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perspective



The causes and biogeographical significance of species' rediscovery

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Abstract. The rediscovery of a species that was putatively considered to be extinct can provide valuable data to test biogeographical hypotheses about population decline and range collapse. Moreover, such rediscoveries often generate much-needed publicity and additional funds for the conservation of rare species and habitats. However, like extinction, rediscovery is challenging to define. In this perspective we argue that the 'loss' of a species and its subsequent rediscovery can be understood in terms of the interplay among four socio-ecological factors: (1) the state of knowledge of species loss and rediscovery; (2) the presence of people and/or organizations with the interest, motivation, resources, skills and technology to find target species; (3) the accessibility of the areas, habitats or sites where the species are thought to survive; and (4) the ease with which a species can be located when it is present within a habitat. Thus, species are 'lost' from scientific knowledge for different reasons and, consequently, not all rediscoveries are equally significant for biogeographical research or conservation. Indeed, rediscoveries of species that underwent a well documented decline and disappearance – and are therefore of greatest potential importance for both conservation and biogeographical research – appear to be poorly represented in the literature compared to rediscovered species that were only known from a handful of museum specimens. Thus, carefully distinguishing between the causes of temporal gaps in zoological records is essential for improving the utility of rediscovery data for biogeographical research and conservation practice.

Keywords: extinction, range collapse, rarity, critically endangered, monitoring

Introduction

Rediscoveries of putatively extinct species are of great potential interest to both conservationists and biogeographers (Crowley 2011). For the former, 'rediscovery' can be a considerable conservation policy and publicity asset (Ladle and Jepson 2008, Ladle et al. 2009) — as testified by recent global initiatives: in 2009 BirdLife International launched a "global bid to try to confirm the continued existence of 47 species of bird that have not been seen for up to 184 years" (BirdLife International 2009). The following year Conservation International launched its "Search for lost Frogs" which involves a dedicated campaign and expedi-

tions to 18 countries seeking to locate 40 species not seen for a decade or more (Conservation International 2010) — at the time of writing 12 species have been rediscovered. Moreover, since rediscovered species are typically exceedingly rare and geographically localized, new knowledge on population status and distribution supports effective conservation interventions. Finally, rediscoveries remove uncertainty from extinction risk assessments; a confirmed new record moves the species from 'extinct' or 'probably extinct' and into an IUCN threat (or data deficient) category.

For biogeographers, species rediscovery has both a practical and conceptual significance. From the practical perspective, the rediscovery of a species that has gone unrecorded for a long period of time improves geographical knowledge about some of the world's rarest species, helping to address the Wallacean shortfall - the inadequacy of our knowledge of the geographical distributions of species (Lomolino et al. 2006, Riddle et al. 2011). The shortfall can often be extreme, with a species known from just one or a few museum specimens collected decades or even centuries earlier. These species are sometimes incorrectly assumed or declared extinct, a phenomenon which Ladle and Jepson (2008) refer to as a Wallacean extinction. As we discuss later, these extreme examples of the Wallacean shortfall are amongst the most frequently rediscovered species.

More recently, biogeographers have started to use information on species rediscoveries to test theories of population decline and range collapse under anthropogenic disturbance (Fisher 2011a,b; Fisher and Blomberg 2011). The underlying idea is both simple and elegant: the location of a rediscovered species relative to its historical range reflects the pattern of range collapse. Thus, if anthropogenic pressures (e.g. unsustainable exploitation) are strongest at the periphery (Channel and Lomolino 2000) the rediscovery will most likely be made near the centre of the historic range. Diana Fisher's (2011a) study of 67 species of rediscovered mammals found a number of clear trends, although these tended to be dependent upon the ecology of the species. For example, one of the strongest patterns observed was that rediscoveries were generally made at higher elevations than the original record (excluding mountain-top and coastally restricted species). This provides some support for the hypothesis that higher elevations can sometimes provide ecological refugia (Towns and Daugherty 1994) and fits with the frequently observed pattern of habitat destruction and population extinction progressing from low to high altitudes (Triantis et al. 2010).

However, like extinction, rediscovery is challenging to define. This should not be surprising since rediscovery and extinction are conceptually intertwined; extinction is the permanent absence of current and future records while redis-

covery reflects the temporary absence of such records. Moreover, rediscovery is the proof required to refute a hypothesis of extinction. Given the close conceptual linkage between the concepts of rediscovery and extinction it is interesting that, until recently, there have been so few studies linking patterns of rediscovery to contemporary theories of population decline and extinction. One impediment to such research is the lack of a systematic approach to species rediscoveries that allow scientists to identify cases of rediscovery that have biogeographical or conservation significance, and which can be subject to meaningful analysis. Here, we propose a conceptual framework for understanding and analyzing species rediscovery, based on the social, institutional and ecological factors that created the temporal gap in occurrence data. We believe that formalizing the concept of rediscovery in this way has the potential to create new measures of the state of knowledge of the world's rarest species, provide a quantifiable metric to support existing endangerment categorizations, and would help to maintain the culture of biogeographical exploration that contributes to the datasets that underpin global conservation target-setting, advocacy and monitoring.

Conceptual framework

The 'loss' of a species and its subsequent rediscovery can be conceptualized as a result of the interplay among four socio-ecological aspects of rediscovery (schematically illustrated in Figure 1): (1) the state of knowledge of species loss and rediscovery; (2) the presence of people and/or organizations with the interest, motivation, resources, skills and technology to find target species; (3) the accessibility of the areas, habitats or sites where the species are thought to survive; and (4) the ease with which a species can be located when it is present within a habitat. It should be noted that although these factors potentially apply to all 'lost' taxa, owing to issues of historical data quality, funding and the culture of scientific exploration, rediscovery research has focused almost exclusively on herptiles, birds and mammals (cf. Scheffers et al. 2011).

Knowledge of 'lost' species

Enormous advances have been made over the last 40 years in enumerating which species are apparently 'lost'. For example, BirdLife International has made significant investments in compiling new and authoritative assessments of threatened species using information from a variety of sources including amateur and university-led research expeditions and major reviews of existing museum specimens. In particular, from the mid 1980s two major regional Red List reviews were compiled for the Americas (Collar et al. 1992) and Asia (Collar et al. 2001), the findings of which were then fed back to the BirdLife network of pioneering professional and amateur ornithologists (Tobias et al. 2006, Butchart 2007).

The knowledge of what is 'lost' is complicated, as rediscoveries can logically be split into four categories that reflect different degrees of uncertainty (and authority) about the continued existence of a target species (Table 1). An additional category could potentially be added to this typology to account for cases where an unrecorded sub-species is elevated to full species status. For example, the Sangihe Shrike-thrush (Colluricincla sanghirensis) was rediscovered in 1985 but its status as a full species was only established in 1999 (Rozendaal and Lambert 1999). Changes in taxonomic status may have profound impacts on survey effort: according to Rasmussen et al. (2000), the demotion of the Sangihe Whiteeye (Zosterops nehrkorni) to sub-specific status by Stresemann (1931) had the effect of making the species of "only marginal, regional interest" and as a consequence "for many years [it] received little attention" (p. 69).

From the perspective of investigating range changes, confounding different categories of rediscovery could seriously influence research findings. For example, we might expect that all other things being equal, species whose habitat or range has not been surveyed for a significant period of time and for which there are no strong reasons to assume have become extinct (Table 1, category 4), are as likely to be rediscovered at the edge or centre of their historic range as are better-known species. Moreover, all four categories of rediscovery may contain species that were only known from a small number of museum specimens - the rediscovery of which may tells us more about the history of biogeographical exploration than the ecology of decline and extinction. Indeed, Scheffers et al. (2011) found that the majority of recently claimed amphibian, bird and mammal rediscoveries represent first documentations since their original scientific description. It should also be noted that such rare species may have remained unrecorded because of intrinsic biological characteristics (e.g. nocturnal habits, cryptic colouration, etc.) rather than a lack of sampling effort and that these factors need to be carefully untangled in any analysis of patterns of rediscovery (see McCarthy 2008; Fisher and Blomberg 2011).

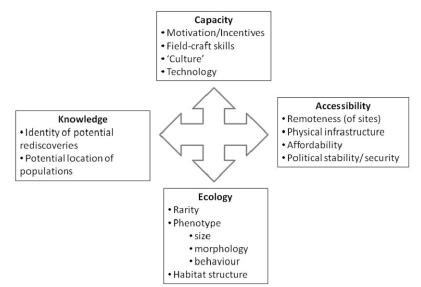


Figure 1. The four major dimensions of species rediscovery (see text).

Туре	Rediscovery of	Example
1.	a species declared extinct by an authoritative source	The Pohnpei Starling (<i>Aplonis pelzelni</i>) was declared extinct by the IUCN (1990) and rediscovered in 1995 (Buden 1996)
2.	a species considered probably extinct by an authoritative source	The Sao Tome Grosbeak (<i>Neospiza concolor</i>) was described as probably extinct by Greenway (1967) and rediscovered in 1991 (Sergeant et al. 1992)
3.	a species believed to be still extant but for which substantive searches over dec- ades have drawn a blank.	According to the NGO BirdLife International the Madagascar Serpent Eagle (<i>Eutriorchis astur</i>) was not definitely recorded between 1930 and 1993 despite considerable search-effort within its habitat.
4.	a species whose habitat or range had not been surveyed for a significant period of time, but for which there is no real rea- son to assume has become extinct	The Chestnut-bellied Flowerpiercer (<i>Diglossa glorio-sissima</i>) was unrecorded for 38 years: since 2003 it has been recorded from three locations (Tobias et al. 2006)

Table 1. A crude typology of species rediscovery based on decreasing level of certainty that the rediscovered species was extinct.

Perhaps the most important type of rediscovery for conservation is where a previously well known species undergoes a population decline, is lost from biogeographical knowledge, and is then rediscovered. A possible example is the Australian Pygmy Blue-tongue Lizard Tiliqua adelaidensis. This rather secretive lizard was relatively well known up to its disappearance in 1959; its rediscovery in 1992 (in the stomach of a snake) confirmed that the species now has "a dramatically reduced geographical range" (Milne and Bull 2000, p. 296). The rediscovery of the Ivory-billed Woodpecker (Campephilus principalis) (Fitzpatrick et al. 2005) would be an even better example, except that this rediscovery is increasingly looking like a case of mistaken identity (Dalton 2005, 2010, Stokstad 2007). The apparent scarcity of such rediscoveries (cf. Scheffers et al. 2011) strongly suggests that a species that undergoes a well documented decline and disappearance is likely to be extinct. However, formally testing this hypothesis would require good information on population trends of rediscovered species prior to their original disappearance – data that rarely exist for older cases of species loss.

A final aspect of the knowledge needed to find 'lost' species is the reliability of biogeographic information on where to search for the species.

Thus, the Black-hooded Antwren (Formicivora erythronotos) was known only from a 19th Century type specimen, for which the type locality was probably incorrect, and which was also put in the wrong genus. Balchon (2007) suggests that this led to researchers "looking in the wrong place, for the wrong sort of bird and listening for inappropriate vocalizations". Thus, 'lost' species can sometimes turn up thousands of kilometres away from where they were last seen, or in completely different habitats. For example, the Large-billed Reed Warbler (Acrocephalus orinus) was previously known from just a single specimen collected in 1867 in the Sutlej Valley, Himachal Pradesh, India. However, a living specimen was trapped in March 2006 at Laem Phak Bia, Phatchaburi Province, south-west Thailand, over 3000 km from the type locality (Round et al. 2007). The renewed interest in this species led to the unearthing of ten new museum specimens (Svensson et al. 2008) and, shortly afterwards, to the discovery of a breeding population in north-east Afghanistan (Timmins et al. 2010).

Institutional, scientific and technical capacity Even when a species is identified as possibly still extant, the institutional and technical capacity to find it may not exist. Such capacity, at a global level, has varied considerably over time and space in response to various cultural and ecological factors. Most notably, the mainstreaming of biodiversity into international development following the 1992 Earth Summit created many new sources of funds and employment opportunities for scientists in less-developed countries. With respect to birds, this increase in local capacity coincided with the creation of BirdLife International in 1993. BirdLife emerged from the International Council for Bird Preservation (founded in 1922) when its leaders devised the compelling proposition of forming an international partnership, under a single name, with smaller, national, bird-orientated conservation organizations (Jepson and Ladle 2010). More generally, increased funding of expeditions by international NGOs has probably been the driving force behind the increasing frequency of rediscoveries of various taxa (Scheffers et al. 2011).

Other trends within science and conservation also help determine the capacity and motivation that enables rediscoveries, especially the introduction of new technology. For example, advances in molecular biology have made it much easier to genetically compare preserved type specimens in museums with contemporary material collected directly or acquired from hunters or from rural markets. This has opened the way for completely new ways of rediscovering lost species, where a fragment of hair or a faecal sample may be sufficient to prove the continuing existence of a species that has still not been physically observed.

An excellent example of such a technology-aided discovery is provided by Pitra et al. (2006), who recently announced the continuing existence of the giant sable antelope (*Hippotragus niger variani*), a sub-species unique to Angola that was feared extinct after almost three decades of civil war. They compared the mitochondrial DNA sequences derived from old museum specimens with samples extracted from dung samples recently collected in the field. Such remotely collected DNA evidence can also be used to discount presumed discoveries or rediscoveries. For example, Hennache et al. (2003) used a range of techniques, including captive hybridization experi-

ments and analysis of mitochondrial DNA and microsatellites, to conclusively demonstrate the hybrid origin of the imperial pheasant (*Lophura imperialis*). This mysterious bird had first been captured in 1924 when a single pair had been shipped to the private aviary of Jean Delacour in France and was not seen again until one was trapped in 1990 (Hennache et al. 2003).

It is not only advances in molecular biology that are facilitating rediscoveries. The ready availability of sophisticated audiovisual equipment has been especially important in the evolution of bird surveying. Two such technological advances, the increased availability of less expensive soundrecording and playback equipment in the late 1990s and the more recent internet-based birdsound archives, have dramatically increased the capacity of both amateurs and professionals to locate and identify rare and cryptic bird species. Moreover, advances in the quality of cameras and lenses, especially digital cameras and video recorders, have also been important in documenting and providing definitive proof of the existence of very rare species. For example, the New Zealand Storm Petrel (Pealeornis maoriana) was identified from the details on a digital image taken in 2003 (Stephenson et al. 2008). It had previously been known only from putative fossil material, and from three specimens collected in the 19th Century, 150 years before its rediscovery.

Accessibility

Even if a species is extant and potential habitats have been located, the species may not be found. Access to suitable habitat may be limited because of political instability/restrictions, or simply the remoteness of potential sites. Although in the era of cheap international air travel this is arguably less important, it may have played a critical role in restricting the intensity of surveys and therefore the rate of rediscoveries in many parts of the globe. Examples of rediscoveries that were probably delayed, and possibly even caused, by political instability include that of the Large-billed Reed Warbler in Afghanistan (see above) and the Gabela Helmet-shrike (*Prionops gabela*), rediscovered in 2003 in Angola (Ryan et al 2004).

A closely related factor is a lack of communication with remote and isolated rural communities who may already have knowledge of the continued existence of a putatively extinct species, or of a species new to science. Thus, a productive route to increasing rediscoveries (and new species discoveries) might be through better communication with remote tribes and communities whose knowledge of local biodiversity may extend considerably beyond that of conservationists. However, Fisher and Blomberg (2011) found that human population overlap did not predict rediscovery rate in mammals, possibly because expeditions and surveys may intentionally focus on more remote areas.

Ecological factors

The final aspect of rediscovery is the ecological characteristics of the putatively extinct species that may make verification of its continued existence problematic. For example, if the species is very rare and/or dispersed, then it may be difficult to locate an individual/population within an area of potentially suitable habitat. Even if the survey team is in the same area as the target species, it may still not be encountered because of phenotypic and ecological traits (e.g. cryptic coloration, lack of vocalizations, skulking behaviour, etc.) that reduce the probability of detection (Scheffers et al. 2011). However, the evidence for this effect is variable: Fisher and Blomberg (2011) found that in mammals many ecological characteristics such as cryptic coloration and arboreal and nocturnal behaviour were not significantly associated with rediscovery - although smaller rediscovered mammals had been missing for longer periods of time (Fisher 2011b).

A possible example of ecology driving the lack of records is the Night Parrot, a species that is known from 23 specimens and many sightings of varying reliability from a wide geographic area of inland Australia (McDougall et al 2009). From what little information exists, the Night Parrot is crepuscular or nocturnal, cryptic, and when approached will only flush at close quarters, then fly low over short distances before plunging back into cover (Forshaw and Cooper 2002). Perhaps unsur-

prisingly, between 1912 and 1990 there were no records of the Night Parrot until one was hit by traffic (Boles et al. 1994).

Rediscoveries reconsidered

Given the very loose usage of the term 'rediscovery' and the varying factors, social and ecological, that contribute to rediscoveries, both biogeography and conservation may benefit from adopting a stricter policy of usage. One strategy would be to strictly confine the term 'rediscovery' to species categorized as extinct in the IUCN system (Mace et al. 2008) or as 'possibly extinct', or 'lost' by authoritative sources (Table 1, categories 1, 2 and 3). It should be noted that many species that are considered possibly extinct are listed as "critically endangered" in the IUCN system. For example, Fisher (2011a) restricts her analysis to rediscovered mammal species that had been previously reported as globally extinct or possibly extinct. It should be noted, however, that this approach will not completely eliminate all the cases of species that are missing through low levels of surveying.

An alternative strategy could be to classify rediscovery purely in terms of the length of time without a formal record. If this were adopted, the only issue would be an appropriate time frame for a given taxon. For example, De Roland et al. (2007) felt justified in claiming the 'rediscovery' of the Madagascar Pochard (*Athya innotata*) just 15 years after the last confirmed sighting – conceivably the same individual.

Using a simple time-based criterion would provide a single, objective definition of rediscovery – whatever the cause of the gap in zoological records. Conservation bodies could potentially use this definition to periodically produce lists of species that may still be extant and, by extension, are in need of rediscovery. These could be categorized according to the time since a species was last recorded (e.g. <25 years ago, 25–49 years ago, 50–100 years ago, >100 years ago, etc.). One advantage of such a system would be to maintain and extend the practice of biogeographical expeditions to remote areas. It would also help guard against the overuse or misrepresentation of redis-

coveries in the media (Ladle et al. 2009). It would offer a viable alternative to the use of terms such as 'possibly extinct' (Butchart et al. 2006) and 'data deficient', and would ensure better quality of data for future biogeographical studies.

Conclusions

The rediscovery of a species that was thought to be extinct can generate global interest and represents a real opportunity for conservationists to reassert core values and raise funds that may help protect poorly known habitats. Moreover, rediscoveries provide a unique source of information about the rarest and least-known species (for certain taxa) that can be used to investigate biogeographic theories about range loss and extinction. Both of these important agendas would benefit from a greater systematization of the concept of rediscovery, acknowledging the varying causes (both social and ecological) of gaps in the temporal records of rare species.

In summary, the study of rediscoveries provides a wonderful opportunity to assess both the subtle ecological and biogeogeographical characteristics of exceptionally rare species of well studied taxa such as amphibians, birds and mammals, and the fascinating historical and cultural trends in zoological surveying and exploration. Considerable efforts are being made to untangle these interacting factors (Fisher 2011a,b; Fisher and Blomberg 2011, Scheffers et al. 2011), while the recent targeting of 'lost species' by international conservation NGOs is generating considerable amounts of valuable new data. Nevertheless, the lack of rediscovered species that were previously well known and which had undergone a well documented process of population decline, fragmentation and local extinction (Scheffers et al. 2011) remains a worrying trend for global conservation.

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