oceanic islands, they are the only indigenous mammals and may play a vital role as 'keystone' species in ecosystems (Cox *et al.*, 1992).

In 1992 Mickleburgh *et al.* (1992) reviewed conservation issues relating to megachiropteran bats, and the conservation status of the Microchiroptera was reviewed by Hutson *et al.* (2001). The publication of these two Action Plans permitted the first overview of conservation

issues relating to bats worldwide. Both documents were aimed at key decision-makers at the governmental level as well as those promoting bat conservation at an international, regional and national level. As such, the documents contained many specific conservation recommendations. The purpose of this review is to synthesize the available information and highlight the key issues that need to be tackled immediately at global, regional and national levels.

### Diversity and conservation status

The greatest bat diversity is in the neotropics, with at least 83 genera and 288 species recorded (Appendix). One hundred and two bat species have been recorded for the Caribbean region, of which 23 are endemic. The country with the greatest number of species is Indonesia with 175. West, Central and Southern Africa and elsewhere in South-east Asia are also rich areas for bat diversity. In many cases the numbers of species recorded are underestimates because systematic surveys are incomplete. Australia has 75 bat species, 20% of which are endemic, neighbouring Papua New Guinea has 91 species, and Europe has 35 species.

The status of all bat species were assessed using the IUCN Red List Categories (IUCN, 1994) (Table 1). Twelve bat species are confirmed as Extinct. A further 238 species, almost a quarter of the total, are threatened (i.e. Critically Endangered, Endangered or Vulnerable).

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**Table 1** Number of bat species in each IUCN Red List category (see IUCN (1994) for details of the categories). All species except those in the Lower Risk: Least Concern category, which are not on the 2000 IUCN Red List, are included in Hilton-Taylor (2000).

Category	Number of Species	% of total
1. Adequate data		
<i>Extinct species</i>		
Extinct	12	1.2
Extinct in the Wild	0	0.0
<i>Threatened species</i>		
Critically Endangered	29	2.9
Endangered	36	3.6
Vulnerable	173	17.3
<i>Lower risk species</i>		
Lower Risk: Near Threatened	212	21.2
Lower Risk: Conservation Dependent	0	0.0
Lower Risk: Least Concern	479	47.8
2. Inadequate data		
Data Deficient	60	6.0
TOTAL	1001	

In the lower risk categories, 212 species are categorised as Near Threatened and 479 as Least Concern (i.e. they are not on the 2000 IUCN Red List). Sixty species are categorised as Data Deficient. In most cases these assessments were made using the limited amount of information currently available. Few bat species have been studied in detail across the whole of their range. Many assessments were made by predicting status based upon knowledge of current threats to habitats or roosts, or to similar species in other areas. In all cases the precautionary principle was applied, and it is likely that assessments will change as more information on biology, ecology, distribution and taxonomy becomes available.

### Major threats

Many of the threats to bats can be directly related to increasing human populations that bring extra demands for land, food and other resources that ultimately results in the degradation or destruction of habitat for bats and other organisms. This pressure is especially acute in tropical countries where a large proportion of the population may live in rural areas and have relatively low incomes.

### Habitat loss or modification

One of the most important but universally threatened habitats for bats is forest or woodland, used for roosting and feeding. While much attention has focused on the

loss of primary forest in tropical and subtropical areas, the situation in temperate areas is equally serious in many cases. Certain forest types are of particular concern, for example dry forests in Latin America and the Caribbean. Some harvesting techniques can be particularly damaging to the forest structure, and logging activities may open up previously inaccessible areas to hunters, settlers and miners.

Landscape elements are important for bats (Verboom, 1998). Tree lines, hedgerows, canals and other linear elements are used by bats during flight and may provide vital connections between roosts and feeding areas, and their loss or disruption because of intensified agricultural practices may be highly detrimental to some species. In areas where agriculture has been practised at a less intensive level, such as in Central Europe, the threat to these cultural landscapes is a great concern for the conservation of bats and other organisms.

Worldwide, agriculture has had a major impact on many bat habitats. The negative effects of 'slash and burn' agriculture on bat populations have recently been seen in Laos (T. Guillen, pers. comm.), where the nomadic peoples of the Nam Et Highlands burn primary forest to plant crops. Slash and burn destroys vegetation cover and may also kill individual bats that use tree crevices as roosts, affecting many of the threatened species of bats. Pesticide usage in agriculture in the developed world has recently moved towards chemicals with reduced mammalian toxicity, but highly toxic alternatives such as DDT are still used in developing countries (Fenton & Rautenbach, 1998). DDT has been widely used in Africa as a way of controlling the *Anopheles* mosquito, which spreads malaria (McGinn, 2001). Safer pyrethroid alternatives are now being used, although the use of DDT has been reintroduced in areas where resistance to pyrethroids has developed (McGinn, 2001). Such pesticides have been implicated in the decline of bat populations in the USA and Australia (Clark, 1981) and McWilliam (1994) showed that spraying with DDT increased the mortality of some bat species in Zimbabwe. Clearly, the threat to bat populations from DDT needs to be weighed against the threat to humans from malaria.

Natural events can also cause problems, especially on small islands in the Indian and Pacific Oceans that are regularly affected by tropical storms. A typhoon that hit Samoa and American Samoa in 1990 had a severe impact on populations of *Pteropus tonganus* and *P. samoensis* (Dashback, 1990). Following the storm many bats foraged on fallen fruit or in fallen trees, but because bats were unable to take flight from the ground they were vulnerable to predation and were killed in large numbers by domestic dogs, cats and pigs. Evidence from the Mariana Islands, Samoa and Vanuatu suggested that a

major cause of post-storm mortality was increased hunting by humans (Pierson & Rainey, 1992). Defoliation made roosting animals more visible, and a reduced food supply forced bats to forage diurnally, increasing opportunities to hunt them.

### Roost site loss or disturbance

Woodland management practices can also negatively affect bats. Removal of dead trees or decaying branches from living trees can reduce the availability of potential roosting sites. Bats may be loyal to an area containing several roosts rather than a specific tree, suggesting that even trees not heavily used by bats may be important to them (Lewis, 1995; Barclay & Brigham, 1996; Pierson, 1998).

Underground sites such as caves and mines are crucial to the survival of many bat species worldwide. In temperate countries such sites may be used for breeding in summer and hibernation in winter, whereas in tropical countries, where bats do not hibernate, caves and mines may provide roosts for large colonies. In areas with few natural caves, such as Australia, mines provide important alternative roost sites. For example, the endemic and vulnerable ghost bat *Macroderma gigas* is heavily reliant on mines in Australia, with one site containing 1,500 animals out of a total population of 10,000 (Phillips, 1990).

Abandoned underground mines may be threatened by resumption of activities such as open cast mining, and the sealing of abandoned workings, usually for safety reasons, can have a dramatic impact on bats. In Wisconsin in the USA more than 600,000 bats of four species were saved when two mines were protected from closure (Tuttle & Taylor, 1998). Quarrying, particularly for limestone, is a major threat to caves in Asia. Samanar Hill in southern India has many caves used by bats, and only the cancelling of new quarrying leases has saved the site (Murphy, 1987).

Some of the larger bat colonies produce sufficient guano for it to be an important economic resource, and uncontrolled guano collection can result in disturbance of colonies. A similar problem exists where bats share caves with cave swiftlets. The nests of cave swiftlets are highly prized as a component of bird's nest soup, with the most valuable nests worth US\$2,000 – 4,000 per kg (Sankaran, 2001). Uncontrolled nest collection can disturb bat colonies, and concerns have been raised over dramatic declines in populations of naked bats *Chieromeles torquatus* in caves in Sarawak (L. S. Hall pers. comm.). Caves are also attractive to speleologists and tourists. Spectacular cave systems are a magnet for tourists, and poorly managed tourism can modify cave ecosystems and adversely affect bat populations. In a number of

countries such as the UK and Australia there are agreements between conservationists and speleologists to minimise impacts on cave ecosystems (Hutson *et al.*, 1995; Watson *et al.*, 1997).

### Health issues

There are human health concerns associated with bats including histoplasmosis, rabies-like lyssaviruses and classical rabies. Histoplasmosis is a group of diseases that have been linked to inhalation of the spores of *Histoplasma capsulatum* in bat caves, although the risk to humans is relatively small (Hutson *et al.*, 2001). In Australia rabies-like lyssavirus has been isolated from megachiropteran bats, although again the threat to humans is small, particularly if appropriate precautions are taken when handling bats (Hall & Richards, 2000).

Rabies is the main health issue associated with bats, particularly amongst vampire bats in Latin America (Brass, 1994). Rabies is also known to be widespread amongst insectivorous bats in the USA and Canada and during 1980–2000, 28 people died of strains of rabies virus associated with bats, particularly *Lasionycteris noctivagans* and *Pipistrellus subflavus* (Jackson & Fenton, 2001). This has led to the issuance of strict guidelines for preventing human rabies (Centers for Disease Control and Prevention, 1999), and could pose a threat to the public image of bats in these countries. Vampire bats, which feed on blood and are vectors of bovine paralytic rabies, are potentially a more serious threat, principally to livestock. On a global scale, over 1929–1990 c. 500 human deaths have been attributed to bats (i.e. an average of <10 per year) (Brass, 1994). However, it has been estimated that an average of 100,000 cattle a year die from rabies, representing a loss of about \$30 million per year (Acha & Arambulo, 1985). Of the three vampire species (*Desmodus rotunda*, *Diphylla ecaudata* and *Diaemus youngi*) only *Desmodus* is common. Most attempts to control the threat from vampire bats have been ineffective, and damaging to non-target species. Caves in Mexico have been sealed because of the purported presence of vampires, threatening non-target species using these sites (Pint, 1994). Bats have been destroyed in their roosts using dynamite, shotguns, smoke and fire, and cyanide gas. Other methods have targeted bats whilst they feed, and have included the application of poisons such as strychnine and arsenic to open wounds on cattle and the administration of low doses of anti-coagulants to cattle that leave them unaffected but which are fatal to bats (Brass, 1994). Vaccination of cattle is the most effective and specific control mechanism for rabies but this is relatively expensive (Arellano-Sota, 1988). Concerns over the 'rabies issue' led to a Resolution at the 11th International Bat Research Conference in Brazil

in 1998 which called for a more carefully managed approach to the issue of vampire bats and rabies (Hutson *et al.*, 2001).

Bats may also be victims of disease. Flying foxes (*Pteropus* species) in the Pacific are thought to have suffered on several occasions from mass mortality resulting from pandemic disease (Rainey, 1998). *Pteropus* species are generally colonial, and there have been reports of the dramatic impacts of disease on Pacific islands such as Fiji, the Solomon Islands, New Caledonia and the Federated States of Micronesia (Rainey, 1998). The origin of these diseases is not known, although the high mortality suggests that the bats were not previously exposed to the pathogen, which might have been inadvertently introduced by humans (Flannery, 1989).

### Persecution

Bats are viewed with suspicion, if not outright fear, in many cultures. A combination of ignorance and perceived risks of damage or disease can lead to deliberate persecution. This is particularly the case where humans share their homes with bats. In Africa, molossid bats such as *Mops condylurus*, *Tadarida aegyptiaca* and *Chaerephon pumilus* frequently roost in houses, and destructive methods of exclusion, such as fumigation, may be used to deal with them (Taylor, 2000). However, in The Netherlands successful education campaigns have ensured that roosts of *Eptesicus serotinus* have remained undisturbed in houses even when the bats have tested positive for rabies (P. H. C. Lina, pers. comm.).

In areas where fruit is grown on a commercial scale and where fruit orchards have replaced forests that would otherwise have been key feeding areas, such as Israel, Australia and South Africa, flying foxes have been the targets of eradication campaigns (Makin & Mendelssohn, 1987; Hall & Richards, 2000). Although flying foxes usually feed on fruit too ripe for commercial use, they may damage other fruits, leading to economic losses. Efforts to control flying foxes have varied from fumigation of caves in Israel, resulting in the deaths of many insectivorous bats (Makin & Mendelssohn, 1987), to culling 75% of the bat population on the Maldives every 3 or 4 years to "maintain a stable population" (Dolbeer *et al.*, 1988). In Australia, conservationists are lobbying for the recognition of *Pteropus poliocephalus* as a threatened species, but this has not stopped plans to cull these animals in Melbourne Botanic Garden because of concerns over possible damage to roosting trees (L. Lumsden, pers. comm.). As with vampire bats, many of the management methods used to deal with this problem have been indiscriminate and ineffective. Only

through closer liaison between conservationists and the fruit-growing industry can this problem be effectively addressed.

### Lack of information

Lack of information makes assessing the status of populations difficult, this in turn hampers the development of appropriate conservation measures. Of the 1,001 species of bats, few have been well studied. For many, information about their status, biology and ecology is limited, and for some there is no information beyond that available when the species was first described. In some regions, particularly in Europe and North America, biologists have collated information on the distribution and status of species, but there are large areas of the world where basic distributional data are lacking. In South-east Asia, for example, recent studies in Viet Nam, Laos and Myanmar have dramatically increased the known numbers of species in these countries (Bates *et al.*, 1997, 2000; Francis *et al.*, 1999). What is known of the distribution of a species is often based on information from specimens in museum collections and may not reflect the actual distribution. Bats may undergo seasonal movements, resulting in their concentration in certain areas at certain times of year, which may give a false impression of their status. Also, the status of colonial species is easier to assess than for those that are widely dispersed. Taxonomic uncertainties make conservation planning difficult. This has been highlighted in Australia, where the status of many taxa remains uncertain (Duncan *et al.*, 1999). Novel techniques, including DNA analysis, are helping to resolve some of these problems. New species of bats are frequently being described, even in relatively well studied areas. Recently, *Pipistrellus pipistrellus*, one of the commonest species in Europe, was found to be two species, the nominate form and *Pipistrellus pygmaeus* (Jones & Barrett, 1999).

### Overexploitation for food

The importance of bats as a food for humans is not well understood. It is known that larger species such as *Pteropus* and *Acerodon* have long been used by humans as a source of protein especially on Indian and Pacific Ocean islands. In the western Pacific there has been a commercial trade in flying foxes, centred on the island of Guam. Between 1981 and 1989 c. 13,000 flying foxes were imported into Guam each year (Wiles, 1992), resulting in declines of populations in exporting countries (Rainey, 1998). In 1989 this trade was largely stopped when all *Pteropus* and *Acerodon* species were included in Appendix I and II of CITES. However, some illegal hunting and international trade probably still occurs

in the northern Marianas (Wiles, 1994; Worthington & Taisacan, 1996). Although the level of exploitation of microchiropteran bats is largely unknown, a study in Laos suggested that this may be a serious threat (Francis *et al.*, 1999). In all survey areas bats were eaten by local villagers and there were reports of large numbers being taken for food. In northern Laos thousands of bats were cooked for sale. In general, it is likely that the consumption of bats is widespread and is not a major threat where it involves common species. However, for some threatened species, or where trade becomes commercialized, the situation may be more serious.

### Conservation priorities

The two Action Plans (Mickleburgh *et al.*, 1992; Hutson *et al.*, 2001) give detailed lists of conservation recom-

mendations for bats worldwide. Some of the more important general issues relating to bat conservation are discussed below.

### Critically Endangered species

Of the 238 species considered to be threatened (Table 1) conservation attention should focus initially on the 29 species that are categorised as Critically Endangered (Table 2). Seven species (*Pteralopex acrodonta*, *P. anceps*, *P. atrata*, *P. pulchra*, *Pteropus insularis*, *P. molossinus* and *P. phaeocephalus*) are found on small islands in the western Pacific where threats from increasing human populations and natural events, such as typhoons, are particularly high (Hutson *et al.*, 2001). Six species (*Nyctimene rabori*, *Hipposideros nequam*, *Paracoelops megalotis*, *Rhinolophus convexus*, *Pipistrellus anthonyi* and *P. joffrei*) are

**Table 2** Critically Endangered Bats, with the criteria used for their categorisation (see IUCN (1994) for details), and their distribution.

Family/Species	Criteria for CR categorisation	Distribution
<b>Megachiroptera</b>		
<b>PTEROPODIDAE</b>		
<i>Aproteles bulmerae</i>	B1 + 2c	Papua New Guinea
<i>Latidens salimalii</i>	B1 + 2c, D	India
<i>Nyctimene rabori</i>	A2c	Philippines (Negros)
<i>Pteralopex acrodonta</i>	A1c, B1 + 2c	Fiji
<i>Pteralopex anceps</i>	A1c	Papua New Guinea, Solomons
<i>Pteralopex atrata</i>	A1c	Solomons
<i>Pteralopex pulchra</i>	A1c	Solomons
<i>Pteropus insularis</i>	A1cd	Federated States of Micronesia
<i>Pteropus livingstonei</i>	A1c + 2cd, B1 + 2c, C2a	Comoros
<i>Pteropus molossinus</i>	B1 + 2ce	Federated States of Micronesia
<i>Pteropus phaeocephalus</i>	B1 + 2e	Federated States of Micronesia
<i>Pteropus pselaphon</i>	B1 + 2ce	Japan
<i>Pteropus rodricensis</i>	B1 + 3d	Mauritius (Rodrigues)
<i>Pteropus voeltzkowi</i>	C2a	Tanzania (Pemba)
<b>Microchiroptera</b>		
<b>EMBALLONURIDAE</b>		
<i>Coleura seychellensis</i>	B1 + 2cde, C2b, D	Seychelles
<i>Taphozousroughtoni</i>	A1ac, B1 + 2abcde, D	Australia
<b>HIPPOSIDERIDAE</b>		
<i>Hipposideros nequam</i>	B1 + 2c	Malaysia
<i>Paracoelops megalotis</i>	B1 + 2c	Viet Nam
<b>RHINOLOPHIDAE</b>		
<i>Rhinolophus convexus</i>	D	Malaysia
<b>VESPERTILIONIDAE</b>		
<i>Myotis cobanensis</i>	B1 + 2c	Guatemala
<i>Myotis planiceps</i>	B1 + 2c	Mexico
<i>Pharotis imogene</i>	B1 + 2c, C2b	Papua New Guinea
<i>Pipistrellus anthonyi</i>	B1 + 2c	Myanmar
<i>Pipistrellus joffrei</i>	B1 + 2c	Myanmar
<i>Scotophilus borbonicus</i>	A1c	Madagascar, Réunion
<i>Murina tenebrosa</i>	B1 + 2c, D	Japan
<b>MOLOSSIDAE</b>		
<i>Chaerephon gallagheri</i>	B1 + 2c	Democratic Republic of Congo
<i>Mops niangarae</i>	B1 + 2c	Democratic Republic of Congo
<i>Otomops wroughtoni</i>	B1 + 2c	India



**Table 3** Families of bats, with number of species, number of threatened species (i.e. Critically Endangered, Endangered or Vulnerable), % threatened and general distribution.

Family	No. of species	No. of threatened species	% threatened	Distribution
Megachiroptera				
Pteropodidae	167	58	34	Europe, Africa, Arabia, Asia, Australia, Oceania
Microchiroptera				
Rhinopomatidae	4	1	25	Africa, Arabia, Asia
Craseonycteridae	1	1	100	Thailand
Emballonuridae	48	14	29	Americas, Europe, Africa, Arabia, Asia, Australia, Oceania
Nycteridae	14	2	14	Africa, Arabia, Asia
Megadermatidae	5	1	20	Africa, Asia, Australia
Hipposideridae	75	18	24	Africa, Arabia, Asia, Australia, Oceania
Rhinolophidae	66	11	17	Europe, Africa, Arabia, Asia, Australia
Noctilionidae	2	0	0	Americas
Mormoopidae	8	1	13	Americas
Phyllostomidae	151	29	19	Americas
Natalidae	5	1	20	Americas
Furipteridae	2	1	50	Americas
Thyropteridae	3	1	33	Americas
Myzopodidae	1	1	100	Madagascar
Vespertilionidae	357	78	22	Americas, Europe, Africa, Arabia, Asia, Australia, New Zealand, Oceania
Mystacinidae	2	1	50	New Zealand
Molossidae	90	19	21	Americas, Europe, Africa, Arabia, Asia, Australia, Oceania

found in South-east Asia, and four (*Pteropus livingstonei*, *P. rodricensis*, *P. voeltzkowi* and *Coleura seychellensis*) are found only on small islands in the Indian Ocean. Only two species are found in mainland Africa (*Chaerephon gallagheri* and *Mops niangarae*) and two in Central America (*Myotis cobanensis* and *M. planiceps*). There are no Critically Endangered species in South America despite the diversity of bats in this area.

### Taxonomically distinct species

There are 18 families of bats, and most are represented by large numbers of species with widespread distributions (Table 3). However, two families, the Craseonycteridae and the Myzopodidae, are represented by a single genus and species: *Craseonycteris thonglongyai* from Thailand is categorised as Endangered and *Myzopoda aurita* from Madagascar as Vulnerable. The family Mystacinidae has one genus with two species, both endemic to New Zealand. One, *Mystacina robusta*, is thought to be Extinct, while the other, *M. tuberculata*, is categorised as Vulnerable. Five other bat families are represented by a single genus: the Rhinopomatidae (4 species), Nycteridae (14), Noctilionidae (2), Natalidae (5) and Thyropteridae (3). All of these families provide important reservoirs of taxonomic diversity and as such should receive particular attention.

### Endemic species

Table 4 lists countries that have >10 endemic bat species. Of particular concern are Australia, Madagascar and Japan, where the bat faunas are relatively small. The general threat to bat species is especially acute in the latter two countries (Hutson *et al.*, 2001).

### Islands

Bats are recorded from many island nations. Many species of the family Pteropodidae are recorded largely or entirely from islands and 13 of the 29 Critically Endangered bats are found only on islands (Table 2). The threats on islands are accentuated by often limited habitat, rapidly increasing human populations and

**Table 4** Countries with 10 or more endemic bat species.

Country	Total no. of bats	Total no. of endemics	% of endemics in bat fauna
Indonesia	175	24	13.7
Australia	75	15	20.0
Madagascar	28	14	50.0
Mexico	137	13	9.5
Japan	39	12	30.7
Malaysia	112	11	9.8
Papua New Guinea	91	10	11.0

natural events such as typhoons and cyclones. Bats often form a significant proportion of the native mammalian fauna and their role as pollinators and seed dispersers in some ecosystems has led to their designation as 'keystone species', the demise of which could lead to a cascade of extinctions (Cox *et al.*, 1992).

### Caves

The largest bat colonies are found in caves, with one site, Bracken Cave in Texas in the United States, containing *c.* 20 million animals (McCracken, 1986). Key cave sites worldwide need to be identified and if necessary management regimens instigated to protect populations of bats and other important cave fauna and flora. Active cave conservation projects are already underway in countries such as the UK and USA (Hensley, 1992; Hutson *et al.*, 1995; National Caving Association, 1997) and these can provide models for other countries. Caves are also of interest to other groups such as archaeologists and speleologists and their involvement can help strengthen the case for protecting sites. Inventories and long-term monitoring are needed for some of the more important sites.

### Education

The general negative human perception of bats stems from an ignorance of their biology, ecology and role in ecosystems. Where educational campaigns have been instigated, views of bats have often changed dramatically. One particularly effective example is in the Comoros, where the establishment of a locally-run survey and educational programme focusing on the Critically Endangered endemic *Pteropus livingstonei* has been particularly successful at raising the profile of bats and their role in forest ecosystems (Action Comores, 1993, 1994, 1997). Educational campaigns need to be targeted not just at the general public, but also at other interest groups whose activities may impact bats. These include the forestry and mining sectors, archaeologists, speleologists, farmers, fruit growers, the tourist industry, the house building and maintenance industry, and local and national governments.

### Legal protection

The legal protection that bats receive at a national level is variable and ranges from full protection of roosts and feeding areas to no protection. In some countries bats are still listed as vermin. Only two international agreements have been formulated specifically for bats: the Agreement on the Conservation of Bats in Europe (under the Bonn Convention) and the Program for

the Conservation of Migratory Bats of Mexico and the United States (Hutson *et al.*, 2001). Efforts should concentrate on improving the legal status of bats, expanding the scope of current international agreements and establishing new ones.

### Discussion

The two IUCN Action Plans have provided for the first time a conservation overview of this important group of mammals. The megachiropteran Plan successfully highlighted conservation issues relating to this group and 15 of the 20 highest priority recommendations have been implemented. These have included the establishment of captive breeding programmes for threatened populations of *Pteropus voeltzkowi* and *P. livingstonei*, surveys of poorly known countries such as the Maldives and Solomon Islands, permanent enforcement personnel on Guam to monitor illegal trade in bats, a review of the interaction between bats and commercial fruit growers and more research on the role of bats as 'keystone species'. The task for microchiropteran bats is much greater, both because of the larger number of species involved and their wide distributions.

This review has highlighted a number of issues that require immediate attention if the conservation problems facing bats are to be tackled at a global scale. Two issues in particular stand out as being areas where a global or regional approach could be most successful. Islands and caves generally receive less attention from the conservation community but are crucial to the survival of bats. A large proportion of the most threatened bats are found on islands (Table 2), and bats are often significant contributors to mammalian diversity in these areas. The threat to bats is often greatest on islands and as such they should be the primary focus of any major bat conservation initiative. There are good examples of successful conservation campaigns on islands, particularly in the Indian Ocean, and these could be used as templates for action in other areas.

Caves house the largest bat colonies on earth and caves and karst have been identified as key habitats globally (Watson *et al.*, 1997). Most of those interested in caves have similar aims, the protection of sites, and there are good examples of collaboration between interest groups (National Caving Association, 1997). A global register of caves that are important for bats would be a first step towards developing management plans for the most valuable caves.

The two Action Plans are just the beginning of a process that will continue for many years. Plans are already in motion to update the megachiropteran Plan and to establish a website that could be regularly updated with new information. Above all, these Plans are meant to be

a stimulus to individuals and organisations to develop further plans that may focus on particular countries, regions, species or issues. The first two priority projects should focus on island bats and on cave conservation worldwide.

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### Biographical sketches

Simon Mickleburgh graduated with a BSc in Biological Sciences from the University of London and an MSc in Ecology from the University College of North Wales. He worked initially on the conservation of the chough *Pyrrhocorax pyrrhocorax* in Britain and on amphibian conservation issues in Central Wales before joining Fauna & Flora International (FFI) as London Bat Officer in 1984. Since that time he has concentrated on bat conservation projects at both a national and international level, particularly the production and implementation of Action Plans. He is currently Senior Conservation Researcher at FFI and is Manager of FFI's grant-giving programme, the 100% Fund.

Tony Hutson worked at the British Museum (Natural History) on insects, especially ectoparasites of bats. In 1984, he joined FFI to establish a bat conservation programme.

When The Bat Conservation Trust was set up in 1991, he became the first Conservation Officer. In 2000, he left to become a freelance consultant biologist, specialising in bats at an international level. He has been Co-Chairman of the IUCN-SSC Chiroptera Specialist Group since 1986. He has been involved in running field projects around the world and in the development and implementation of bat conservation initiatives and research at home and abroad.

Paul Racey graduated from the University of Cambridge with a degree in Zoology and carried out his PhD work on the reproductive biology of bats at the Zoological Society of London. Since moving to Aberdeen in 1973 he has worked on the ecology and conservation biology of bats, initially at temperate latitudes but more recently in the tropics, particularly Madagascar. He was founding Chairman of The Bat Conservation Trust, is Co-Chair of IUCN's Chiroptera Specialist Group and chairs the Conservation Committee of FFI.

### Appendix

Number of bat species, IUCN Red List species and endemic species for countries of the world.

*IUCN Red List species.* These are species listed in the 2000 *IUCN Red List of Threatened Species* (Hilton-Taylor, 2000) CR = Critically Endangered, EN = Endangered, VU = Vulnerable, LRcd = Lower Risk: Conservation Dependent, LRnt = Lower Risk: Near Threatened, EX = Extinct, DD = Data Deficient.

*Endemics.* Total number of species recorded only from that country.

*Total species.* The total number of bat species recorded from that country. Mega = bats in Suborder Megachiroptera, Micro = bats in Suborder Microchiroptera. Sources for these figures are given and included in the reference list. For many countries, detailed and up to date lists are not available and it is likely that these figures will change as more research is undertaken.

Country	IUCN Red List species								Total endemics	Total species			
	CR	EN	VU	LRcd	LRnt	EX	DD	Total		Mega	Micro	Total	Source
Afghanistan	0	0	5	0	6	0	0	11	0	0	37	37	(1)
Albania	0	0	2	0	4	0	0	6	0	0	24	24	(2)
Algeria	0	0	4	0	4	0	0	8	0	0	26	26	(3)
Am. Samoa	0	1	0	0	0	0	1	2	0	2	2	4	(4)
Am. Virgin Is.	0	0	1	0	0	0	0	1	0	0	5	5	(5)
Andorra	0	0	3	0	2	0	0	5	0	0	11	11	(6)
Angola	0	0	3	0	6	0	2	11	0	15	43	58	(7)
Anguilla	0	0	0	0	1	0	0	1	0	0	5	5	(8)
Antigua and Barbuda	0	0	0	0	2	0	0	2	0	0	7	7	(9)
Argentina	0	0	3	0	7	0	0	10	1	0	57	57	(10)
Armenia	0	1	5	0	5	0	0	11	0	0	24	24	(11)
Aruba	0	0	1	0	0	0	0	1	0	0	4	4	(12)
Australia	1	0	7	0	14	1	1	24	15	12	63	75	(13)
Austria	0	0	4	0	4	0	0	8	0	0	24	24	(14)
Azerbaijan	0	0	6	0	5	0	0	11	0	0	27	27	(15)
Bahamas	0	0	1	0	3	0	0	4	1	0	12	12	(16)
Bahrain	0	0	0	0	0	0	0	0	0	0	4	4	(17)
Bangladesh	0	0	0	0	0	0	0	0	0	3	15	18	(18)
Barbados	0	0	0	0	2	0	0	2	0	0	6	6	(19)
Belarus	0	0	3	0	3	0	0	6	0	0	17	17	(20)
Belgium	0	0	3	0	5	0	0	8	0	0	18	18	(21)
Belize	0	0	1	0	8	0	0	9	0	0	69	69	(22)
Benin	0	0	1	0	0	0	0	1	0	4	28	32	(23)
Bermuda	0	0	0	0	0	0	0	0	0	0	4	4	(24)
Bhutan	0	0	0	0	0	0	0	0	0	3	2	5	(25)



Country	IUCN Red List species								Total endemics	Total species			Source
	CR	EN	VU	LRcd	LRnt	EX	DD	Total		Mega	Micro	Total	
Bolivia	0	0	1	0	9	0	0	10	0	0	107	107	(26)
Bosnia	0	0	7	0	4	0	0	11	0	0	22	22	(27)
Botswana	0	0	0	0	5	0	1	6	0	3	31	34	(28)
Brazil	0	0	14	0	23	0	3	40	6	0	137	137	(29)
Br. Virgin Is.	0	0	0	0	0	0	0	0	0	0	3	3	(30)
Brunei	0	0	0	0	1	0	0	1	0	11	11	22	(31)
Bulgaria	0	0	7	0	6	0	0	13	0	0	29	29	(32)
Burkina Faso	0	0	0	0	2	0	0	2	0	5	28	33	(33)
Burundi	0	0	0	0	0	0	1	1	0	6	18	24	(34)
Cambodia	0	0	0	0	2	0	0	2	0	10	28	38	(35)
Cameroon	0	0	2	0	16	0	0	18	0	14	57	71	(36)
Canada	0	0	1	0	0	0	0	1	0	0	20	20	(37)
Cape Verde Is.	0	0	0	0	0	0	0	0	0	0	2	2	(38)
Cayman Is.	0	0	0	0	3	0	0	3	0	0	8	8	(39)
C.A.R. (1)	0	0	1	0	1	0	0	2	0	13	32	45	(40)
Chad	0	0	1	0	0	0	0	1	0	3	18	21	(41)
Chile	0	0	3	0	3	0	0	6	0	0	10	10	(42)
China	0	0	2	0	20	0	3	25	6	8	82	90	(43)
Colombia	0	1	10	0	33	0	0	44	2	0	170	170	(44)
C.N.M.I. (2)	0	1	0	0	0	0	0	1	0	1	1	2	(45)
Comoros	0	0	0	0	2	0	0	2	0	3	2	5	(46)
Congo Rep.	0	0	1	0	7	0	1	9	1	12	36	48	(47)
Cook Islands	0	0	0	0	0	0	0	0	0	1	0	1	(48)
Costa Rica	0	0	2	0	11	0	0	13	0	0	107	107	(49)
Côte d'Ivoire	0	0	3	0	4	0	1	8	0	12	60	72	(50)
Croatia	0	0	7	0	4	0	0	11	0	0	28	28	(51)
Cuba	0	0	2	0	7	0	0	9	1	0	27	27	(52)
Cyprus	0	0	1	0	3	0	0	4	0	1	15	16	(53)
Czech Rep.	0	0	5	0	3	0	0	8	0	0	21	21	(54)
D.R.C. (3)	2	0	5	0	25	0	1	33	2	17	78	95	(55)
Denmark	0	0	2	0	0	0	0	2	0	0	15	15	(56)
Djibouti	0	0	1	0	1	0	0	2	0	0	17	17	(57)
Dominica	0	0	1	0	3	0	0	4	0	0	12	12	(58)
Dominican Rep.	0	0	0	0	6	0	0	6	0	0	18	18	(59)
Ecuador	0	1	7	0	12	0	0	20	1	0	125	125	(60)
Egypt	0	0	4	0	1	0	0	5	0	1	21	22	(61)
El Salvador	0	0	2	0	6	0	1	9	0	0	58	58	(62)
Eq. Guinea	0	0	1	0	8	0	0	9	0	9	39	48	(63)
Eritrea	0	0	2	0	0	0	0	2	0	0	11	11	(64)
Estonia	0	0	1	0	0	0	0	1	0	0	11	11	(65)
Ethiopia	0	0	7	0	12	0	1	20	1	8	58	66	(66)
Falkland Is. (4)	0	0	0	0	0	0	0	0	0	0	0	0	(67)
F.S.M. (5)	0	1	0	0	0	0	0	1	0	4	1	5	(68)
Fiji	0	1	0	0	1	0	0	2	0	4	2	6	(69)
Finland	0	0	0	0	0	0	0	0	0	0	8	8	(70)
France	0	0	8	0	5	0	0	13	0	0	29	29	(71)
French Guiana	0	0	2	0	8	0	2	12	0	0	102	102	(72)
Gabon	0	0	1	0	5	0	0	6	0	9	23	32	(73)
Gambia	0	0	0	0	1	0	0	1	0	4	23	27	(74)
Georgia	0	0	6	0	4	0	0	10	0	0	25	25	(75)
Germany	0	0	5	0	4	0	0	9	0	0	23	23	(76)
Ghana	0	0	2	0	16	0	1	19	0	13	71	84	(77)
Gibraltar	0	0	0	0	1	0	0	1	0	0	4	4	(78)
Greece	0	0	5	0	6	0	0	11	0	0	28	28	(79)
Grenada	0	0	0	0	0	0	0	0	0	0	13	13	(80)
Guadeloupe	0	1	3	0	3	0	0	7	2	0	12	12	(81)
Guam	0	1	0	0	0	0	0	1	0	1	1	2	(82)
Guatemala	1	1	1	0	11	0	0	14	1	0	94	94	(83)
Guinea	0	0	1	0	6	0	1	8	1	9	37	46	(84)

Country	IUCN Red List species								Total endemics	Total species			
	CR	EN	VU	LRcd	LRnt	EX	DD	Total		Mega	Micro	Total	Source
Guinea-Bissau	0	0	0	0	5	0	0	5	0	7	28	35	(85)
Guyana	0	0	3	0	10	0	2	15	0	0	107	107	(86)
Haiti	0	0	0	0	6	0	0	6	0	0	17	17	(87)
Honduras	0	0	3	0	12	0	1	16	0	0	98	98	(88)
Hungary	0	1	6	0	5	0	0	12	0	0	26	26	(89)
Iceland (6)	0	0	0	0	0	0	0	0	0	0	0	0	(90)
India	1	1	6	0	15	0	5	28	9	13	96	109	(91)
Indonesia	0	4	14	0	25	0	4	47	24	63	112	175	(92)
Iran	0	1	7	0	5	0	0	13	0	1	37	38	(93)
Iraq	0	0	5	0	2	0	0	7	0	0	19	19	(94)
Ireland	0	0	1	0	1	0	0	2	0	0	7	7	(95)
Israel	0	0	6	0	5	0	0	11	0	1	32	33	(96)
Italy	0	0	7	0	6	0	0	13	0	0	30	30	(97)
Jamaica	0	1	2	0	5	0	0	8	2	0	21	21	(98)
Japan	1	5	3	0	8	0	2	19	12	3	36	39	(99)
Jordan	0	0	5	0	4	0	0	9	0	0	14	14	(102)
Kazakhstan	0	0	3	0	3	0	0	6	0	0	27	27	(101)
Kenya	0	0	5	0	17	0	2	24	1	11	84	95	(102)
Kuwait	0	0	0	0	0	0	0	0	0	0	1	1	(103)
Kyrgyzstan	0	0	2	0	1	0	0	3	0	0	16	16	(104)
Laos	0	0	1	0	18	0	2	21	0	8	82	90	(105)
Latvia	0	0	2	0	1	0	0	3	0	0	15	15	(106)
Lebanon	0	0	4	0	3	0	0	7	0	1	15	16	(107)
Lesotho	0	0	0	0	0	0	0	0	0	2	6	8	(108)
Liberia	0	0	2	0	8	0	1	11	0	11	57	68	(109)
Libya	0	0	1	0	2	0	0	3	0	0	14	14	(110)
Liechtenstein	0	0	3	0	3	0	0	6	0	0	18	18	(111)
Lithuania	0	0	2	0	1	0	0	3	0	0	17	17	(112)
Luxembourg	0	0	3	0	3	0	0	6	0	0	17	17	(113)
Macedonia	0	0	7	0	4	0	0	11	0	0	23	23	(114)
Madagascar	1	0	6	0	7	0	8	22	14	3	25	28	(115)
Malawi	0	0	0	0	8	0	1	9	0	6	51	57	(116)
Malaysia	2	1	3	0	22	0	3	31	11	17	95	112	(117)
Maldives	0	0	0	0	0	0	0	0	0	2	0	2	(118)
Mali	0	0	0	0	3	0	0	3	0	3	15	18	(119)
Malta	0	0	1	0	3	0	0	4	0	0	10	10	(120)
Martinique	0	0	0	0	4	0	0	4	0	0	10	10	(121)
Mauritania	0	0	0	0	0	0	0	0	0	5	40	45	(122)
Mauritius	0	0	1	0	0	0	0	1	0	1	2	3	(123)
Mayotte	0	0	0	0	0	0	0	0	0	1	1	2	(124)
Mexico	1	4	9	0	17	0	0	31	13	0	137	137	(125)
Moldova	0	0	4	0	3	0	0	7	0	0	20	20	(126)
Monaco	0	0	0	0	0	0	0	0	0	0	5	5	(127)
Mongolia	0	0	0	0	0	0	0	0	0	0	12	12	(128)
Montserrat	0	1	0	0	3	0	0	4	0	0	10	10	(129)
Morocco	0	0	6	0	4	0	0	10	0	0	26	26	(130)
Mozambique	1	0	0	0	7	0	1	9	1	5	40	45	(131)
Myanmar	2	0	0	0	16	0	3	21	3	12	76	88	(132)
Namibia	0	1	1	0	3	0	1	6	1	2	24	26	(133)
Nepal	0	0	2	0	7	0	3	12	1	4	47	51	(134)
Netherlands	0	0	4	0	3	0	0	7	0	0	19	19	(135)
Neth. Antilles	0	0	1	0	3	0	0	4	0	0	10	10	(136)
New Caledonia	0	2	0	0	0	1	0	3	2	4	4	8	(137)
New Zealand	0	0	2	0	0	1	0	3	3	0	3	3	(138)
Nicaragua	0	0	1	0	11	0	1	13	0	0	88	88	(139)
Niger	0	0	0	0	0	0	0	0	0	2	19	21	(140)
Nigeria	0	0	2	0	11	0	0	13	0	12	59	71	(141)
Niue	0	0	0	0	0	0	0	0	0	1	0	1	(142)
North Korea	0	1	0	0	6	0	1	8	0	0	21	21	(143)

Country	IUCN Red List species								Total endemics	Total species			Source
	CR	EN	VU	LRcd	LRnt	EX	DD	Total		Mega	Micro	Total	
Norway	0	0	1	0	0	0	0	1	0	0	11	11	(144)
Oman	0	0	3	0	2	0	0	5	1	1	16	17	(145)
Pakistan	0	0	2	0	5	0	0	7	0	4	43	47	(146)
Palau	0	1	0	0	0	0	0	1	0	2	1	3	(147)
Panama	0	0	1	0	10	0	0	11	0	0	111	111	(148)
P.N.G. (7)	1	0	13	0	12	0	1	27	10	34	57	91	(149)
Paraguay	0	0	1	0	4	0	0	5	0	0	49	49	(150)
Peru	0	1	14	0	21	0	1	37	5	0	152	152	(151)
Philippines	0	0	1	0	13	0	3	17	9	24	46	70	(152)
Poland	0	0	5	0	3	0	0	8	0	0	23	23	(153)
Portugal	0	0	8	0	5	0	0	13	1	0	24	24	(154)
Puerto Rico	0	0	1	0	3	1	0	5	1	0	13	13	(155)
Qatar	0	0	0	0	0	0	0	0	0	0	2	2	(156)
Réunion	1	0	1	0	0	0	0	2	0	2	3	5	(157)
Romania	0	0	7	0	6	0	0	13	0	0	26	26	(158)
Russia	0	1	8	0	7	0	1	17	1	0	41	41	(159)
Rwanda	0	0	1	0	3	0	0	4	0	8	33	41	(160)
St. Kitts & Nevis	0	0	0	0	1	0	0	1	0	0	4	4	(161)
St. Lucia	0	0	0	0	3	0	0	3	0	0	8	8	(162)
St. Vincent	0	0	0	0	2	0	0	2	0	0	12	12	(163)
Samoa	0	1	0	0	0	0	1	2	0	2	2	4	(164)
San Marino	0	0	1	0	2	0	0	3	0	0	6	6	(165)
São Tomé and Príncipe	0	0	1	0	1	0	0	2	1	3	6	9	(166)
Saudi Arabia	0	0	4	0	4	0	0	8	0	2	21	23	(167)
Senegal	0	0	2	0	5	0	1	8	0	5	40	45	(168)
Seychelles	1	0	2	0	0	0	0	3	2	1	3	4	(169)
Sierra Leone	0	0	0	0	9	0	1	10	0	10	46	56	(170)
Singapore	0	0	1	0	0	0	1	2	1	5	4	9	(171)
Slovakia	0	0	6	0	5	0	0	11	0	0	24	24	(172)
Slovenia	0	0	7	0	5	0	0	12	0	0	27	27	(173)
Solomon Is.	0	0	3	0	4	0	0	7	3	20	13	33	(174)
Somalia	0	0	1	0	6	0	0	7	0	2	35	37	(175)
South Africa	0	0	5	0	10	0	2	17	3	4	52	56	(176)
South Korea	0	1	0	0	4	0	1	6	0	0	16	16	(177)
Spain	0	0	9	1	4	0	0	14	1	0	27	27	(178)
Sri Lanka	0	0	0	0	2	0	0	2	0	4	28	32	(179)
Sudan	0	0	3	0	10	0	0	13	0	9	58	67	(180)
Suriname	0	0	3	0	9	0	2	14	0	0	62	62	(181)
Swaziland	0	0	0	0	1	0	0	1	0	3	17	20	(182)
Sweden	0	0	3	0	0	0	0	3	0	0	16	16	(183)
Switzerland	0	0	4	0	5	0	0	9	0	0	26	26	(184)
Syria	0	0	1	0	4	0	0	5	0	1	10	11	(185)
Taiwan	0	0	2	0	2	0	1	5	4	0	20	20	(186)
Tajikistan	0	0	2	0	3	0	0	5	0	0	19	19	(187)
Tanzania	0	0	2	0	13	0	3	18	2	13	66	79	(188)
Thailand	0	2	2	0	21	0	3	28	4	17	91	108	(189)
Togo	0	0	0	0	3	0	0	3	0	9	31	40	(190)
Tonga	0	1	0	0	0	0	0	1	0	1	1	2	(191)
Trinidad and Tobago	0	0	0	0	5	0	0	5	0	0	63	63	(192)
Tunisia	0	0	4	0	3	0	0	7	0	0	12	12	(193)
Turkey	0	0	7	0	6	0	0	13	0	1	30	31	(194)
Turkmenistan	0	0	3	0	3	0	0	6	0	0	21	21	(195)
Turks and Caicos Islands	0	0	0	0	2	0	0	2	0	0	7	7	(196)
Uganda	0	0	1	0	13	0	0	14	0	11	51	62	(197)
Ukraine	0	0	5	0	4	0	0	9	0	0	27	27	(198)
U. A. E. (8)	0	0	0	0	0	0	0	0	0	0	6	6	(199)
United Kingdom	0	0	3	0	3	0	0	6	0	0	16	16	(200)
United States	0	3	4	0	4	0	0	11	3	0	45	45	(201)
Uruguay	0	0	1	0	1	0	0	2	0	0	15	15	(202)

Country	IUCN Red List species								Total endemics	Total species			Source
	CR	EN	VU	LRcd	LRnt	EX	DD	Total		Mega	Micro	Total	
Uzbekistan	0	0	3	0	4	0	0	7	0	0	21	21	(203)
Vanuatu	0	0	0	0	1	0	0	1	0	4	7	11	(204)
Vatican City (9)	—	—	—	—	—	—	—	—	—	—	—	—	
Venezuela	0	0	6	0	23	0	3	32	3	0	154	154	(205)
Viet Nam	1	1	2	0	10	0	1	15	1	11	53	64	(206)
Wallis & Futuna Islands	0	0	0	0	0	0	0	0	0	1	0	1	(207)
Yemen	0	0	2	0	3	0	0	5	0	2	22	24	(208)
Yugoslavia	0	0	8	0	5	0	0	13	0	0	26	26	(209)
Zambia	0	0	2	0	8	0	0	10	0	11	54	65	(210)
Zimbabwe	0	0	2	0	8	0	1	11	0	6	55	61	(211)

## Notes:

- (1) – Central African Republic  
(2) – Commonwealth of the Northern Mariana Islands  
(3) – Democratic Republic of Congo (formerly Zaire)  
(4) – Only two bats have been recorded from the Falkland Islands, both probable imports.  
(5) – Federated States of Micronesia  
(6) – The only bats recorded from Iceland are vagrants.  
(7) – Papua New Guinea  
(8) – United Arab Emirates

(9) – As far as the authors are aware, there is no information on bats in the Vatican City.

SOURCES: (1) – Corbet, 1978, (2) – Mitchell-Jones *et al.*, 1999, (3) – Gaisler, 1983–84; Kowalski & Rzebik-Kowalska, 1991, (4) – Mickleburgh *et al.*, 1992; Koopman, 1993; Flannery, 1995b, (5) – McFarlane, 1991, (6) – S.S. Guitart, pers. comm., (7) – Bergmans, 1988, 1989, 1990, 1994, 1997; Skinner & Smithers, 1990, (8) – Breuil & Masson, 1991; McFarlane, 1991, (9) – Breuil & Masson, 1991; McFarlane, 1991, (10) – Barquez *et al.*, 1999, (11) – E.G. Yavrovyan, pers. comm., (12) – Husson, 1960, (13) – Churchill, 1998, (14) – F. Spitzenberger, pers. comm., (15) – Rakhmatulina, 1989, 1996a,b, (16) – Koopman *et al.*, 1957; Hill, 1985, (17) – Harrison & Bates, 1991, (18) – Bates & Harrison, 1997, (19) – McFarlane, 1991, (20) – A. Borissenko, pers. comm., (21) – J. Fairon, pers. comm., (22) – McCarthy *et al.*, 1993, (23) – Robbins, 1980, (24) – Koopman, 1993, (25) – Bates & Harrison, 1997, (26) – L.F. 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