Nature Conservation 15: 1–9 (2016)
doi: 10.3897/natureconservation.15.8259
http://natureconservation.pensoft.net

RESEARCH ARTICLE

A peer-reviewed open-access journal
Nature Conservation
Launched to accelerate biodiversity conservation

An open door for illegal trade: online sale of *Strombocactus disciformis* (Cactaceae)

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Academic editor: *D. Evans* | Received 24 February 2016 | Accepted 4 July 2016 | Published 22 September 2016

http://zoobank.org/C07EDF96-B251-4176-A764-317D87421767

Citation: Olmos-Lau VR, Mandujano MC (2016) An open door for illegal trade: online sale of *Strombocactus disciformis* (Cactaceae). Nature Conservation 15: 1–9. doi: 10.3897/natureconservation.15.8259

Abstract

Online trade of CITES listed species has become a persistent threat which is difficult to measure and control. The use of online markets is growing day by the day as technology becomes more available and familiar to people of all ages and interests. Species trade can now be propagated remotely hardly without any real human interaction. We develop a quick-easy method to assess the online availability of the genus *Strombocactus*, a highly collectible cactus, to understand the real magnitude of this new form of threat and the possible menace it could be for these Mexican cacti. We used the Google.com site to do an online search in four languages (Spanish, English, French and German) for the offer of adult plants or seeds. We found specimens and seeds available in major online markets like ebay, amazon, cactusplaza.com and mercado libre. Plant price range from €10.00 to €30.00 plus shipping and handling. The plants were also offered in local online stores in countries like the USA, France, Germany, Australia, Czech Republic, the United Kingdom, and others; some sellers claim they have no obstacles for "shipping across countries" and others openly declare the natural localities where seeds were extracted. Only a minority of these online stores openly stated that the cacti were obtained from CITES registered nurseries or that the cacti were grown through propagules or seeds. Our method is easily transferable to estimate the illegal market for any species. There is an active online trade of *Strombocactus* species and other species listed in CITES without the necessary documentation. Compliance or other regulation mechanisms are needed in order to promote species conservation.

Keywords

Cactaceae, CITES, online trade, ornamental plant trade, wildlife trade

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Introduction

Mexico is the main hot spot of native cacti biodiversity, there are approximately 600 species of Cactaceae family of which 80% are endemic (Ortega-Baes and Godínez-Álvarez 2006, 2007, Ortega-Baes et al. 2010, Novoa et al. 2014); because of their beauty and rarity, they are of great interest and are well represented in the ornamental plant market, particularly in Europe, and more recently also in Asia (Álvarez et al. 2004, Novoa et al. 2014). *Strombocactus disciformis* is one of the Mexican endemic species listed as vulnerable in the IUCN, due to its limited range restricted to ten localities and the population decline due to illegal overcollection of mature individuals (Gómez-Hinostrosa et al. 2013), and it is included in Appendix I of CITES (CITES 2014). It is also included in the Mexican red list (NOM-ECOL-2010, SEMARNAT 2010) as threatened, therefore a collection permit is needed for seeds and individuals and no commercial trade of wild specimens is allowed (SEMARNAT 2010).

Online trade has become a new threat for CITES species (CITES 2011). The use of online stores by the general public increases each day as technology becomes more accessible and familiar to people of all ages and interests. In present days the trade of species can be done without any real human interaction and distance is no longer an obstacle. Contacting a seller is simplified by finding an offer in an online store and by the use of e-mail. Although conventional trade routes are maintained through the shipping of goods, the widespread use and the unregulated nature of the internet make e-commerce a great concern to the Convention on International Trade in Endangered Species of Wild Fauna and Flora, since plants and their derivatives have become a widespread commodity in this new type of trade (Ceballos and Kepel 2009).

Only species subject to international trade can be included in the CITES Appendices, inclusion in the Appendices allows the regulation of international trade in endangered wild species through the issuing and control of permits which aim to guarantee that the trade of individuals is not detrimental to the survival of the species in the wild. These apply to regular and internet trade (Sajeva et al. 2013). All members of the Cactaceae, with the exception of 3 genera (*Pereskia*, *Pereskiopsis*, and *Quiabentia*) are listed in either Appendix I or II. International trade of plants listed in Appendix I for commercial purposes is prohibited and they can only be traded if they are artificially propagated, in which case they are treated as if they were included in Appendix II, for which an export permit must be issued (Article VII, paragraph 4 of the Convention) (Sajeva et al. 2013). Artificially produced hybrids may be traded with an artificial propagation certificate, while seeds, flowers and other derivatives of these hybrids are not subject to the Convention (CITES 2014). Seeds of CITES Appendix I cacti, including seeds from artificially propagated plants, require CITES permits (U.S. Fish and Wildlife Service 2010; CITES 2014). This also applies to seeds from all Cactaceae spp. exported from Mexico (CITES 2014).

Illegal international trade in species of wild flora, in addition to threatening survival of species, may be detrimental for the local use and fair sharing of benefits from utilization of species (CBD 2012). Mexico being the most important centre of biodiversity

of cacti (Jiménez-Sierra and Torres-Orozco 2003, Ortega-Baes and Godínez-Álvarez 2006, Carrillo et al. 2005, Jiménez-Sierra and Torres-Orozco 2003, Martínez-Peralta and Mandujano 2009, Novoa et al. 2014), plays no important role in the commercial reproduction of cacti for trade and propagation activities are often hard to begin due to strong national regulations (Bárcenas 2003). This leaves locals in the sites of origin, who are usually low income peasants, with no other way of making use of the biological richness other than allowing collection by any visitor for a low income through illegal trade.

Internet monitoring of the illegal trade of species has focused mainly on animals (Kepel et al. 2004, CEEWeb 2007, Ceballos and Kepel 2009, Xianlin 2009, Pistoni and Toledo 2010). A study in 2013 concerning the cacti family suggested that only 10% of the plants traded through the internet were potentially legal (Sajeva et al. 2013). All reports have agreed that internet commerce is a growing threat to the regulation of illegal trade, but presents an opportunity to understand its scale and main targets. Internet monitoring can give a picture of the actual scale of trade (CEEWeb 2007). Taxon-specific internet monitoring allows the understanding of market opportunity as well as the threat presented by potentially unregulated commercial trade.

Methods

This methodology is relatively simple and easy to replicate to obtain a snapshot of internet commerce of a any species or genus.

An online search for the offer of adult plants and seeds of the genus *Strombocactus* was made during the period of March-April 2014, and reviewed at the end of 2015, using the https://www.google.com. The search was made in four languages using the following phrases: compra *Strombocactus* (Spanish), buy *Strombocactus* (English), acheter *Strombocactus* (French), and *Strombocactus* kaufen (German). Each website shown as a result in the browser was visited to determine if the website offered plants for sale, this was repeated until websites stopped being relevant on plant sales. The use of a common name for the search was not considered for this genus.

A database was constructed to organize the data and a summary chart was made to organize the information in the following categories: store name, link for the website, type (plant or seeds), quantity (number of seeds or size of the plants), species (different varieties recognized by collectors were considered), country of origin for the website, currency used, price, if they have or offer CITES documentation, and any other observations. For independent stores' websites, information on CITES was usually found under the terms and conditions or shopping tab. Advertisements in auction sites or big online websites like eBay or Amazon were also considered. All websites that didn't mention CITES information were contacted by e-mail, as potential buyer, inquiring about the need for CITES documentation and the origin of the plant or seeds.

An analysis of the UNEP-WCMC CITES Database, which holds the official record of CITES documented trade as reported by the countries member to the Conven-

tion, for the genus was also carried out (http://trade.cites.org/) (CITES 2013, 2015) using the following filters: year range as from 1975 to 2014 and species as *Strombocactus*, no other filter was used.

Results

The genus *Strombocactus* is sold under different names recognized by collectors (Table 1). Some varieties of *Strombocactus disciformis* are more valuable than others. However, we notice the online market price for this species is no more than €30 for the biggest and therefore most ancient individuals and also considerably cheap prices for the seeds.

We found 32 online stores where either whole plants or seeds of the genus *Strombocactus* were available. Only six (19%) state the plants they sell were obtained from CITES certified nurseries and will provide the documentation necessary: Duben Kaktus on eBay, Seeds Cactus, B&T World Seeds, Kakteen-Haage, Uhlig-Kakteen, and Mesa Garden.

Out of the rest; 5 (16%) mention CITES papers are necessary for the export but do not hold themselves responsible, 4 (13%) don't deliver outside of the European Union and are therefore exempted of the need for CITES papers, 12 (38%) mention that both plants and seeds are nursery cultivated from seed, *in vitro* or through grafting; and 8 (25%) include the name of localities from which seed or plants have been collected of which 3 (9%) include field collection numbers. These categories are not exclusive.

Regarding big online stores and auction sites such as eBay, Amazon and Mercadolibre, 24 publications were found. eBay contains the greatest number of publications, a total of 21, where only one of these sells plants from a CITES certified nursery, and another twelve declared specimens (both plants and seeds) came from nurseries or in the case of the latter where obtained from plants from a private collection.

Some online stores provide CITES documentation for international trade, 17% of stores in Germany, 25% in the Czech Republic, 33% in France and 50% in Italy. Only two online stores out of the previously mentioned (one based out of Germany and one out of Czech Republic) sell plants directly from CITES certified nurseries (Figure 1).

Online commerce of seeds is abundant. Most of the seeds of this genus are sold in quantities of less than 100 seeds, but offers were found in some stores for 500-1000 seeds. As well, in some private websites and through the e-mail answers we received, the harvesting of seeds from the wild is admitted openly (Table 2), and some even provide information regarding a collectors code or the locality were they were obtained. *Strombocactus* seeds measure about 0.5 mm (Rojas-Aréchiga et al. 2013), therefore a single envelope can serve as a mean to move thousands of propagules unnoticed.

According to the UNEP-WCMC (United Nations Environmental Program's World Conservation Monitoring Centre) CITES trade database up until 1984 only whole live individuals were sold; subsequently trade in seeds began. Since 1976, 326 879 plants and 325 433 seeds have been exported with CITES documentation. This last type of trade becomes more common than trade in whole plants from 1987 to the present day. The database also shows that since 1990 Mexico being the only country

Table 1. Online price of the different species and varieties of the genus *Strombocactus* (Cactaceae) for one unit in the case of plants and for 100 units in the case of seeds, during the period of March-April 2014, and reviewed at the end of 2015, using the https://www.google.com.

Species	Seed prices (×100)	Plant prices
Strombocactus disciformis	2–10 euros	6–30 euros (depending on size)
Strombocactus corregidorae	7–12 euros	13 euros
Strombocactus disciformis var. *jarmilae*	2.5–15 euros	–
S. pulcherrimus (*S. disciformis* ssp. *esperanzae*)	2–12 euros	21–26 euros
Strombocactus disciformis var. *seidelli*	2.7–3.6 euros	–

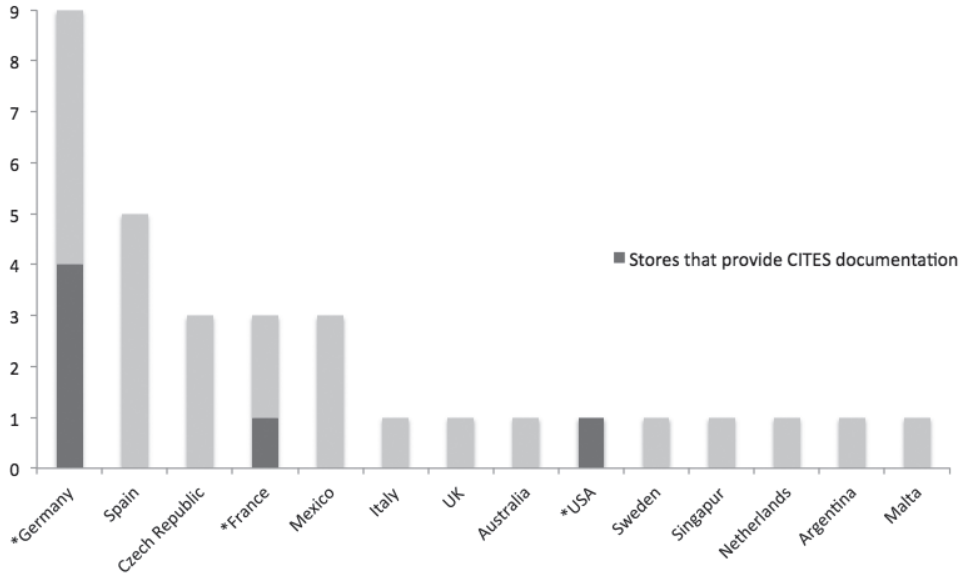

Figure 1. Number of online stores per country that sell *Strombocactus*. The asterisk (*) represents countries where at least one online store offers CITES certified cacti.

Table 2. Number of online stores localities (abbreviated state in Mexico).

No. of stores	Locality
5	Xichu, Gto.
5	Peñamiller, Qro.
3	Las Adjuntas, Gto.
3	Peña Blanca, Qro.
1	Vizarrón, Qro.
1	Maconi, Qro.
1	Jalpán, Qro.

which holds *Strombocactus* in its natural habitat, began importing seeds from the USA, allowing non-range countries to profit from its national resources. Mexico has also imported live plants for reintroduction and scientific purposes (CITES 2015).

Discussion

Most online stores may be implicated in illegal trade if they deliver specimens (both plants and seeds) internationally without CITES papers. The availability of seeds collected from wild specimens is particularly concerning. Plants can be easily sent in boxes marked with store codes, or seeds placed in envelopes. Generally, most stores that traded without the CITES documentation, didn't hold themselves responsible in case of confiscation but mentioned having no problem shipping internationally and that they do it often. This is particularly alarming due to the growing number of people that can easily offer CITES species in these stores protected by virtual anonymity, where once the publication is finished the user can leave the website making the identification of traders harder in the virtual world.

Research like this is relevant since it allows the use of an accessible and free tool like the internet to understand the magnitude of species trade. The UNEP-WCMC CITES database can be used to determine volumes of legitimate trade reported by CITES Parties and consistency between imports and exports (D'Cruze et al. 2015). We can find out which species are the most valuable, wanted and/or available; which may be useful to understand if the production of cultivated plants satisfies the demand for plants in the market. We can even track the appearance of recently described species in the international market of ornamental plants. Answers to these questions are especially vital for policy making by the bodies responsible for enforcing regulations, nature conservation and sustainable trade, as well as for possible future law amendments (Kepel 2004). The countries with the greatest volumes of production and sales can be identified, and most importantly it allows us to know which localities are the most visited for wild collection, especially of seeds, and so determine whether this is legal and sustainable or not. Once the harvesting localities have been determined, action plans can be created to keep these localities under surveillance during the time of fruit production. These localities can also be used as study areas to understand the population dynamics under constant harvesting.

There already exists a growing concern for the regulation of – illegally collected plants sold on the Internet (Sajeva et al. 2013, Lavorgna 2014). At this point, eBay offers the option of reporting items on sale based on their prohibited and restricted items list, which includes plants and seeds. However, this policy is focused on limiting the spread of pests and weeds and not on wildlife protection (eBay 2015). Its international trading policy expects the seller to be aware of international trade laws before listing an item and warns items could be removed if these laws are not respected; the same is applied to its animals and wildlife product policy. In this study, we see that although the policies exist they are not reflected in practice; particularly in the case of plants there is a gap of regulation in regard of protected species trade.

In the case of major online stores like eBay, Mercado Libre and Amazon we propose they apply a policy based on filtering the publications which contain the name of CITES species; for example through a downloadable format, signed by the seller

assuming responsibility for the legal origin of the product or/and a pop up window allowing the buyer to understand what a CITES species is and what its acquisition involves. Most times the lack of compliance with regulations for wildlife trade is more a matter of ignorance rather than disobedience (see Kepel 2004). This is especially important since often buyers assume that if a product is offered on a well-known service, then it must be legal.

In regard of the cheap online prices found for this species and considering their extremely low growth rates, late and annual reproduction events, and the rare establishment of new plants in the wild; we can argue the price for this species and probably for many other cacti and slow-growing plants is undervalued. Even in the case of abundant supply or low market demand, the valorisation of this and other species is not reflecting their particularly long life cycles and the services they bring to many pollinators. Just as diamonds take a long time to form, so do many cacti take a long time to reach the aesthetically appreciated form collectors want and it takes an equally long time for new individuals to establish in wild populations; however, they are clearly valued differently.

Conclusion

We found that most of the *Strombocactus* plants and seeds offered for sale on-line do not mention or follow CITES international trade regulations, therefore both the legal origin of the specimens and the assurance that it was non-detrimental for the survival of the species in the wild, can be questioned.

We emphasize that most of these stores also offer other cacti (close to 50 species) listed in CITES Appendix I. This type of trade must be acknowledged and complied with to promote species conservation. Throughout this study, and in compliance with the results of Kepel (2004), amongst breeders and artificial propagators we find general acceptance for breaking nature preservation laws. So we must ask ourselves why is this so? How can we fix it? And do current regulations make it too difficult to obtain the proper documentation for those who wish to trade honestly?

Especially in species rich countries, like Mexico, we need to open our eyes to the demand for wildlife and how it can be satisfied through fair trade schemes that benefit local landowners.

Acknowledgements

This research was completed through grants from Consejo Nacional de Ciencia y Teconología and Secretaría del Medio Ambiente y Recursos Naturales (project SEMARNAT/CONACyT 0350) and Ciencia básica del Conacyt (Conacyt 221362), and by Universidad Nacional Autónoma de Mexico (project PAPIIT IN 207411) and PASPA-DGAPA-UNAM for sabbatical leave to MCM.

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Nature Conservation 15: 11–22 (2016)
doi: 10.3897/natureconservation.15.9616
http://natureconservation.pensoft.net

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Pollinator species richness: Are the declines slowing down?

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Academic editor: *K. Henle* | Received 20 June 2016 | Accepted 11 July 2016 | Published 22 September 2016

http://zoobank.org/ECD71ECF-842D-4E87-AB97-50C8C03B4F48

Citation: Van Dooren TJM (2016) Pollinator species richness: Are the declines slowing down?. Nature Conservation 15: 11–22. doi: 10.3897/natureconservation.15.9616

Abstract

Changes in pollinator abundances and diversity are of major concern. A recent study inferred that pollinator species richnesses are decreasing more slowly in recent decades in several taxa and European countries. A more careful interpretation of these results reveals that this conclusion cannot be drawn and that we can only infer that declines decelerate for bees (*Anthophila*) in the Netherlands.

Keywords

Species richness, rarefaction, pollinators, species accumulation curve, diversity decline

Introduction

In a recent paper investigating different plant and pollinator groups in three countries, Carvalheiro et al. (2013, CA2013 hereafter) conclude that "Over more recent decades [...] declines in species richness [...] slowed down for many of the studied taxa and countries", a statement subsequently expressed less firmly as "past declines in some pollinator groups may have recently slowed or even partially reversed" (Kunin 2013). This conclusion on decelerating declines has been adopted in the recent UN IPBES Pollination Report draft summary (Potts et al. 2016, status "established but incomplete"). Carvalheiro and co-authors (2013) rightly state that a general deceleration would be

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highly relevant for conservation biology and biodiversity management and suggest in their concluding remarks that European Union (EU) policy could have played a role in the effect they infer. Ambitions in terms of biodiversity management seem reduced in recent EU legislation (Pe'er et al. 2014), unproblematic if the loss of diversity already slows down. I reassess the CA2013 statement that species richness declines have decreased in magnitude for many taxa and countries. The data and statistics presented in that publication are considered, as well as elements of the scripts provided by the authors to anyone interested. My own scripts used to carry out this assessment using R (R Core Team 2015) are available upon request.

Inference of decelerating declines in CA2013

The analysis in CA2013 is based on comparisons of species accumulation curves (Colwell et al. 2012) between periods (Figure 1). These curves express the dependence of the number of species in a sample on a variable representing sampling effort, and the horizontal asymptote of the curve is species richness. The comparisons in CA2013 are between three 20-year periods (1950–1969, 1970–1989 and 1990–2009). Per pair of successive periods, richness change was estimated as the difference between the log transformed numbers of species in the second minus the first period, where these numbers of species were predicted at a sampling effort (number of records) specific to each difference. Differences were calculated per group of species, country or per grid cell at smaller spatial scales. The differences between logged numbers of species were predicted at three times the numbers of records of the least sampled period, either by extrapolation when numbers of records in both periods were smaller than that, or by inter- and extrapolation combined (Fig. 1). The standard deviation of each difference was estimated using a bootstrap approximation. For spatial scales with multiple grid cells, random effects models that use squared standard deviations as the known error variances (Viechtbauer 2010) were fitted to the estimated changes per grid cell. The average effect across grid cells was used as a measure of richness change. As a check of robustness of results, the analysis was repeated with only interpolation (rarefaction) or only extrapolation and also with standard deviations of the logged difference estimated with an analytical expression (Colwell et al. 2012, CA2013). CA2013 inferred that rates of decline have decreased from observing that estimates became less accentuated, or that significant species number increases occur between the most recent periods when there had been a decrease before. Per taxon and country, Table 1 lists the statements from the text that the authors used to support their conclusion of a decelerating decline in species richness in several taxa and countries. All statements in the table can be found in CA2013's Results section on changes since 1990. When a spatial scale is mentioned in CA2013, I list the spatial scales to which the statement applies. Eight out of fifteen taxon/country combinations have statements in support of a decelerating decline. CA2013 state that this is independent of the way in which they carried out the analysis, hence robust.

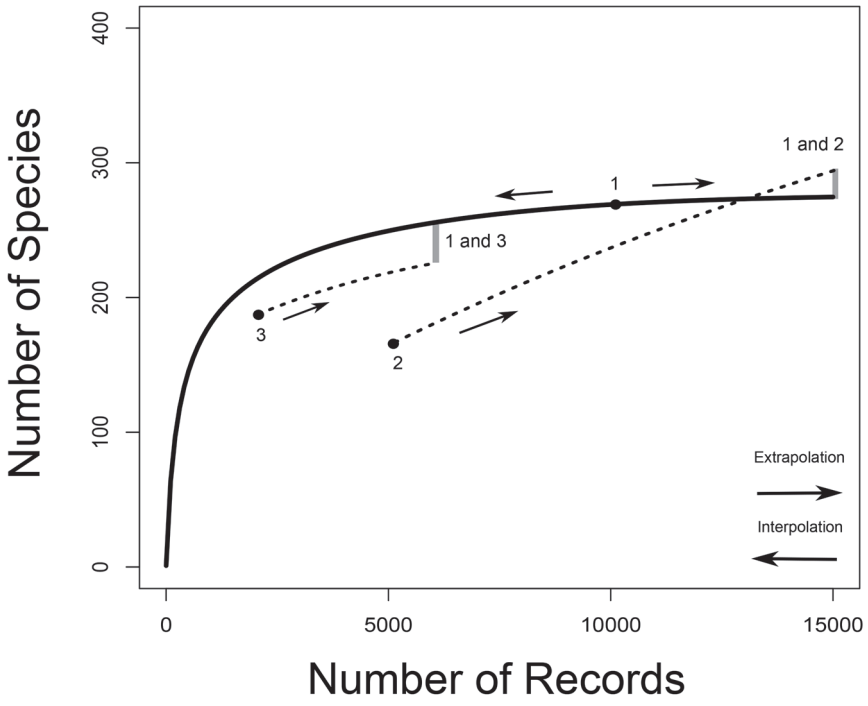

Figure 1. Species accumulation curves. Species richness is the asymptote of a species accumulation curve, which expresses the dependence on sampling effort of the number of species sampled from an assemblage. In CA2013, sampling effort is given by the number of records from which the number of species is calculated. For illustrative purposes, an example with three arbitrary samples (for 10000, 5000 and 2000 records, labeled from one to three) is drawn. For sample one, a predicted species accumulation curve is added that gradually increases from one species sampled to the predicted species richness for that assemblage (full line). Such curves are constructed on the basis of interpolation and extrapolation. For samples two and three only segments of extrapolated curves are drawn (dotted lines). For sample two, a curve that crosses the species accumulation curve of sample one is sketched. For samples one and three species accumulation curves are more or less proportional. The way in which the species richness differences between samples are assessed in CA2013 is illustrated by indicating on the species accumulation curves at which numbers of records pairwise comparisons would be made between two sample pairs (1 vs. 2 and 1 vs. 3). The number of species of the sample with the smallest number of records is extrapolated to the number expected at three times the number of records. When the number of records of the other sample is still larger than that, the number of species of the second sample is interpolated (rarefied), otherwise it is extrapolated as well.

A reassessment is required

Note that species richness was nowhere estimated in CA2013, rather numbers of species at particular finite sampling efforts were used as proxies for species richness.

As Table 1 shows, CA2013 does not contain any test for differences in rates of richness change between the pairs of twenty-year time periods considered. They did

Table 1. Statements in CA2013 supporting a slowing down of species richness decline. The column with spatial scales to which a statement applies lists either the grid sizes (as length of a grid side in km) or the country level. $: The changes on Figure 1 and in Table S2 are in fact decreases. *: It is unclear if this result is interpreted as a slowing down of the decline, since no significant change between the first two periods is reported. For all other groups with statements, a decline in an earlier period is reported.

Species group/Country	Statement on the change between the two most recent periods	Spatial scale
Non-*Bombus* bees		
Belgium	–	–
Great Britain	Significant increase	10/20/40/80/160
Netherlands	Significant increase	10/20/40/80
Bumblebees		
Belgium	–	–
Great Britain	Declines less accentuated	–
Great Britain	Significant increase	Country level
Netherlands	Declines less accentuated	
Butterflies		
Belgium	–	–
Great Britain	–	–
Netherlands	Declines less accentuated	10/20
Netherlands	Significant increase[$]	10/20
Hoverflies		
Belgium	Significant increase[*]	–
Great Britain	–	–
Netherlands	–	–
Plants		
Belgium	–	–
Great Britain	Recovery of species richness	10/20/40
Netherlands	Recovery of species richness	Country level

not aim to reject the null hypothesis that species numbers change at a constant rate. One cannot infer a change in species number decrease by checking which confidence intervals overlap with zero change and which ones not. For example if confidence intervals for declines would have been [-2, -0.2] between the first pair of twenty-year periods and [-1, 0.2] between the second pair, these intervals should not be interpreted as evidence of a change in decline as they do overlap, while the estimates would indeed have become less accentuated.

While appropriate tests for a slowing down of richness decline are lacking in CA2013, we can still check ourselves whether confidence intervals for changes overlap between interval pairs, and conclude on the significance of decelerations in species richness from the absence of overlaps.

Methods

I assess limits of confidence intervals in tables and figures of CA2013 to construct tests for a significant deceleration in richness decline. When these numbers are provided, limits of intervals are calculated from parameter estimates and their standard deviations using the normal approximation for 95% intervals ($z = 1.96$), otherwise limits of confidence intervals in the figures are inspected. I will conclude that a species richness decline has slowed down when (1) there is a significant species richness decrease between the first two periods. In terms of the analysis of CA2013 that translates into a negative response variable for the change between the first two periods, with a confidence interval that does not overlap zero. (2) The species richness decrease becomes less. The confidence interval in CA2013 for the change between the last two periods does not overlap with that for the previous two periods, and the estimate is larger.

I believe that the parallel analyses in CA2013 with different estimators of species number variance, for rarefaction and for extrapolation are to some extent a valid way of assessing the robustness of the inference. Comparing results when differences are predicted at different numbers of records implicitly checks whether crossing species accumulation curves might be present. With such crossings, the sign of species number differences will depend on the number of records where the difference is assessed (Fig. 1, comparison sample 1 vs. 2). I will require that decelerating declines, which are detected when combinations of inter- and extrapolation are used, also need to be detected for extrapolation to be considered robust.

Unfortunately, the robustness assessment in CA2013 is affected by anti-conservative inference, duplications of statistics and errors as explained in the following sections, such that a number of assessments are removed from consideration. This makes the assessment of robustness more limited than originally intended.

In the reassessment, I will give less importance to results at smaller spatial scales than at country level. First of all, the conclusion re-investigated here was formulated at country level. Second, for comparisons at smaller scales sample sizes are smaller. Hence the risk that predicted species numbers badly reflect species richness can be increased. Third, there is no guarantee and no evidence that the local grid cells compared between the first two and the last two periods are the same or samples from sets with identical properties. Fourth, I will show below that regression corrections carried out in CA2013 for the smaller spatial scales carry an additional risk of anticonservative inference and bias.

Increased risk of anti-conservative inference

In part of their calculations, CA2013 have used a bootstrap estimate of the variance of predicted species number. After inspection of the R code used, it turns out that their estimate is neither bootstrap variance nor bootstrap accuracy (e.g., Walther and

Moore 2005), so not a regular bootstrap estimate of variance. In their paper as published before correction, they sum the absolute value of the bootstrap estimated bias and the squared bootstrap average of Colwell et al.'s (2012) expression for the standard deviation of predicted species richness. CA2013 intended the bootstrap to account for additional uncertainty caused by potential non-random sampling, thus variances "corrected" in this manner should rarely become smaller than the analytical expression based on multinomial sampling. However, simulations using samples from the EIS bee and bumblebee dataset used in CA2013 indicate that they often do.

CA2013's script contained a calculation error: the bias on species number in the earlier period is used in calculations where it should have been that of the later period. In a modified script distributed with their corrigendum (Carvalheiro et al. 2013b) and used to produce a modified Figure 1, this error has been corrected. At the same time, however, a second change has been implemented: the bootstrap standard deviation of species number is now calculated as the product of the bootstrap average of the estimate of standard deviation based on multinomial sampling, times a scaling factor which is equal to one plus the absolute value of the ratio of the bootstrap estimated bias in predicted species number divided by the original estimate of species number. In my simulations, this quantity is smaller than the analytical expression in over 90% of samples simulated using random (multinomial) draws from the EIS bee data species distribution. As the CA2013 bootstrap confidence intervals are obtained using non-standard approaches, we know little about their performance in frequentist inference, except for the simulations I mention here which suggest that they have undesirable properties that lead to anticonservative inference.

The unweighted tests in Table S5 of CA2013, where we expect standard deviations to be calculated automatically from the data variances, all use averages of the bootstrap standard deviations as weights. They are therefore all weighted in an unexpected manner and should not be considered.

In Table S5 of CA2013, the three listed tests per taxon/country for effects at the national scale are in fact always the same test pasted in three times, namely the test based on a bootstrapped variance estimate. The R script of the authors does not contain any calculations for non-bootstrap weighted tests for national data, such that there is no robustness assessment possible. An unweighted test is impossible to carry out at the national level, as there are too few values to calculate data variances per species group/country. I am forced to rely solely on CA2013's bootstrap statistics for the country-level comparisons. Statistics in Tables S2 and S5 of CA2013 and the supplementary figures have not been adapted to the new heuristic to estimate bootstrap standard deviation, we therefore need to inspect the corrected Figure 1 of CA2013 to assess comparisons based on bootstrapped statistics and the uncorrected figures of the supplement (by comparing plotted limits of confidence intervals with a ruler). Table 2 summarizes the different estimates CA2013 provides and problems arising when one wants to use them further. A proper assessment of robustness is difficult, as in fact nearly any category of estimates either has uncorrected errors, is not provided, or not available at the national level. Nevertheless, I will use rarefaction and extrapolation

Table 2. Species number statistics. CA2013 presents standard deviations of species number change estimated in different ways and at different sampling efforts (NA: not available). Each of these statistics available from the paper or its figures is calculated in an unexpected manner. Categories where remarks are in bold are used for the reassessment.

	Unweighted standard deviation	**Analytical standard deviation**	**Bootstrapped standard deviation**
Rarefaction (Interpolation)	NA	NA	**Calculation error not corrected**
Extrapolation + Interpolation	Bootstrapped standard deviation	**Bootstrapped standard deviation at country level**	**Risk of anticonservative inference**
Extrapolation	NA	NA	**Calculation error not corrected**

results in my assessment, and will proceed as if their standard deviations had been correctly calculated. When such estimates will affect conclusions, I will note whether the uncorrected standard deviations play an important role in that or whether just the estimates of species number change would lead to the same conclusion.

Bias

CA2013 assume that their response variable (log-ratio of predicted species numbers at a particular sampling effort) is directly comparable between different sampling efforts. This is only expected when non-linear species accumulation curves for different periods are proportional and will often not hold good when these curves for example cross (Fig. 1).

CA2013 call it a bias that their response variable often becomes larger with larger differences in data sample sizes between periods. To correct for this presumed bias, they included the difference of the logged numbers of records in the two time periods as covariate in the random effects models. That the difference in species number often becomes larger with larger differences in sample sizes is an absolutely normal pattern if species accumulation curves are not proportional and sample sizes where species numbers are interpolated are not randomly distributed (for example consistently smaller in one period). It is not difficult to sketch a pair of species accumulation curves where unbiased estimation and a non-random set of sample sizes per period would produce this pattern. Applying the proposed regression correction here would distort the pattern of real differences. On the other hand, we also need to check whether it removes estimation bias when differences are calculated between different samples from the same assemblage.

Simulating data from a single species accumulation curve based on the EIS bee data, I found that the "regression correction" approach CA2013 used in their analysis of species richness change patterns at spatial resolutions smaller than the national scale does not remove bias on the intercept. When the ratio of sample sizes between periods is on average different from one in these simulations, tests on the intercept or on the

partial residuals used in this regression approach too often conclude that species accumulation curves have changed. These tests have anticonservative amounts of type I errors and also show estimation bias. When the sample in the second period is on average larger (smaller), the intercept is negative (resp. positive).

Additionally, the variances of partial residuals used for "corrected" per-grid tests in CA2013 were not taking variances of estimated regression parameters into account neither the random effect variance of the model fitted (Viechtbauer 2010). Also here, simulations indicate that the variance used is often smaller than that of the partial residual when calculated correctly. Thus tests on small spatial scale differences can be expected to be anticonservative due to a biased estimator and underestimated errors, even if the regression correction were appropriate. This completes my arguments to give sub-national analyses much less importance. I will focus on the tests at the national level as much as possible, even while anticonservative inference is expected there too.

Further irregularities

There are further irregularities in the analysis of CA2013. In the functions used to predict species accumulation curves, which I originally wrote, zero values have been replaced by positive numbers, and where functions should produce missing values or zeroes, shortcuts have been inserted that return other values. The threshold for the rma.uni() function used for weighted regression is not set at the default value of 10^-5 but at 0.01, which makes convergence of the algorithm on a decent estimate of unexplained heterogeneity in the data uncertain. In one instance, a 0.06 tail probability is used to conclude on significance of a test and not 0.05 as would be standard. Numbers of cells significantly declining or increasing in Tables S2 and S5 of CA2013: The authors have applied a two-sided test, not one-sided ones. They have counted as significant declines cells that had tail probabilities below 0.05 for that two-sided test and with a negative log-ratio value. These are thus not one-sided tests at 5% level as suggested by the verbal statement, but one-sided tests at the 2.5% significance level. The numbers of significant increasing cells are wrong altogether. Authors have counted number of grid cells with tail probabilities above 0.05 and a positive coefficient as significant, instead of the cells with a probability below 0.05. This error is made for all weighting methods, inter- and extrapolation. Thus entire columns "significant increases" are wrong.

Results

From the comparisons of confidence intervals extracted from CA2013's corrected Figure 1 and from the supplementary tables and figures, I conclude the following. For only six country/taxon combinations, confidence intervals of earlier rates of change are below zero and these of earlier and recent rates of change do not overlap in at least one test at the national level (Table 3). There are thus at most six combinations that need

Table 3. A reassessment of results in CA2013. Confidence intervals are extracted and calculated from figures and tables in CA2013. Cells with value "1" indicate taxa and countries where a significant decline in number of species between the two first periods is followed by a change in species number between the two most recent periods, which is significantly less negative (with non-overlapping 95% confidence intervals). Columns "nat" indicate comparisons at the national level and are in bold. I attach a larger importance to them as explained in the text. "NA" indicates missing values, where some data were lacking to carry out the comparison. Rows for which I would conclude from CA2013 that there is a decreased decline (provided that further inference problems are ignored) are in grey.

	Figure 1 (From Corrigendum)						**Table S5 Non-Bootstrap Weights**					**Supplementary Figures**			
												Extrapolation		**Rarefaction**	
Spatial scale	***nat***	160	80	40	20	10	160	80	40	20	10	**nat**	10	**nat**	10
Non-Bombus bees															
Belgium	**0**	NA	0	0	0	0	NA	0	0	0	0	**0**	0	**0**	NA
Great Britain	**0**	0	0	0	0	0	0	0	0	0	0	**0**	0	**0**	0
Netherlands	**1**	NA	0	1	1	1	NA	0	1	1	1	**1**	1	**1**	1
Bumblebees															
Belgium	**0**	NA	1	NA	NA	NA	NA	0	0	0	0	**0**	NA	**0**	NA
Great Britain	**0**	0	1	0	0	0	0	0	0	0	0	**0**	0	**0**	NA
Netherlands	**1**	NA	1	1	1	NA	NA	1	0	1	1	**1**	1	**0**	1
Butterflies															
Belgium	**0**	NA	0	NA	NA	NA	NA	0	0	0	0	**0**	NA	**0**	NA
Great Britain	**0**	0	0	0	0	0	0	0	0	0	0	**0**	0	**0**	0
Netherlands	**0**	NA	0	0	1	1	NA	0	0	1	1	**0**	1	**0**	0
Hoverflies															
Belgium	**1**	NA	0	0	0	0	NA	0	0	0	0	**0**	0	**1**	0
Great Britain	**0**	0	0	0	0	0	0	0	0	0	0	**0**	0	**0**	0
Netherlands	**0**	NA	0	0	0	0	NA	0	0	0	0	**0**	0	**0**	0
Plants with Intermediate Dependence on Insects															
Belgium	**0**	NA	0	0	0	0	NA	0	0	0	0	**0**	0	**0**	1
Great Britain	**0**	0	0	1	1	1	0	0	1	1	1	**0**	0	**0**	1
Netherlands	**0**	NA	0	0	0	0	NA	0	0	0	0	**0**	0	**1**	0
Plants Independent of Insects															
Belgium	**0**	NA	0	0	0	0	NA	0	0	0	0	**0**	0	**0**	1
Great Britain	**0**	0	0	0	1	1	0	0	0	1	1	**0**	0	**0**	1
Netherlands	**1**	NA	0	0	0	0	NA	0	0	0	0	**0**	0	**1**	0
Plants Dependent on Insects															
Belgium	**0**	NA	0	0	0	0	NA	0	0	0	1	**0**	0	**0**	1
Great Britain	**0**	0	0	1	1	1	0	0	1	1	1	**0**	0	**0**	1
Netherlands	**1**	NA	0	0	0	0	NA	0	0	0	0	**0**	0	**1**	0

further scrutiny, to check whether the decelerating decline suggested in at least one test might be there with some robustness.

For bumblebees and other bees in the Netherlands, the pattern is found in Figure 1 of CA2013, for extrapolation, at smaller spatial scales and for rarefaction (non-*Bombus* bees). This seems the most robust evidence for a decrease in biodiversity loss in CA2013, given the choice of inference method, and assuming anti-conservative approaches and calculation errors have limited effect. For three groups of plants in the Netherlands, the tests are significant when rarefying species numbers. The significance disappears in one group in Figure 1 of CA2013 and completely for extrapolation and at smaller spatial scales. For extrapolation, the estimates are not species number decreases. I conclude that this evidence on a reduced loss is non-robust and could be due to crossing species accumulation curves. For hoverflies in Belgium, the difference is significant at the national level for the new Figure 1, but not significant for spatial levels below national and not for the extrapolation. The estimates of species number change are all positive for extrapolation. I conclude that this result is not robust and could be due to crossing species accumulation curves. Plants in Great Britain at the smallest spatial scales suggest a reduced rate of changes, but the results for larger spatial scales are not significant. The same holds for butterflies in the Netherlands.

Taken together, the inference in CA2013 only provides robust inference of a slowing down of species richness decline in two out of fifteen taxon/country combinations. This is in fact one taxon, the bees *Anthophila*, in a single country, the Netherlands.

Discussion

Table 1 illustrates that CA2013 does not contain a test for a slowing down of species richness decline. When I construct such tests based on the confidence intervals provided in the paper (Table 2), and apply the procedure to check robustness proposed by the authors as much as possible, only two out of fifteen taxon/country combinations show evidence of decelerating declines. If I would have given the analyses at small spatial scales the same weight in my assessment as the country level, the conclusion would be slightly different. Butterflies in the Netherlands at the smallest spatial scale show a decelerating decline, which is also detected when an analytical expression for species number variance is used, and for extrapolation. If we conclude that this is evidence of a decelerating decline, we would then have detected it for two taxa in a single country. However, on top of arguments given in the previous sections, the data on butterflies in the Netherlands show a massive increase in numbers of records between periods (from 29,496 records to 162,102 and 1,835,545; CA2013 Table S1) and for the second estimate of richness change, 40% more 10 km grid cells are used than for the comparison of the first two periods. Figure S1.1 of CA2013 suggests that these 40% are not randomly distributed. I therefore conclude that this comparison at small spatial scales is insufficiently reliable to be presented as evidence.

Alternatively, we could forgo trying to draw conclusions on the separate species groups and countries altogether and just inspect estimates and the relative occurrence among them of species number decreases between the first two periods, and whether the last periods would often have increased values for species number change relative to the previous period. Such an approach would be akin to CA2013's statements that estimates have become less accentuated. Please note that such a procedure would be sensitive to estimation bias. At the same time, we would assume that all data heterogeneity can be ignored. Note that this inspection can easily generate bias itself: We should not select a subset of data points with negative changes between the first periods to assess further. In the case of independent changes between pairs of periods, just inspecting groups with the smallest values between the first pair of periods would bias the estimates for the second pair of periods to be larger than the first more often. Neither should we use all estimates provided in CA2013, as estimates for different spatial scales on the same group are not independent but re-calculations on the same data. If we count the changes at the national level from the corrected Figure 1 and the supplements, we do find decreases relatively often (15/21 estimates negative), and many more positive (less negative) recent changes (15/21 changes larger than between first periods). However, this pattern is again not robust. For extrapolated estimates, the decreases are a minority (8/21 estimates negative) and the estimates of recent change are not more often positive than what one could expect by chance (12/21 estimates larger). Sign tests (Conover 1999) could be used to test null hypotheses on these counts, but the raw numbers already show that we would have only weak support for a conclusion that the median species number decline become smaller. The lack of robustness points again to the possibility that results found in the data can be due to changes in the shapes of species accumulation curves. This approach and the hypotheses it can test would not allow us to draw conclusions on declines in individual countries and taxa. This is possible when considering standard deviations of the estimates as was done above. These standard deviations also allow us to distinguish more reliable estimates from less reliable ones, when calculated correctly and appropriately.

My reassessment and the brief discussion of what a simplified analysis and hypothesis testing scheme would provide do accept the inference method based on extrapolating and rarefying species numbers as valid. One can argue against that. Species richnesses were not estimated in CA2013, and the paper did not provide statistics that allowed tests at the country level without using bootstrap estimates of standard deviations. The time period was arbitrarily binned in three time intervals. If declines and decelerations occur, they don't have to be synchronous across taxa and countries and match with the time intervals. Moreover, O'Hara (2005) has stated that "Estimating species richness [...] seems futile, as it is impossible to know how bad the estimates are", pointing out known general difficulties with assessing bias and precision of species richness estimates. Given these additional arguments regarding the type of analysis CA2013 used, a new analysis using different methods still seems warranted and could further adjust the present conclusion. Therefore the status of the statement on decelerating declines in the Pollination Report (Potts et al. 2016) should be adjusted accordingly.

Acknowledgements

I thank Menno Reemer for providing the EIS (Invertebrate Survey Netherlands) bee dataset. An anonymous peer provided extremely useful comments through Peerage of Science.

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Nature Conservation 15: 23–45 (2016)
doi: 10.3897/natureconservation.15.9800
http://natureconservation.pensoft.net

RESEARCH ARTICLE

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Does timing of breeding matter less where the grass is greener? Seasonal declines in breeding performance differ between regions in an endangered endemic raptor

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Academic editor: *K. Henle* | Received 8 July 2016 | Accepted 15 July 2016 | Published 22 September 2016

http://zoobank.org/71343564-DECC-4DB6-A7A8-0C2FB331D023

Citation: Garcia-Heras M-S, Arroyo B, Mougeot F, Amar A, Simmons RE (2016) Does timing of breeding matter less where the grass is greener? Seasonal declines in breeding performance differ between regions in an endangered endemic raptor. Nature Conservation 15: 23–45. doi: 10.3897/natureconservation.15.9800

Abstract

The timing of breeding can strongly influence individual breeding performance and fitness. Seasonal declines in breeding parameters have been often documented in birds, particularly in the Northern Hemisphere. Fewer studies have investigated whether seasonal declines in productivity vary in space, which would have implications for a species' population dynamics across its distributional range. We report here on variation in the timing of breeding in the Black Harrier (*Circus maurus*), an endangered and endemic raptor to Southern Africa. We investigated how key breeding parameters (clutch size, nesting success and productivity) varied with the timing of breeding, weather conditions (rainfall and temperature) and between contrasted regions (coastal vs. interior-mountain). Black Harrier onset of breeding extended over an 8-month period, with a peak of laying between mid-August and end of September. We show a marked seasonal decline in all breeding parameters. Importantly, for clutch size and productivity these seasonal declines differed regionally, being more pronounced in interior-mountain than in coastal regions, where the breeding season was overall shorter. Timing of breeding, clutch size and productivity were also partly explained by weather conditions. In coastal regions, where environmental conditions, in particular rainfall, appear to be less variable, the timing of breeding matters less for breeding output than in interior-mountain regions, and breeding attempts thus occurred over a longer period. The former areas may act as

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population sources and be key in protecting the long-term population viability of this threatened endemic raptor. This study provides unique evidence for a regionally variable seasonal decline in breeding performance with implications for population biology and conservation.

Keywords
Black Harrier, *Circus maurus*, Conservation, Breeding success, Productivity, Fynbos, Karoo, South Africa

Introduction

Understanding spatial-temporal variations in breeding parameters is an essential component of population ecology, and is particularly important for species that are of conservation concern, as this may help identify reasons for population decline or scarcity (Newton 1979, 1998, Krebs 1985). In this context, understanding variation in the timing of breeding and its potential fitness consequences is an essential intermediate step, and may reveal limiting factors for the species (Perrins 1970, Verhulst 2008). Quality of the breeding area, predation risk, inter- and intra-specific competition, individual quality and time of migration (Newton 1998) have all been found to affect timing of breeding in bird species. Overall, weather conditions (Charmantier et al. 2008, Visser et al. 2009) and food abundance (Newton 1998, Verboven et al. 2001) are generally considered the two main drivers influencing variation in the timing of breeding in bird species. In tropical birds, breeding onset may occur throughout the year as a result of a less seasonal climate and more constant food availability and abundance (Simmons 2000, De Marchi et al. 2015). On the other extreme, breeding onset in Arctic species depends on snow cover in spring and is restricted to a very narrow temporal window (Dickey et al. 2008).

The timing of breeding is a key determinant of breeding success and productivity (e.g. Verhulst 2008, Dunn and Moller 2014, Martin et al. 2014). In many woodland passerines, laying usually occurs so that the nestling period matches the seasonal peak in caterpillar abundance, which in turn is determined by weather conditions, such as temperatures in spring (Lof et al. 2012). Breeding too early or too late in relation to optimal conditions may lead to lower breeding performance (Robb et al. 2008). Seasonal declines in breeding outputs have been observed in many species, with birds breeding earlier in the season having higher reproductive outputs than those breeding later on (Verboven and Visser 1998, Mougeot and Bretagnolle 2006, Verhulst and Nilsson 2008). This pattern may arise when individuals breeding earlier in the season are of better quality, and/or when environmental conditions degrade as the season progresses (e.g. worsening weather conditions, reduced food abundance and quality, degrading breeding habitat vegetation; Verhulst et al. 1995, Verhulst and Nilsson 2008). The latter scenario implies that optimal conditions for breeding are temporally limited within a breeding season. In a context of climate change and rapidly changing environmental conditions, a preexisting synchrony between the timing of breeding and the availability of key breeding resources (seasonal food peak) may be disrupted leading to biodiversity loss (Visser et al. 2004), but more investigation is needed on this topic (e.g. Visser and Both 2005, Reed et al. 2013, Grimm et al. 2015).

Recent research has also indicated that seasonal declines in breeding performance may vary in strength depending on habitat type or location. For example, Zarybnick et al. (2015) found that Tengmalm's Owl (*Aegolius funereus*) showed different seasonal declines in productivity in temperate and boreal areas, principally due to differences in nestling mortality rates across the season. In the Great Tit *Parus major*, clutch size declines through the breeding season have been reported in rural, but not in urban areas (Wawrzyniak et al. 2015). This may imply that conditions for breeding in the latter habitat are more stable or last longer in the year, which may have implications for the ecology of these populations. However, with these few exceptions, the variability in declines of seasonal reproductive performance remains poorly studied or explored.

Research on the relationship between timing of breeding (i.e. lay date) and breeding output (e.g. clutch size, success or productivity) in birds, up until now, has been mainly conducted in temperate and boreal regions (Barnard et al. 1987, Amar et al. 2012, Dunn and Møller 2014). Relatively few studies exploring the association between timing of breeding and breeding outputs have been conducted in the Southern Hemisphere, particularly in Africa (Simmons 2000, Lepage and Lloyd 2004, Martin et al. 2014, Murgatroyd et al. 2016). Identifying these associations may contribute to our understanding of why some populations are more or less successful under certain circumstances and conditions than others. This may be particularly important when dealing with endangered species, as it may allow prioritizing conservation efforts of target species in space or time (Green et al. 2006, Amar et al. 2008, Gangoso et al. 2009).

The Black Harrier (*Circus maurus*) is a ground-nesting medium-sized bird of prey, endemic to southern Africa. The species is very scarce with an estimated total world population of less than 1000 mature breeding birds, a distribution range of approximately 500,000 km^2 and a far more restricted breeding range of approximately 170,000 km^2 (van der Merwe 1981, Siegfried 1992, Simmons 2000). This endemic species to Southern Africa is listed as endangered in both South Africa and Namibia (Taylor et al. 2015, Simmons et al. 2015), the two countries encompassing the totality of the breeding range. Black Harriers breed in both coastal regions and in the interior mountains of south-western South Africa (Curtis et al. 2004, Curtis 2005), but the species remains very understudied (Van der Merwe 1981, Simmons et al. 1998, Curtis et al. 2004, Curtis 2005, Simmons et al. 2005, Jenkins et al. 2013) and information on breeding parameters is particularly scarce. Curtis et al. (2004) explored variation in breeding parameters between nests in coastal or interior-mountain regions, finding that clutch sizes and productivity were greater in coastal regions. However, this study used data from only 3 years (2000–2002) and their analyses did not account for variations due to the timing of breeding or the influence of weather. Black Harriers are known to lay clutches over an extended period (from mid-May to mid-December, Simmons et al. 2005), but information about variation in the timing of breeding between years or regions is currently lacking. The breeding range of the Black Harrier mainly coincides with the Mediterranean climate zone of South Africa, characterized by cold and wet winters (May-September), and warm and dry summers (October–April). The seasonal fluctuations characterizing this climatic zone may in-

fluence the timing of breeding for Black Harriers, which may also differ between the main nesting regions.

In this study, we use a large data set of nearly 400 breeding events of this scarce endemic species collected over 15 years (2000–2014) in South Africa to investigate spatial-temporal variations in breeding performance. We first report on regional variation in the timing of breeding, and its association with weather conditions (i.e. rainfall and temperature). We then investigate whether key breeding parameters (clutch size, nesting success and productivity) vary depending on the timing of breeding, geographical location (coastal vs. interior-mountain regions) and weather conditions. Lastly we evaluate whether seasonal declines in breeding performance differ in strength between regions, and the potential implications this might have for the conservation of this species.

Material and methods

Study area

Breeding data were collected opportunistically over a large area (ca. 170,000 km^2) of temperate southwestern South Africa (29°-34°S; 17°-27°E) from 2000 to 2011. More focused studies took place along the west coast of the Western Cape Province and inland in the Northern Cape Province around Nieuwoudtville (31°19'S; 19°05'E) first from 2000 to 2002, and then from 2012 to 2014. Nests were located in and around national parks (i.e. South African National Parks – SANParks), provincial protected reserves (i.e. Cape Nature), or on private lands. They were spread across a mosaic of different biomes with diverse habitats and vegetation types, many of which are nationally and internationally protected and considered of high biological and ecological values (see e.g. Manning 2007). Climate across the study area varies between provinces: the west of the Eastern Cape, and Western Cape have a more temperate climate and a winter rainfall regime (April to September), while the coastal Northern Cape also experiences a winter rainfall regime but with more fluctuating temperatures (South African Weather Services: http://www.weathersa.co.za).

Black Harriers are ground-nesting birds and, unlike other raptor species, breeders rarely re-use the same nest over the years (Simmons et al. 2005). It is as yet unclear if the same individuals breed together as a pair year after year, although some evidence suggests this is not the case (Garcia-Heras et al., unpublished data). Breeding sites were located by observing areas where Black Harriers were previously known to breed and/or where perched adults were detected. As in other raptor species, the females take care of the chicks at the nests and perform all brooding, while the male captures and provides the food in the early nestling period (Simmons 2000, Redpath et al. 2002a). Thus, nests were located by following prey-carrying males and observing where females landed after a food pass (Simmons 2000).

Breeding parameters

After discovery, nests were visited regularly (usually 2–3 times per breeding event) where possible to assess nesting success and productivity. However, because of the extensive nature of the study area, not all breeding areas and nest sites were monitored consistently each year, and for some remote areas, nests sites were only visited once, or were last visited prior to fledging. During each nest visit, we noted the nest contents (i.e. number of eggs or nestlings) and, if the nests contained nestlings, a visual estimate of age was taken. In a subsample of nests, wing, tail and tarsus length (mm), and mass (g) of chicks were measured. Nest visits were kept as brief as possible (< 20 min) and an effort was made to leave the vegetation around the nest undisturbed. The location of nests was recorded using a global positioning system (GPS). A total of 490 nests were located between 2000 and 2014, although not all variables examined in this study were available for each breeding attempt, so sample size varies among analyses.

Lay dates were estimated by subtracting 31 days (Simmons et al. 2005) from hatch date, which was in turn estimated either directly when a clutch was found with an egg hatching or a newly hatched chick (aged 1–3 days old) or indirectly from nestling age. Nestling age was estimated either visually (see above) or through body measurements (using data from a subsample of nests that were visited more regularly, we could build growth curves of wing-length for this species, Garcia-Heras et al. unpublished data). Given the variation in precision of lay dates among nests, we finally attributed the laying date for each nest to a 15-day period (where 1 = 1–15 May, 2 = 16–31 May, etc., up to 15 = 1–15 December). For the sake of simplicity, we henceforth refer to these lay date periods as "lay date" even though they are not exact dates. Lay date could not be determined for nests located during the incubation period and visited only once or that failed before the second visit (n = 70), or for nests discovered after fledging or for breeding records without a precise visit date (n = 18); therefore, data from these nests were excluded from the breeding phenology analyses. Overall, lay date was estimated for 402 breeding events.

Clutch size was defined as the maximum number of eggs laid. When possible, nests were visited twice during the incubation period with the second visit timed to coincide with the estimated date of hatch. This ensured that we recorded the exact number of eggs laid per breeding event. Nests that were visited before the clutch was finished and that subsequently failed, or only during the nestling period were excluded from clutch size analyses. Clutch size was known for 191 breeding attempts.

Breeding output was measured in two ways, nesting success (known for n = 263 breeding attempts) and productivity (n = 261). Nesting success was classified as 1 for those nests where at least one young was raised to 35 days old, or 0 otherwise. Productivity was defined as the number of young reaching 35 days of age (range 0–4) for pairs that laid a clutch. Black Harriers fledge at approximately 40 days old (Simmons et al. 2005) but in many cases our last visit occurred before that age; however, in harriers, as in many other species there is usually little mortality during this late nestling stage (Redpath et al. 2002a). Thus, we assume that any nestlings alive at 35 days old would have fledged.

Topographic parameters

Nest coordinates were incorporated in a geographical information system (QGIS Valmiera 2.2.0), projected on WGS84-UTM-34S as the coordinate reference system. Using this GIS, we calculated and identified the following variables for each nest: i) Altitude, from the Shuttle Radar Topography Mission (SRTM) 90 m Digital Elevation Database v4.1 (Srtm90m). ii) Region (coastal and interior-mountain) was defined using a combination of nest altitude (from SRTM) and distance to the coast. Coastal nests were defined as those located within 15 km from the coast and with a maximal altitude of 100 mASL (n = 328). Nests located further than 15 km from the coast and with an altitude higher than 100 mASL were considered as interior-mountain (n = 146). However, this classification excluded nine nests that were located higher than 100 mASL (average of 118 m), but within 15 km from the coast and for the purpose of our analysis these were classified as coastal. Another eight nests were located at an altitude lower than 100 m, but 45 km from the coast, and these were classified as interior-mountain. In both cases, we believe our classification to more accurately describe conditions for those 17 nests. This regional classification was initiated by Curtis et al. (2004) to explore regional differences in lay dates and productivity of Black Harriers. That study also further differentiated between nests in mountain and interior-lowland areas. However, overall sample size of interior-lowland areas was too small to allow meaningful comparisons, and so these two categories were grouped together as a single region (interior-mountain) for our study.

Weather data

Weather data were obtained for the period 2000–2014 from 17 weather stations distributed throughout the study area (source: South African Weather Services: http://www.weathersa.co.za) (Figure 1). For some stations, weather data were lacking in certain months or years (due to technical problems or stations not being active at the beginning of our study period). For each weather station, we obtained daily rainfall (mm) and daily maximum and minimum temperature (°C). From these, we calculated monthly averages for daily temperature and daily rainfall for all the weather stations and years when data were available. Each weather station was classified as "coastal" or "interior-mountain" depending on its location, using the same criteria as for nests. We attributed to each nest the weather data from the nearest weather station located within the same region. An exception was however made for 18 nests located in interior-mountain regions, but for which the corresponding closest weather station was located 230 km away: for these we instead used the closest coastal weather station, as the distance between these nests and this weather station was relatively small (i.e. between 35 and 70 km away), and because they had a similar altitude. On the other hand, we excluded weather data entirely for 6 nests for which the distance between them and their closest weather station was further away than 120 km. Overall, our sample size included 475 nesting events with associated weather data from weather stations that were located on average 29 ± 22 (SD) km away from study nests (Figure 1).

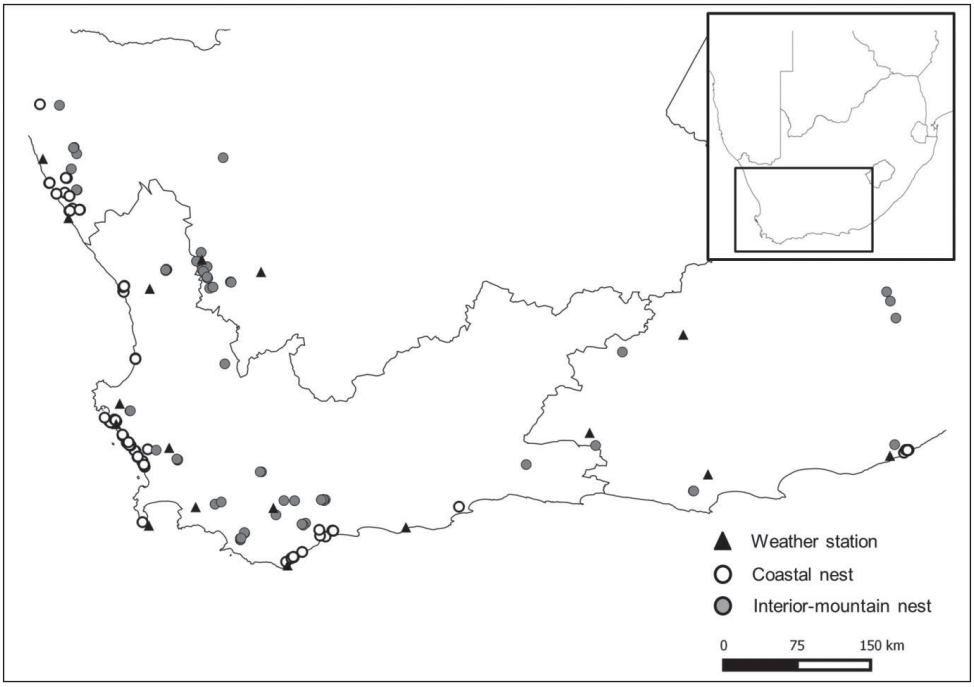

Figure 1. Location of study nests within South Africa for which weather data were available (n = 475), during 2000–2014. White circles: coastal nests; dark grey circles: interior-mountain nests; black triangles: weather stations that provided data for the purpose of the study.

Statistical analysis

All statistical analyses were conducted using R 3.2.3 (the R Foundation for statistical computing 2015).

To reduce the number of weather variables and to account for potential collinearity among them, we conducted a Principal Component Analysis (PCA) on monthly rainfall and temperature data for each station and study year. We selected the first four weather Principal Components (PCs) for subsequent analyses (a scree plot showed a marked drop in explained variance between the fourth and the fifth PC). PCs were chosen for analyses on the effect of weather on breeding parameters, rather than using raw weather data, because we did not have a strong *a priori* hypothesis of the time period over which weather may be more influential. Therefore, using raw data would have meant exploring the effect of a high number of potential explanatory variables (weather over different time periods). Furthermore, our PCs had clear biological meanings (see results), which helped in interpreting the relationships found. However, because PCs include information about weather in all months, in our discussion we placed most emphasis on the meaning of each PC for the months prior to the variable in question (e.g., for the relationship between lay date and weather, we focus on the meaning of each PC for the months prior to laying, not subsequently).

We investigated regional differences in the weather PCs using General Linear Mixed Models (GLMMs, statistical package lme4, Bates et al. 2012) that included the weather station identity as a random effect (to take into account the non-independence of the data coming from the same station) and the factors region (coastal vs. interior-mountain) and year (14 levels) as explanatory variables. This analysis was run on a data set that had only one data point for each weather station and year (n = 88).

To analyse factors affecting variation in breeding phenology, we used GLMMs that included year as a random effect, so that we could identify patterns that would describe what happens in an average year. The "lay date" of each nest (response variable) was fitted with a Gaussian distribution and an identity link function. The initial model included the explanatory variables of region and weather variables (the first four weather PCs). These models were conducted on a subsample of 393 nests for which both lay date and weather data were available.

GLMMs with year as a random effect were also used to explore clutch size, nesting success and productivity (response variables) in relation to region, lay date, and weather (explanatory variables). Initial models also included the interaction between region and lay date to look for regional differences in seasonal variations in breeding performance. For models where this interaction was significant, we re-ran the same model but without the interaction to test for differences between regions. Nesting success was fitted with a binomial distribution, and clutch size and productivity were fitted with a Gaussian distribution. Even though the latter may not be ideal for productivity data, using a Poisson distribution produced models with large dispersion parameters, whereas Gaussian models performed well and model residuals were normally distributed. Analyses of clutch size were conducted on a subsample of 183 breeding events for which clutch size, lay date and weather data were available. Analyses of variation in nesting success and productivity were conducted on a subsample of 223 and 222 breeding events, respectively, for which lay date and weather data were also available.

A stepwise backward procedure was performed for model selection (with the function drop1), and likelihood ratio chi^2 tests (LRT) on AIC differences were used to select the best models.

Samples sizes differed between regions and our slope estimates for the relationships between lay date and breeding parameters could be influenced by this or hinge on data from a few very early or very late nests (see Figure 3). In order to be confident that regional differences were not simply a consequence of these potential biases, we randomly selected a reduced and equal number of nests in each region and re-estimated the slope of the relationships and their 95% confidence intervals using a bootstrap analysis implemented in R 3.2.3. For the relationships between lay date and clutch size, our sample sizes included 144 and 42 nests in the coastal and interior-mountain regions, respectively, so we re-estimated the slope using 1000 random samplings of 30 nests from each region. For the relationships between lay date and productivity, our sample sizes included 163 and 64 nests in the coastal and interior-mountain regions, respectively, and we re-estimated the slope using 1000 random samplings of 50 nests from each region.

Results

Weather: seasonality and regional differences

Study regions were characterized by different weather conditions (Figure 2a, b). Both regions experienced higher temperatures and little rain during summer months (December-March) than winter months (May-September). However, temperature differences between summer and winter were more pronounced in interior-mountain than in coastal regions. Additionally, coefficients of variation for both temperature and rainfall were greater from April to October in the interior-mountain than in the coastal region, indicating that weather conditions in interior-mountain regions at that time were more variable in space (among nest localities) or time (years) than those in coastal regions. Rainfall levels strongly decreased (by half) between August and September in both regions, coinciding with the peak of lay date in Black Harriers (Figure 2b, c).

The PCA analysis on monthly rainfall and temperature data rendered four PCs explaining approximately 60% of the variance (Table 1). PC1 was positively related to temperature during all months, although the relationship was less marked during the winter months (June-August) when temperatures were overall lower (Figure 2a). PC2 was positively related to rainfall during all months, although the relationship was less marked during the summer and early autumn months (December-March), when rainfall levels were overall lower (Figure 2b). PC3 contrasted high temperatures in summer and early autumn (December-March) but low in late autumn and winter (May-August), with lower temperatures in summer and higher in autumn-winter. Therefore, this PC refers to temperature seasonality. Finally, PC4 identified situations with higher rainfall in summer and early autumn (December-March), but lower rainfall in late autumn and winter months (May-August), thus referring to rainfall seasonality.

All weather PCs varied significantly among years, but only PC1 and PC3 were significantly different between regions (Table 2). PC1 values were lower in the coastal region (LS means: -1.15 ± 0.70), indicating cooler temperatures (particularly in springs, summers and autumns) than in the interior-mountain (LS means: 0.93 ± 0.64). PC3 values were also lower in coastal than interior-mountain region (LS means: -1.43 ± 0.34 and 1.18 ± 0.31, respectively), indicating that temperature variation throughout the year was more pronounced in interior-mountain regions.

Timing of breeding

Lay date (n = 393 nests) was remarkably well spread through the year, spanning 8 months, from mid-May to mid-December, and followed a unimodal distribution in each region (Shapiro normality test, $w = 0.98$, $p = <0.0001$, $n = 287$ for coastal region; $w = 0.95$, $p = 0.0009$, $n = 106$ for interior-mountain region) with a peak during mid-August to end of September (Figure 2c).

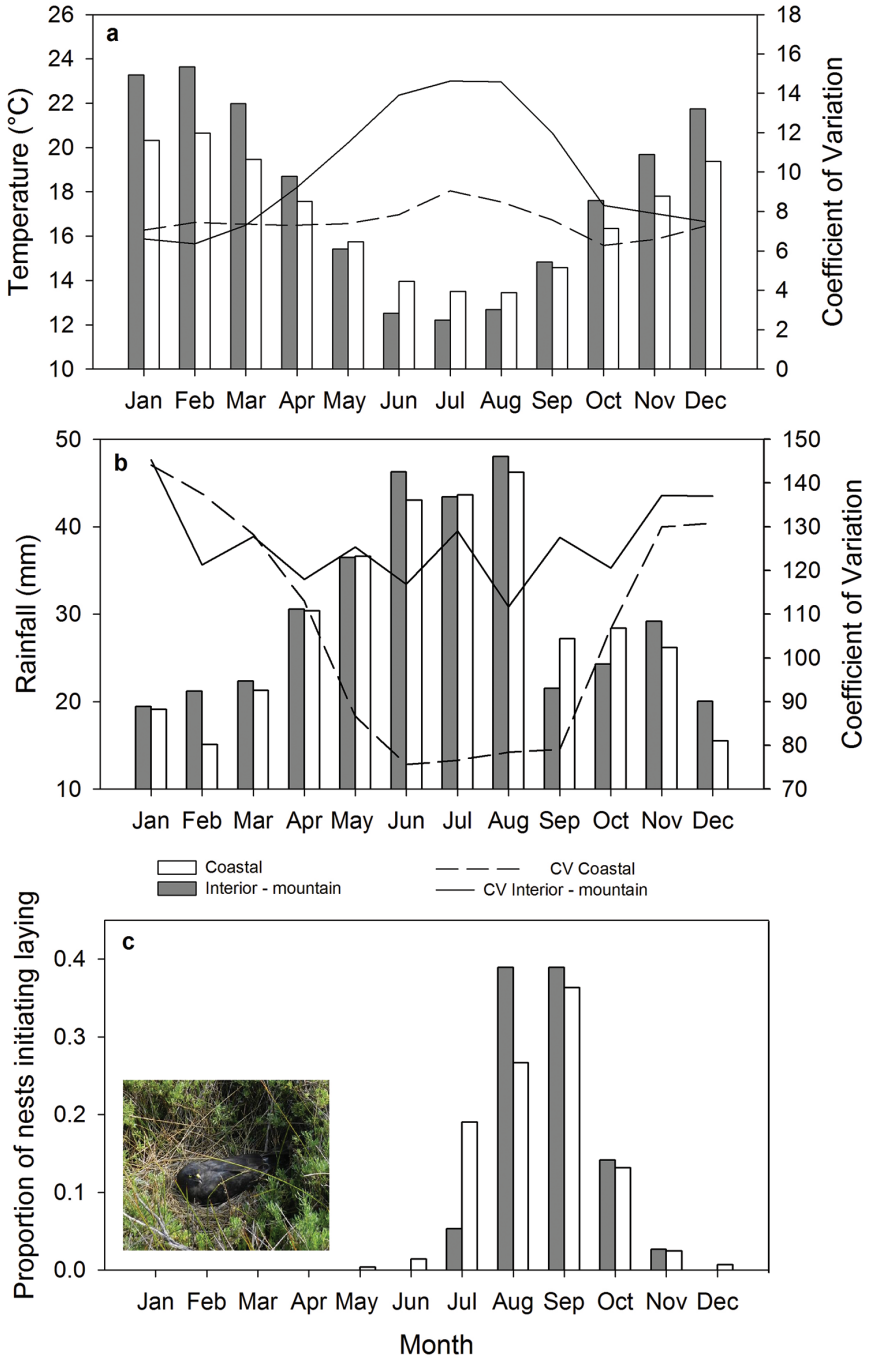

Figure 2. Monthly average temperature (**a**) and rainfall (**b**), according to region (coastal, white bars; interior-mountain, dark grey bars). Also presented are Coefficient of Variation (100x SD/Mean) for both climatic variables (dashed line for coastal, solid line for interior-mountain), as well as frequency distribution of breeding initiation (n = 402) (**c**) during the study period (2000–2014).

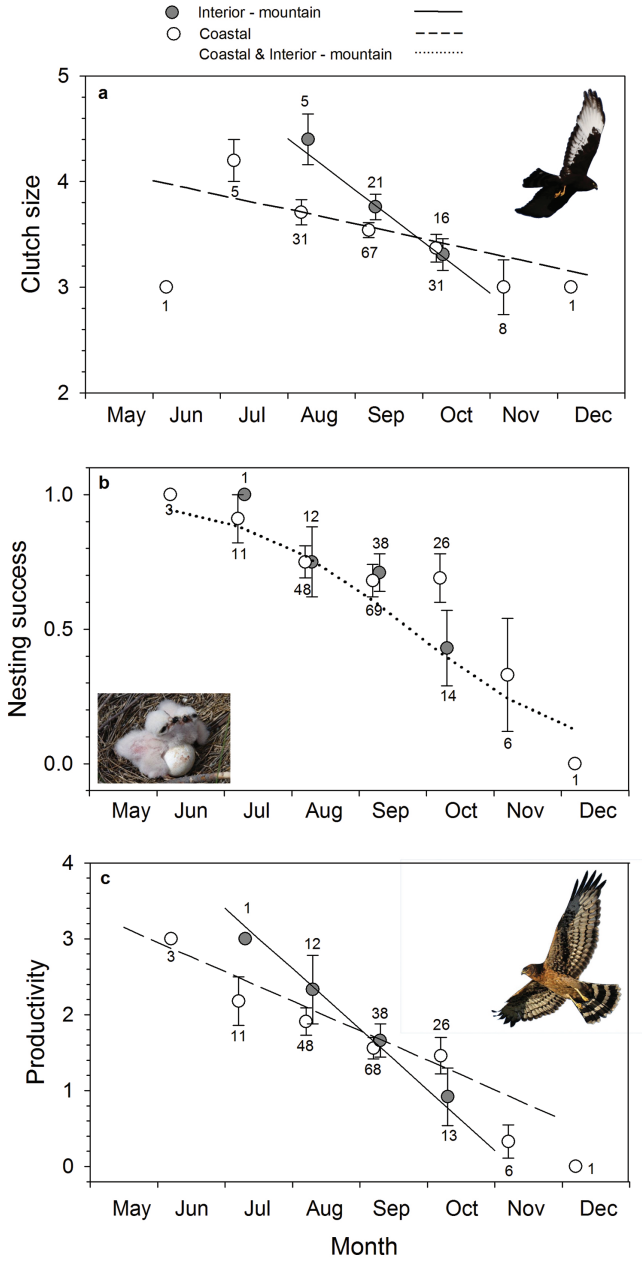

Figure 3. Black Harrier breeding performance (**a** clutch size **b** nesting success **c** productivity) variation according to lay date and region (coastal nests: white circles/dashed line; interior-mountain nests: grey dark circles/ solid line). Lines represent modelled data from the GLMM results (Table 3). Raw data (circles) are also shown for illustration purposes and have been averaged over two consecutive 15-days periods. Sample sizes (number of nests) are indicated above the error bars. The point line represents the breeding success variation with laying date for both coastal and interior-mountain regions (this relationship did not differ between regions).

Table 1. Results of the Principal Component Analysis conducted on weather data (monthly averages of daily rainfall and daily temperatures) collected in 2000–2014 at 17 weather stations (see Figure 1). "Temp" represents the average of the daily maximum and minimum temperatures (°C), per month. "Rain" corresponds to the average of the daily rainfall (mm) per month. Variable loadings greater than 0.2 or lower than -0.2 are highlighted in bold. The months during which Black Harriers usually breed are highlighted in grey.

	PC1	PC2	PC3	PC4
Rain. JAN	0.014443	0.129292	-0.01123	**0.353204**
Rain. FEB	-0.02877	0.171029	0.098396	**0.416038**
Rain. MAR	-0.01663	0.196125	0.032239	**0.45707**
Rain. APR	-0.06009	**0.303045**	0.03444	0.067087
Rain. MAY	-0.11894	**0.281114**	0.093557	**-0.23835**
Rain. JUN	-0.12415	**0.308008**	0.131795	**-0.26365**
Rain. JUL	-0.124	**0.302469**	0.084539	**-0.23318**
Rain. AUG	-0.13295	**0.325751**	0.102831	**-0.27611**
Rain. SEP	-0.09693	**0.350088**	-0.01698	-0.04674
Rain. OCT	-0.0634	**0.28149**	0.001479	0.105491
Rain. NOV	-0.07844	**0.32201**	0.029495	0.174901
Rain. DEC	0.006074	0.168862	0.060451	**0.290475**
Temp. JAN	**0.292895**	0.057873	**0.310684**	0.011043
Temp. FEB	**0.315231**	0.065366	**0.257761**	-0.01914
Temp. MAR	**0.303027**	0.066636	**0.231843**	-0.11742
Temp. APR	**0.335735**	0.082603	-0.02066	**-0.20133**
Temp. MAY	**0.230807**	0.16073	**-0.29901**	-0.07898
Temp. JUN	0.127701	0.149213	**-0.44499**	-0.0962
Temp. JUL	0.127055	0.120859	**-0.43149**	-0.10167
Temp. AUG	0.190731	0.153715	**-0.36607**	0.128207
Temp. SEP	**0.272202**	0.082607	-0.18223	0.075789
Temp. OCT	**0.352615**	0.052975	0.017441	0.024666
Temp. NOV	**0.344244**	0.035273	0.119129	-0.00367
Temp. DEC	**0.290036**	0.046253	**0.258563**	0.009631
Variance explained				
Proportion	0.254	0.1554	0.1361	0.08704
Cumulative	0.254	0.4084	0.5454	0.63249

Lay date was negatively associated with weather PC2 (slope = -0.26 ± 0.07) and PC4 (slope = -0.27 ± 0.10; Table 3), indicating that laying occurred relatively earlier under rainier conditions, particularly when rain was more intense in autumn, winter and spring, and when summers preceding laying were wetter. Lay date was also significantly different between regions (Table 3): nests located in coastal regions had overall earlier lay dates (LS means: 8.40 ± 0.22, 15–30 August) than those located in mountain regions (LS means: 9.36 ± 0.28, 1–15 September). Individuals in coastal regions also laid over a more extended period, with breeding events in this region occurring up to two months earlier and one month later than in the interior-mountain regions (Figure 2c).

Table 2. Results of the General Linear Mixed Models (GLMMs) testing for differences between years and regions (coastal vs. interior-mountain) in weather variables (PC1, PC2, PC3, and PC4; see Table 1). The "weather station" identity was included as a random effect to take into account for the non-independence of data from the same locality. DF: Degree of Freedom, LRT: Likelihood Ratio Tests.

Dependent variables	Explanatory variables	DF	LRT	P
PC1	Year	15	82.15	<0.0001
	Region	1	4.67	0.031
PC2	Year	15	32.11	0.006
	Region	1	0.02	0.88
PC3	Year	15	214.52	<0.0001
	Region	1	21.11	<0.0001
PC4	Year	15	95.19	<0.0001
	Region	1	0.04	0.83

Table 3. Results of the Generalized Linear Mixed Models (GLMMs) testing for variations in lay date (15-day periods), clutch size, nesting success and productivity. "Year" was included as a random effect in all models. Initial models included region (coastal vs. interior-mountain), weather variables (PCs) and lay date (for clutch size, nesting success and productivity), as well as interactions between region and lay date. Stepwise backward model selection was performed based on AIC values. We present the results of final models.

Dependent variables	Explanatory variables	DF	LRT	P
Lay date	PC2	1	15.00	0.0001
	PC4	1	7.28	0.007
	Region	1	16.14	<0.0001
Clutch size	PC2	1	4.23	0.039
	Region×Lay date	1	7.45	0.006
Nesting success	Lay Date	1	17.59	<0.0001
Productivity	PC2	1	5.08	0.024
	Region×Lay Date	1	2.84	0.092

Breeding parameters

Clutch size averaged 3.58 ± 0.64 eggs (range: 2–5; n = 183 nests). Clutch size varied with rainfall (PC2, Table 3), with larger clutches being associated with rainier conditions (slope = 0.08 ± 0.04), particularly in autumn, winter and spring. Clutch size also

varied significantly with the interaction between lay date and region (Table 3): clutch size declined markedly as the season progressed, but this decline was more pronounced in the interior-mountain (slope: -0.25 ± 0.07) than in the coastal region (-0.05 ± 0.03) (Figure 3a). Bootstrapping analyses using 1000 random samplings of 30 nests from each region indicated very little overlap between the estimates of slopes for each region (95% confidence intervals of -0.17 to 0.05 for coastal nests and of -0.39 to -0.15 for interior mountain nests). When removing the interaction region x lay date from the model, clutch sizes were not significantly different between regions (LRT = 0.37, P = 0.54).

In total, 31% of nests (n = 223) monitored during the study period failed to produce fledglings. Nesting success declined significantly with lay date (Table 3; slope: -0.40 ± 0.10), and this decline was similar between regions (non-significant region × lay date interaction; Figure 3b). Once controlling for lay date, no significant differences in nesting success were found between regions, nor any relationships between nesting success and weather variables (Table 3).

Productivity among monitored nests averaged 1.66 ± 1.30 fledglings (range 0 - 4 fledglings, n = 222 nests). Productivity was positively associated with weather PC2 (Table 3; slope = 0.12 ± 0.05), indicating that productivity increased in rainier conditions. Productivity also declined as lay date increased (Table 3; Figure 3c). As for clutch size, there was an indication that this seasonal decline in productivity differed between study regions (marginally significant region × lay date interaction; Table 3; P = 0.09), with a steeper decline in the interior-mountain region (slope = - 0.40 ± 0.12) than in the coastal region (slope = -0.20 ± 0.05; Figure 3c). Bootstrapping analyses using 1000 random samplings of 50 nests from each region showed that there was some overlap between the estimates of the calculated slopes for each region (Mean, SD, and 95% confidence intervals: -0.20 ± 0.05, -0.30 to -0.08 for coastal nests; and -0.35 ± 0.14, -0.59 to -0.12 for interior-mountain nests). When removing the interaction region x lay date from the model, there was no significant difference in productivity between regions (LRT = 0.002, P = 0.98).

Discussion

This study revealed an extended breeding period for the Black Harrier and profound consequences of the timing of breeding on breeding performance. Moreover, it is one of the few studies that document a seasonal decline in breeding performance in a southern African species (Simmons 2000, Martin et al. 2014, Murgatroyd et al. 2016) and one of the few studies overall to highlight a regional difference in the strength of this seasonal decline. Seasonal declines in breeding performance appeared more pronounced in interior-mountain regions, characterized by more seasonally variable weather conditions, than in coastal regions. These observations may explain why coastal regions are seemingly more used by this scarce endemic species and have conservation implications, which we develop below.

Seasonal declines in breeding performance

Most strikingly, we found that seasonal declines varied among regions for clutch size and also (less markedly) for productivity. The seasonal decline in these parameters was progressive and moderate in coastal regions but much more abrupt in interior-mountain regions. Thus, clutch size and productivity were overall higher in interior-mountain than in coastal regions early in the season (until September), but differences were not found or values were higher in coastal regions for nests initiated from October onwards (Figure 3ac). Interestingly, we did not find a significant difference between regions for nesting success, suggesting that regional differences in declines in productivity may simply result from differences in clutch size patterns. Additionally, this suggests that differences between regions are more influential early in the breeding cycle. Ultimately, neither clutch size nor productivity were, on average, significantly different between regions, indicating that differences between regions early and late in the season balanced each other out.

Seasonal declines in breeding performance can be explained by differences in the quality of individuals breeding early or late and/or by a worsening of environmental conditions as the breeding season progresses (Verhulst et al. 1995, Verhulst and Nilsson 2008). The overall seasonal decline observed in the Black Harrier population may reflect a difference in the quality of individuals breeding earlier vs. later in the season (with e.g. older and more experienced birds breeding earlier in the season). However, the observed regional differences in the seasonal declines are unlikely to be explained by differences in individual quality alone, particularly for a mobile species like the Black Harrier (evidence from satellite tagged birds indicate that the same individual can breed in both the coastal and the interior-mountain regions in different years, Garcia-Heras et al., unpublished data). Our results thus indicate that changes in environmental conditions likely play an important role in explaining seasonal changes in breeding performance, and furthermore that this degradation in environmental condition is stronger in interior-mountain than in coastal regions.

Temperature was overall higher in coastal regions until August, when clutch sizes were smaller there, but the opposite pattern was found from October onwards, when clutch sizes were greater in coastal regions. Temperature variation could thus be an indicator of the temporal variation in quality of environmental conditions among regions. However, temperature (PC1) did not significantly influence clutch size (or any other breeding performance parameter), so differences are likely to be related to other factors, such as food availability or habitat quality. Black Harriers mostly feed on small mammals (ca. 65% of the diet), particularly on Four-Striped Mouse (*Rhabdomys pumilio*) and African Vlei Rats (*Otomys* sp.) (Jenkins et al. 2013, Garcia-Heras et al. unpublished data), so the smaller clutch size in interior-mountain areas for pairs starting to lay late in the season may reflect lower small mammal availability there at that time. Population dynamics and breeding output of the striped mouse are known to vary strongly with rainfall (see Taylor and Green 1976, Meynard et al. 2012, Rymer et

al. 2013). This, together with our results (relationship between PC2 and both clutch size and productivity), suggests that greater rainfall during autumn and winter could positively influence the abundance of small mammals such as Four-Striped Mouse, which may in turn influence breeding performance in Black Harriers, as found for other species (Korpimäki 1992, Salamolard et al. 2000, Redpath et al. 2002b). Future studies should investigate the relationship between Black Harrier's breeding and food availability, and how this varies in space and time.

Factors affecting lay date variations

Black Harriers showed a remarkably extended breeding period, with the onset of laying spread over 8 months (mid-May to mid-December). A wide spread in timing of breeding has been reported in other raptors from the Southern Hemisphere [e.g., 8 months for the Black Sparrowhawk (*Accipiter melanoleucus*), Martin et al. 2014], including other harrier species, such as the African Marsh Harrier *Circus ranivorus* (9 months, Simmons 2000, Simmons et al. 2005), the Cinereous Harrier (*Circus cinereus*) (7 months, del Hoyo et al. 1994) or the Spotted Harrier (*Circus assimilis*) (5 months, del Hoyo et al. 1994). This contrasts to what is usually observed in harrier species breeding in the Palearctic, for which the timing of breeding rarely exceeds 3 months [e.g., Pallid Harrier (*Circus macrourus*), Montagu's Harrier (*Circus pygargus*), Hen/Northern Harrier (*Circus cyaneus/hudsonius*), (Schipper 1979, Simmons et al. 1986, Arroyo et al. 1998, Simmons 2000, Amar et al. 2005, Terraube et al. 2009). These large scale differences in the extent of the timing of breeding are likely related to climate, the Northern Hemisphere being in general characterized by a more pronounced seasonality in rainfall and temperature regimes (Garcia and Arroyo 2001, Redpath et al. 2002a) than the Southern Hemisphere, limiting in time the conditions that are suitable for successful breeding, and also suggest that conditions for breeding are suitable over a longer time for Black Harriers, as for other African raptors.

Nevertheless, we found a clear seasonal peak, with most laying (ca. 50% of clutches) occurring between mid-August and the end of September. This, together with the strong seasonal decline in breeding performance observed, indicates that optimal timing for breeding is limited for this species, despite the overall large extended breeding period. This peak coincides with a sharp drop in rainfall levels and an increase in temperature (Figure 2), suggesting that high rainfall levels may impair laying. However, models showed that, overall, laying occurred earlier under more rainy conditions (negative relationships with PC2 and PC4), and particularly if rainfall was greater in autumn-spring periods and when summers preceding laying were wetter. The latter may reflect the east-west rainfall conditions in South Africa, as laying is earlier in eastern locations, where rainfall levels are overall higher particularly in winter months. This may also be associated with food availability: wetter summers may contribute to a greater primary productivity and subsequent rains just before (April-May) and during the time of breeding may lead to greater food abundance during Black Harrier's whole breeding cycle (see above).

The strong associations between timing of breeding, temperature and rainfall also indicate that climate change may further influence shifts in breeding phenology of southern African birds (Simmons et al. 2004, Cunningham et al. 2013), including raptors (Martin et al. 2014), most notably in the southern and western regions where a warming trend has been detected during the past 50 years, and rainfall is predicted to decline (Hockey et al. 2011, Cunningham et al. 2015). Our results highlight that weather conditions, and most notably rainfall regime, play an important role in determining the timing of breeding of Black Harriers, and likely shapes the regional differences encountered in lay date. However, the timing of breeding may also depend on the seasonal fluctuation of other variables responsive to environmental cues that change with weather conditions, but that were not tested here. These more likely would be either variations in food supply (Perrins 1970, Verhulst 2008) or arrival dates from the non-breeding grounds, as suggested for other raptor species (Newton 1998, Ketterson et al. 2015).

We also found differences in lay date between regions: Black Harriers breeding in coastal regions started laying on average about 15 days earlier, and clutches occurred over a more extended period than those breeding in interior-mountain (Figure 2c). These patterns suggest that optimal conditions for breeding might be achieved at different times in different geographical zones, but also indicate that suitable conditions for breeding may last longer in coastal than in interior-mountain regions.

Conservation implications

Black Harriers have been described as Fynbos specialists (Curtis et al. 2004), due to a greater number of breeding events in this vegetation type along the coast and a higher productivity in coastal regions compared with interior-mountain regions. However, our results, based on a larger sample size over a longer study period, differ from those of that study: while the number of monitored breeding events was indeed larger along the coast, we found that overall productivity was equal in interior-mountain and coastal regions. This was mainly explained by the regional differences in seasonal decline observed in breeding parameters, with clutch size and productivity being greater in interior-mountain regions early in the season, but the subsequent decline being more abrupt. Environmental conditions in interior-mountain regions might be more suitable than in coastal regions, but only for a limited period of about 1.5 months. Before, they seem to be unsuitable to allow breeding, and afterwards, they quickly deteriorate inducing a reduced breeding performance later in the season. Weather conditions at the beginning of the harrier breeding season (until October) also appeared much more variable among sites and years in interior-mountain regions (greater coefficient of variation; Figure 2ab). This implies that, even if average conditions are better at that time, in certain years or regions, conditions may not be suitable for breeding. In coastal regions, environmental conditions remain more stable throughout the harrier breeding season, which allows productive breeding to occur over a longer period of time (4 months). Thus, the more

stable weather in coastal regions within and among years may mean that it is overall a safer choice for Black Harriers to breed there than in interior-mountain regions. This may explain why breeding Black Harriers were more commonly found at the coast (i.e. 3 times more breeding events along the coast than in interior-mountain regions; Curtis et al. 2004), although we recognise that these figures do not control for search effort.

Recent changes in climate conditions within Africa during the last decades (Hockey et al. 2011, Kruger and Sekele 2012, Cunningham et al. 2015) may exacerbate the differences among regions and present a challenge for species like the Black Harrier. Indeed, a shift in rainfall and temperature patterns has occurred in South Africa and most notably in the south-west of the country, where most harriers breed: temperatures are getting warmer with less rain falling inland (the same pattern is expected in the western part of the Northern Cape Province, where many "interior-mountain" Black Harrier nests occur), while the opposite trend is expected along the coast (Cunningham et al. 2015). In addition, anthropogenic modifications in land use during the last century in South Africa such as the conversion of the Fynbos vegetation into agriculture or urbanization, might also negatively affect the Black Harrier population (Curtis et al. 2004). Only two records have mentioned Black Harriers breeding in cultivated areas (Steyn 1982, Chadwick 1997), which suggests that the species might not be capable of adapting to breed in non-natural habitats (Curtis et al. 2004, Jenkins et al. 2013), contrary to Palearctic harriers (Arroyo et al. 2002, Millon et al. 2002) and other south African raptors (Murgatroyd et al. 2016). Further land use change may "force" even more Black Harriers to breed along the coast, in Fynbos vegetation, where environmental conditions remain more stable within and among years in comparison to other available sites (e.g., Karoo biome in interior-mountain regions) that may become drier and colder. This highlights the importance that the coastal Fynbos may have for the stability and sustainability of the Black Harrier population in the future. Conservation measures have already prioritized the protection of Fynbos vegetation, through the creation of national parks and private reserves, and should continue in order to conserve the species in the long term.

Conclusions

This study provides unique evidence for spatial variation in the strength of seasonal declines in breeding performance. This main finding has broad implications for population biology and conservation. Environmental heterogeneity needs to be accounted for when considering overall population viability, and our findings suggest that where environmental conditions are less variable and more predictable, the timing of breeding may have less importance for the production of young. Relative differences in individual quality between early and late breeders, which can explain the breeding seasonal declines (Verhulst and Nilsson 2008) would also potentially matter less. These areas may therefore constitute population sources and play a key role for overall population viability. In areas where seasonal declines are more pronounced, a mistiming of breed-

ing will reduce offspring production and populations will be less buffered from rapid, unpredictable environmental changes. Studying spatial variations in the strength of seasonal productivity declines, as we did with the scarce and endemic Black Harrier, could help identify important breeding areas for long-term population viability.

Acknowledgements

This study was funded by the NRF (National Research Foundation, South Africa; Grant no. 90582 to R.E.Simmons), by the DST-NRF Center of Excellence at the Percy FitzPatrick Institute, University of Cape Town, by CSIC (Consejo Superior de Investigaciones Cientificas- PIE 201330E106) and by private landowners and organizations. Particular thanks for economic support are due to BirdLife South Africa, Inkwazi and Wits Bird Club, "Golden Fleece Merino", URC (University Research Council), Jakkalsfontein Private Nature Reserve, TOSS (Two Oceans Slope Soarers), Natural Research UK, Hawk Mountain (USA), the Peregrine Fund, Sven Carlsson-Smith, Nial Perrins, Chris Cory, Gisela Ortner and James Smith. We are also grateful to Graham Cumming to help M-S Garcia-Heras with financial support in 2014. We also thank SANParks and Cape Nature to access to study sites, and the South African Weather Services for the acquisition of weather data. We also thank Andrew Jenkins, Odette Curtis, Anne Williams, Bettie Bester, Binks Mackenzie, Txuso Garcia, Juan Jose Luque-Larena and all the students from the Percy FitzPatrick Institute of African Ornithology who helped with fieldwork and data collection, and an anonymous reviewer for comments on the manuscript.

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Nature Conservation 15: 47–63 (2016)
doi: 10.3897/natureconservation.15.10005
http://natureconservation.pensoft.net

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A review of global trends in CITES live wildlife confiscations

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Academic editor: *K. Henle* | Received 25 July 2016 | Accepted 9 September 2016 | Published 22 September 2016

http://zoobank.org/36EE2B57-7594-4A4F-9FD5-AED3AC5FEBD7

Citation: D'Cruze N, Macdonald DW (2016) A review of global trends in CITES live wildlife confiscations. Nature Conservation 15: 47–63. doi: 10.3897/natureconservation.15.10005

Abstract

We assessed the global scope and scale of confiscated live wild vertebrates using information from the annual Convention on International Trade in Endangered Species of Flora and Fauna (CITES) reports. These reports documented a total of 64,143 individual animals (from 359 species), confiscated by 54 countries party to CITES, between 2010 and 2014. Reptiles represented 95% of individuals seized and posed a particular management challenge during this time. From a conservation perspective, 19% of all individuals reported as seized are currently considered as "Threatened" according to the IUCN Red List and 1% are listed on CITES Appendix I. During this time period, relevant national enforcement agencies have had to effectively detect and quickly deal with illegal live shipments involving a diverse array of vertebrate species with varying psychological attributes, physiological attributes and conservation value. However, we raise pre-existing concerns that CITES records are incomplete, with no data on live seizures provided by 70% of countries party to CITES. Data on the disposal of confiscated live animals is also lacking as providing them is not currently a formal CITES requirement. This lack of information impedes the proper allocation of available resources and prevents the effective monitoring and evaluation of management outcomes. Therefore, we recommend that the management authorities improve reporting compliance, and we encourage the CITES trade database (and other associate national, regional and global databases) to include information on the disposal of all live seizures.

Keywords

Animal Welfare, Conservation, Enforcement, Illegal Wildlife Trade, Seizures

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Introduction

Poaching of threatened species to supply the illicit global wildlife trade (IWT) is estimated to be worth between $8 and $10 billion per year (Lawson and Vines 2014). As the global human population increases, and as the economies of developing countries grow rapidly, demand for wildlife and hence the IWT flourishes (Baker et al. 2013; Zhou et al. 2015a). International travel and transport of goods are now commonplace, and they facilitate movement of live wild animals and products derived from them (e.g. ivory, shells and scales) through illegal and irregular (i.e. under the guise of legal) pathways (Dutton et al. 2013; Zhou et al. 2014a). New media platforms are also having a strong influence promoting IWT, with increased online advertisement and access to information further stimulating demand (Bush et al. 2014; Moorhouse et al. 2016).

IWT is a substantial threat to wild populations through biodiversity loss, species loss, the introduction of invasive species, irresponsible wild release of confiscated animals and disease (Bush et al. 2014; Zhou et al. 2014a). IWT also has negative impacts on animal welfare during illegal capture, improper captive breeding, transport, sale and subsequent use (Baker et al. 2013). IWT embraces wider societal issues, such as a zoonotic risk to human health (Macdonald and Laurenson 2006) and disease risk to livestock (Gómez and Aguirre 2008). Increased understanding of the links with other forms of organized criminal activity is also highlighting how IWT could threaten the stability and security of some societies (Lawson and Vines 2014).

In recognition of these threats, improved regulation of wildlife trade and associated enforcement action has led to an increase in the number of illegal and irregular wildlife shipments intercepted by government authorities (CITES 2010). Yet efforts to try and bypass enforcement agencies continue, with criminal actors employing tactics involving both wild caught and captive bred wild animals that include: (1) concealment of contraband live wild animals and their derivatives within shipments; (2) false declaration of numbers within shipments; (3) false declaration of wild-caught specimens as 'captive bred'; and (4) false declaration of the source as "pre-convention" or "seized" (Kasterine et al. 2012; Lyons and Natusch 2011; Williams et al. 2015; Zhou et al. 2014b; Zhou et al. 2015b). With regards to live wild animals, these tactics are used to meet consumer demand for working animals, pets, companionship, entertainment, and status symbols (Baker et al. 2013).

In order to effectively detect, monitor and address IWT, national authorities require detailed centralized information (such as the source, date, location, species, quantity, intended destination and purpose) regarding seized shipments (UNODC 2012). Currently, a small number of countries are reported to maintain national databases that record such information (UNODC 2012). In addition, this type of data is also recorded in a number of regional [e.g. the European Union's Trade in Wildlife Information Exchange (EUTWIX; www.eutwix.org)] and international databases [e.g. The World Customs Organization's (WCO) Customs Enforcement Network (CEN);

and the World Wildlife Seizure database (World Wise), a developing initiative led by the United Nations Office on Drugs and Crime (UNODC)]. However, of the existing IWT databases, only seizure information from the Convention on International Trade in Endangered Species of Flora and Fauna (CITES) trade database is currently made fully available to the public for subsequent interpretation and analysis.

CITES is an international agreement that operates as a licensing system through which imports and exports of listed species must be authorized by Parties (UNEP-WCMC 2014). There are currently 182 Parties to CITES, who are under obligation to enact this international framework within their own national legislative system (CITES 2014) with varying degrees of effectiveness (D'Cruze and Macdonald 2015). Countries that are party to CITES are required to submit annual reports of international trade, including seizures of listed species, which are made available on the United Nations Environment Program World Conservation Monitoring Centre (UNEP-WCMC) CITES trade database (http://trade.cites.org/). Poor reporting compliance, for example non-standardized, insufficient and absent data have been identified as an on-going issue of concern associated with the CITES trade database (UNEP CITES 2014). However, these data have still proved revealing in previous studies of trade in wild animals (e.g. Bush et al. 2014; Harrington 2015; D'Cruze and Macdonald 2015).

Herein, we review the annual CITES reports between 2010–2014 to examine the current extent of live wild vertebrate trade seizures with respect to the five classes of vertebrates principally involved (amphibians, birds, fish, mammals and reptiles). Specifically, we asked: (1) what taxonomic groups are being seized most frequently; (2) how many individual animals are involved; (3) what are their conservation and legislative status; and (4) where are these seizures most frequently taking place. We intend the information gathered to guide existing efforts to both conserve remaining wild populations and to safeguard the welfare of individual confiscated wild animals.

Methods

We queried the CITES trade database for all live wild animal seizures for the years 2010–2014 inclusive. Trade data on CITES live animal seizures were supplied in the form of a Comparative Tabulation Table (data collated 01 Jan 2016 — see UNEP-WCMC (2014) for detailed explanation on data) (Suppl. material 1). This output was chosen deliberately because in addition to export and import data, it also provides information on the source and purpose of wildlife trade transactions (UNEP-WCMC 2014). Information regarding the conservation status and the regional distribution of wild populations for the species involved in wildlife seizures was gathered from the IUCN Red List of Threatened species (IUCN 2016).

We specifically requested data only using the "live" trade term and the CITES source code "I" which refers to illegal trade seizure records as outlined in Notifica-

tion 2002/022 (UNEP-WCMC 2014). We focussed our analyses on the following five taxonomic classes of vertebrate provided in the database: Actinopterygii ('bony' fish), Aves (birds), Amphibia (amphibians), Mammalia (mammals) and Reptilia (reptiles). We chose to exclude records of wildlife derivatives from our study as a lack of information on volumes seized is already known to hinder such analyses (UNEP-WCMC 2014; D'Cruze and Macdonald 2015). Seizure data were available in the CITES trade database from 54 different countries, with 30% of the countries party to CITES, in Asia (n = 10; 6%), Africa (n = 5; 3%); Australasia (n = 2; 1%), Europe (n = 25; 14%), North America (n = 2; 1%), and South America (n = 6; 3%) (Suppl. material 1).

All purpose codes outlined in Notification 2002/022 that are available to CITES Parties were used in the analysis including: captive breeding (CITES purpose code B), circus (Q), commercial (T), educational (E), personal (P), scientific (S), and zoo (Z) use (UNEP-WCMC 2014). All Appendix classifications used by CITES were also included in the analysis: Appendix I (trade permitted only under exceptional circumstances), Appendix II (non-detriment finding and export permit are required for trade), Appendix III (one Party has asked other CITES Parties for assistance in controlling trade), or non-CITES (CITES 1973).

Following the completion of this review we described tabulated categorical data using descriptive statistics, including percentages, pie charts and bar charts. We used a contingency table to test the hypothesis that the proportions of endangerment classes were similar among taxonomic groups. We used general linear models with mean separation tests using SPSS statistical software (version 22.0, IBM SPSS Statistics, New York, USA) to test for trends in numbers with year and for differences between taxa. We also tested the hypothesis that temporal trends among taxa were similar by including the interaction term between year and group. For all analyses we used the declared state of origin over exporting country if data were available and were different.

Results

During the period 2010–2014, a total of 785 live vertebrate seizure records, comprised of both illegal and irregular shipments, were officially received by CITES according to the comparative tabulation report (Suppl. material 1). These seizures involved 64,143 individual animals belonging to 359 different species. A total of 24 records could not be identified down to species level and were recorded as "spp." (e.g. Falconidae spp.). However, the remaining 335 species were all identified to species level in the CITES reports (Suppl. material 1). Information regarding the regional distribution of wild populations was available for 292 of the species officially reported as seizures in the CITES trade database (IUCN 2016). A total of 100 (34%) of these 292 species are known to have extant wild populations in Asia; 95 species (33%) are present in Africa; 94 species (32%) are present in South America; 75 species (26%) are present in North America; 43 species (15%) are present in Australasia; and 31 species (11%) are present in Europe (Suppl. material 1).

Most targeted taxa

According to CITES trade database, reptiles were the most species-rich taxonomic class reported as live seizures, followed by birds, mammals, fish and amphibians (Fig. 1). Psittaciformes (parrots etc.) were the most species-rich taxonomic order recorded as live seizures, followed by Sauria (lizards etc.), Testudines (turtles etc.), Serpentes (snakes etc.), Primata, Carnivora, and Falconiformes (falcons etc.) (Fig. 1). With regards to the number of individual live animals, reptiles were the class most commonly reported as live seizures, followed by fish, birds, mammals and amphibians (Fig. 2).

Within reptiles, the False Map Turtle [*Graptemys pseudogeographica* (23,201 individuals; 8 separate seizures)] was the species most commonly reported among live seizures (Fig. 3; Suppl. material 1). The Ball Python [*Python regius* (12,172 individuals; 23 separate sei-

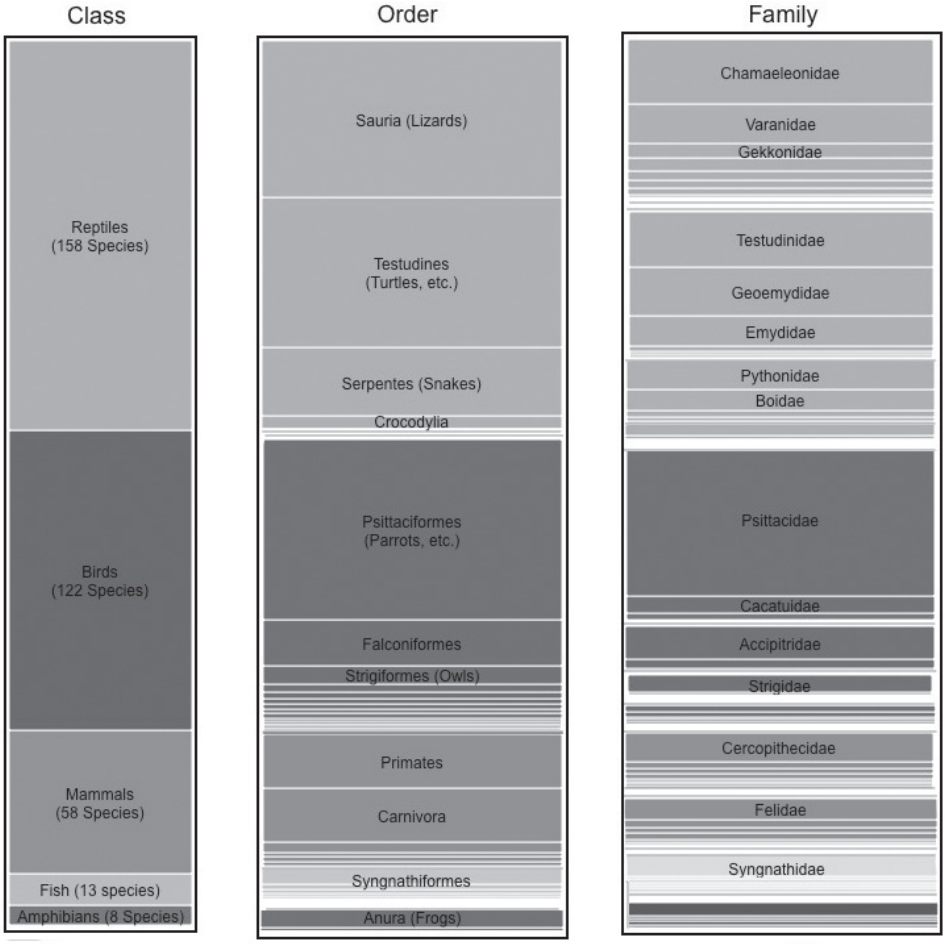

Figure 1. Proportion of species reported as live vertebrate seizures, according to different taxonomic groups, between 2010–2014. Data source: CITES trade database.

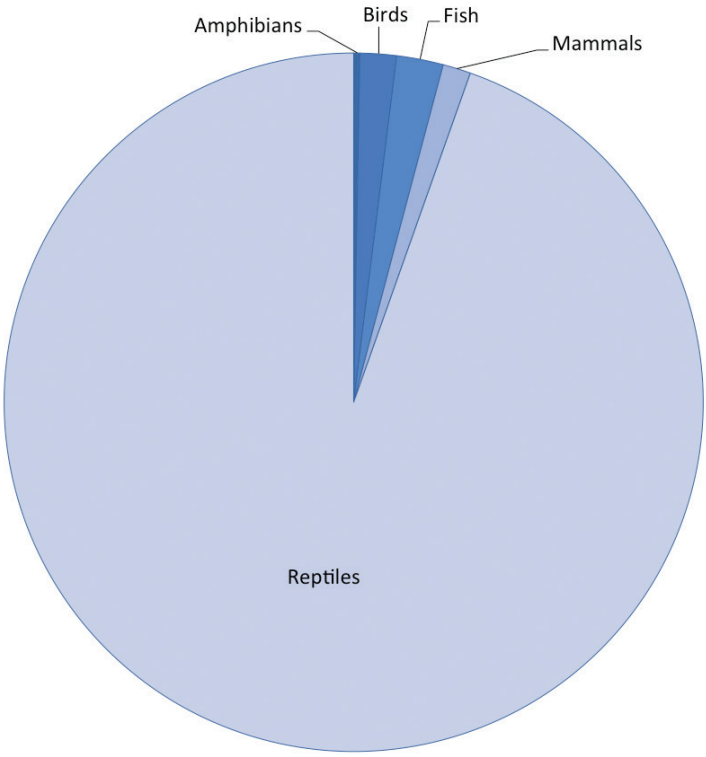

Figure 2. Total numbers and proportions of individual live wild vertebrates seized, according to taxonomic group, between 2010-2014. Data Source: CITES trade database.

zures)] was the second most commonly reported species followed by the Russian Tortoise [*Testudo horsfieldii* (7,115 individuals; 7 separate seizures)], an unknown Map Turtle hybrid [*Graptemys* spp. (4,500 individuals; 2 separate seizures)] and the Ouachita Map Turtle [*Graptemys ouachitensis* (2,630 individuals; 3 separate seizures)] (Fig. 3; Suppl. material 1).

The only non-reptile species among the ten most commonly reported species was the Crab-Eating Macaque [*Macaca fasicularis* (482 individuals; three seizure records)] (Fig. 3; Suppl. material 1). The Common Seahorse [*Hippocampus kuda* (465 individuals; 5 seizure records)] the Long-Snout Seahorse [*Hippocampus reidi* (267 individuals; 7 seizure records)] and the European Eel [*Anguilla anguilla* (235 individuals; 1 seizure record)] were the only other non-reptile species among the 20 most commonly reported species according to CITES records (Suppl. material 1).

Taxonomic trends

A peak of 21,425 animals was seized in 2011 and the lowest number of live animals seized (n = 6,049) was reported from 2014 (Suppl. material 1). There was no evidence

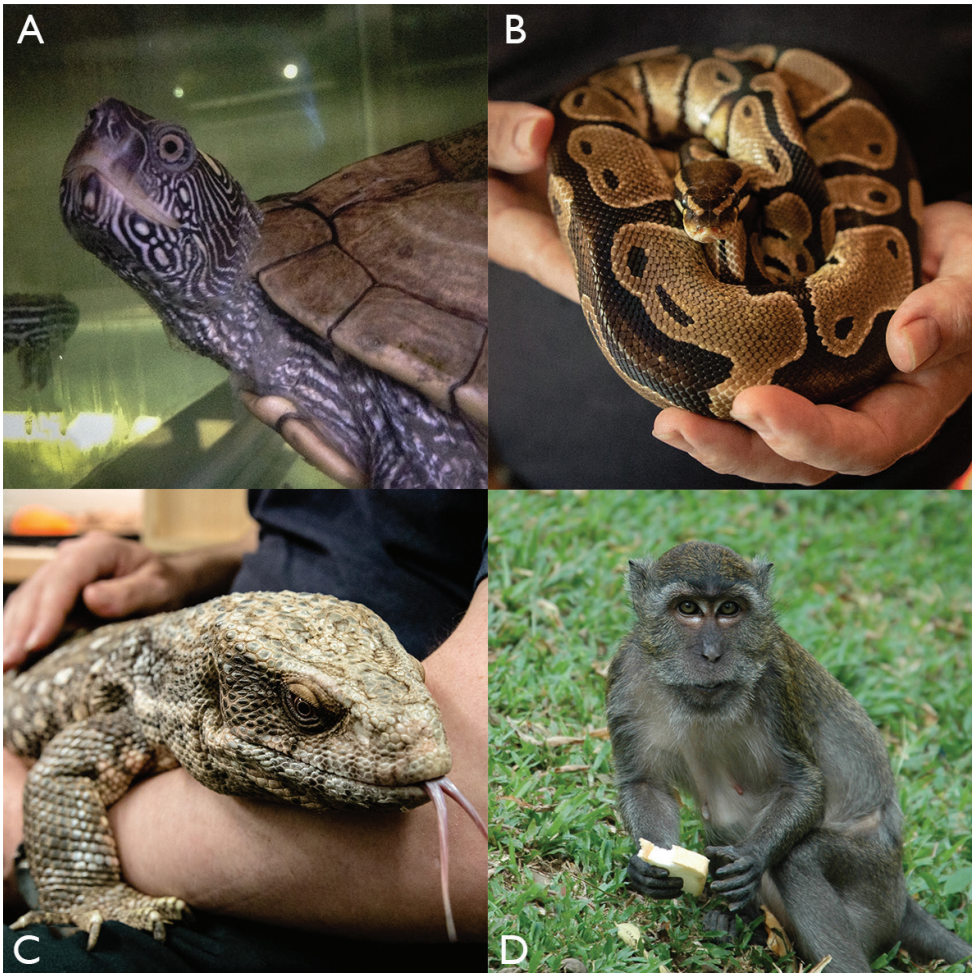

Figure 3. Species commonly reported as live wild vertebrate seizures by CITES between 2010–2014. **A** False Map Turtle (23,201 individuals seized) **B** Ball Python (12,172 individuals seized) **C** Bosc's Monitor (1,705 individuals seized) **D** Crab-Eating Macaque (482 individuals seized). Photo credit **A** Maxine Bradley **B, C** Neil D'Cruze **D** Jan Schmidt-Burbach (credited permission to use these images has been provided by owners).

for an overall trend in numbers of live individuals seized with year ($F_{1,15}$ = 0.24, P = > 0.05) or that this differed among taxonomic groups ($F_{4,15}$ = 0.16, P = 0.96). There was strong evidence that the number of live individuals seized differed among taxonomic groups (F = 28.22, P < 0.001) – reptiles are more numerous than the other groups (Tukey means separation procedure).

With regards to trade purpose, the vast majority of seized live animals (*n* = 60,850; 95%) were intended for commercial use according to CITES records (Suppl. material 1). Law enforcement (e.g. judicial and or forensic) use (*n* = 1072; 2%) was the second most common intended trade purpose reported, followed by breeding in captivity (*n*

= 354; 1%), personal use (*n* = 338; 1%), zoological use (*n* = 185; <1%), medical use (*n* = 137; <1%), reintroduction into the wild (*n* = 111; <1%), scientific use (*n* = 30; <1%), educational use (*n* = 13; <1%) and circus use (*n* = 6; <1%) (Suppl. material 1). No purpose data were provided for 1,056 (2%) of the live individual animals seized, recorded by CITES during the period 2010–2014 (Suppl. material 1).

Conservation and legislative status

In terms of conservation status, there was strong evidence that the proportions of different IUCN Red List categories differed among taxa (X^2 = 23,304, P < 0.001, DF = 36). Overall the majority of individual animals seized belong to species currently considered as "Least Concern" on the IUCN Red List of Threatened species (*n* = 44,371; 69%) (Fig. 4). In total, 11,902 of all individuals seized (19%) are currently considered to have "Threatened" status according to the IUCN Red List (i.e. they are listed as either "Critically Endangered", "Endangered" or "Vulnerable" (Fig. 4).

With regards to their CITES status, overall the largest proportion of individuals belong to species that are currently listed on CITES Appendix III (*n* = 30,602; 48% of all individuals recorded in seizures) (Fig. 5). A further 29,202 (46%) of individuals belong to species currently listed on CITES Appendix II. A total of 852 (1%) are currently listed on CITES Appendix I, and a further 10 individuals (<1%) are not currently listed on any of the CITES Appendices (Fig. 5).

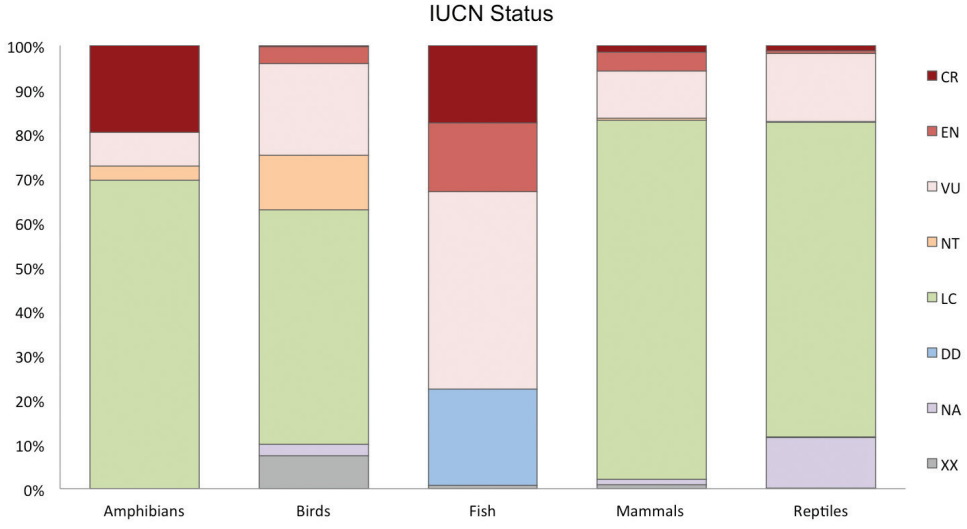

Figure 4. Proportion of individuals reported as live wild vertebrate seizures, according to IUCN Red List status, between 2010–2014. (IUCN Red List assessment categories: CR, critically endangered; EN, endangered; VU, vulnerable; NT, near threatened; LC, least concern; DD, data deficient; NA, not yet assessed; XX, not listed). Data source: CITES trade database.

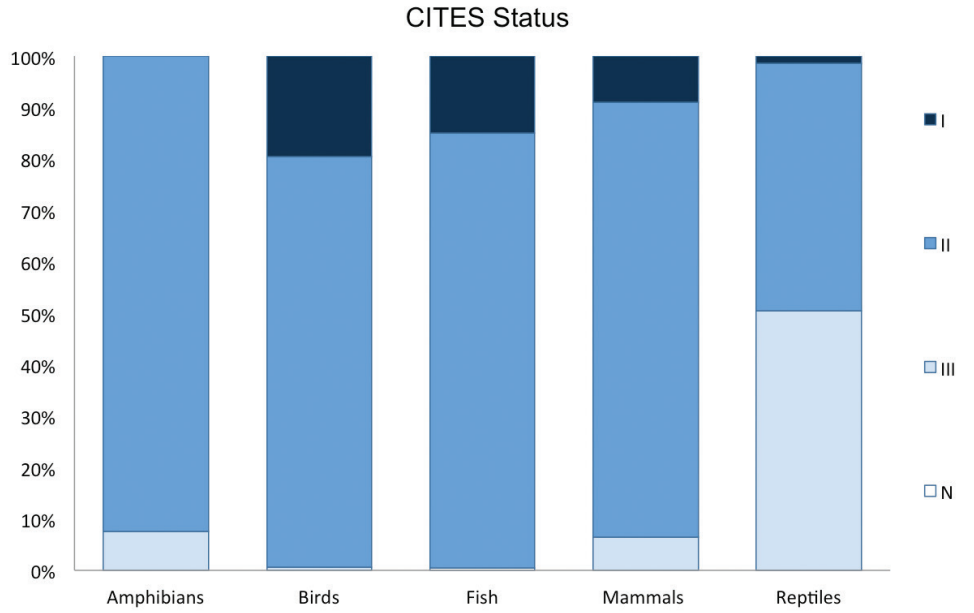

Figure 5. Proportion of individuals reported as live wild vertebrate seizures, according to CITES status, between 2010–2014. (CITES appendix listings: I, CITES Appendix I; II, CITES Appendix II; III, CITES Appendix III; N, not listed). Data source: CITES trade database.

Site of seizure

In total, 36,746 individual live animals were seized by relevant national enforcement authorities upon export and a further 27,397 individuals were seized during import (Suppl. material 1). The number of live wild vertebrates seized during import [amphibians (n = 146 individuals), birds (n = 678), fish (n = 1,374) and mammals (n = 710)] was higher than those seized upon export for all taxonomic groups except reptiles. In contrast, 27,397 individual reptiles were seized upon import whereas 36,177 individual reptiles were seized upon export. With regards to the 11,902 seized live wild animals that are currently considered as Threatened according the IUCN Red List, in total 7,036 individuals (59%) were seized upon import [amphibians (n = 23 individuals), birds (n = 117), fish (n = 1,073), mammals (n = 75) and reptiles (n = 5,748).

Seizure data regarding live wild vertebrates confiscated between 2010–2014 were available in the CITES trade database from 54 different countries which represent 30% of all countries party to CITES. The majority of individuals were seized in the USA (90%), followed by Uzbekistan (5%), Malaysia (1%), Portugal (1%) and the United Arab Emirates (<1%). A total of 2,072 animals were reported as seized by all of the remaining 49 countries combined (Fig. 6).

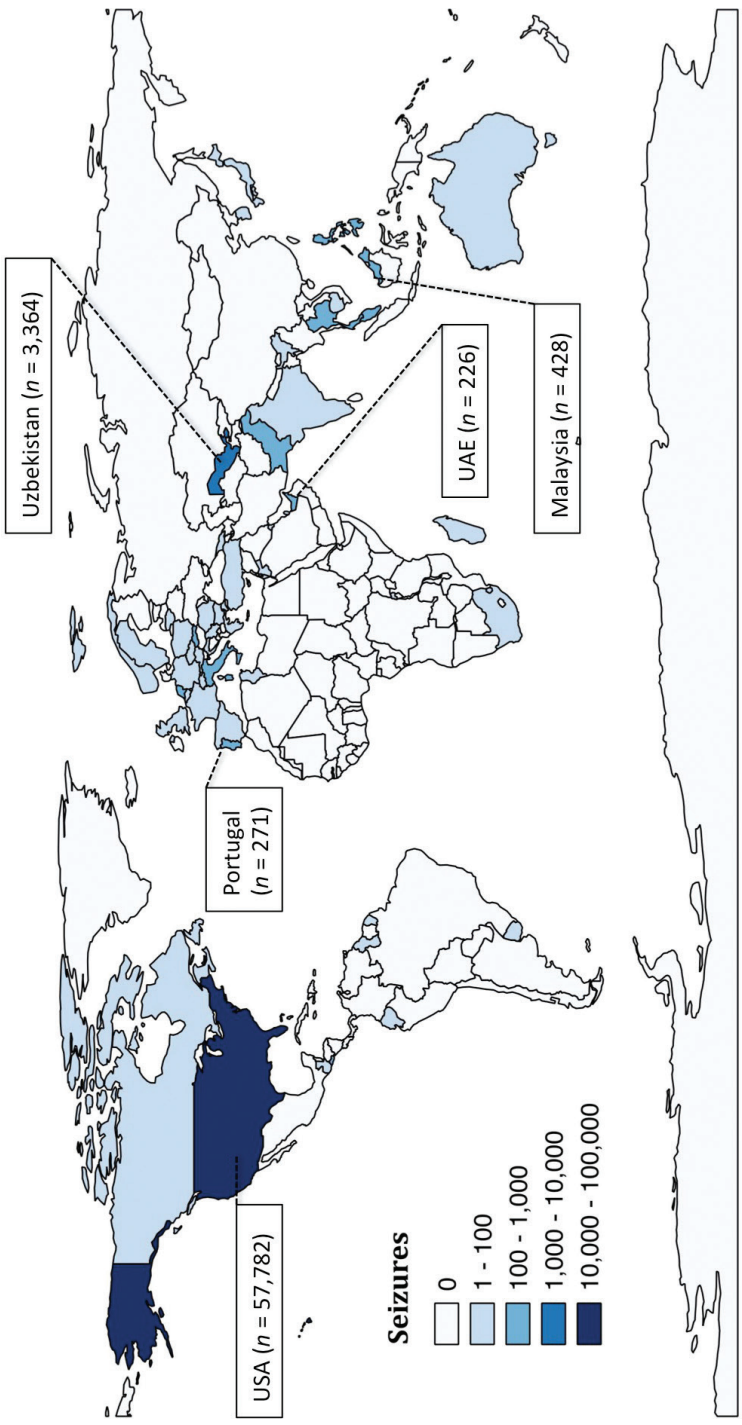

Figure 6. The number of individual live wild vertebrates (across all taxonomic groups) reported as live seizures during import and export, according to confiscating country, between 2010–2014. Data Source: CITES trade database.

Discussion

We reviewed the annual CITES reports to assess the scope and scale of live wild vertebrate trade seizures made between 2010–2014. Overall, our findings are comparable to other studies, for example Rosen and Smith (2010) reported that 191,936 live wild animals were seized between 1996 and 2008 according to TRAFFIC records. Similarly, our study demonstrates that over the past five years, relevant national enforcement agencies in more than 50 different countries have had to effectively detect and quickly deal with illegal and irregular live shipments involving at least 60,143 live individual animals from 359 different wild vertebrate species with varying psychological attributes, physiological attributes and conservation value (e.g. Nijman et al. 2010; TRAFFIC 2008; TRAFFIC 2013).

Following each of these seizures, the relevant CITES Management authorities were expected to have dealt with these confiscated live wild vertebrates in a humane manner that maximized their conservation value and that did not promote further unsustainable illegal wildlife trade (CITES 2010; IUCN 2013). Allowable options available to them fall into three principal categories: (1) maintenance of the individuals in captivity; (2) returning the individuals in question to some form of life in the wild; and (3) euthanasia (CITES 2010; IUCN 2013), dependent on other legal, economic and social factors such as cultural attitudes (Chris Newman pers. comms.). The impact of their decisions in this regard would have important ramifications for both animal welfare and the conservation of wild populations.

Conservation Implications

Overall, the largest proportion of live wild vertebrates seized between 2010–2014 involved species that are currently considered to be of relatively low risk of extinction. Specifically, 69% of all individuals reported are currently considered as "Least Concern" according to the IUCN Red List and 48% are listed on CITES Appendix III. As such, the majority of individuals seized during this time do not appear to be of immediate conservation concern. However, it is important to note that IWT is recognised to be a big and burgeoning business (Baker et al. 2013). Given that it has also been identified as one of the main challenges to conservation (Lawson and Vines 2014), special attention should be paid to ensure that on-going unregulated illegal trade in these species does not become a threat to species survival in the future.

A far smaller proportion of live wild vertebrates seized between 2010–2014 involved species that are currently considered to be of relatively high risk of extinction. Specifically, only 19% of all individuals reported as seized are currently considered as "Threatened" according to the IUCN Red List and only 1% are listed on CITES Appendix I. However, despite the relatively small number of individuals involved, the impact of this IWT on remaining wild populations and the conservation value of these "Threatened" wild animals should not be underestimated. For example, the poaching

of even a small number of "Critically Endangered" individuals could prove catastrophic for remaining wild populations. Similarly, the incorporation of these confiscated live animals into official wild release programmes could help to safe guard their future survival if managed properly (CITES 2010; IUCN 2013).

It should be noted that agency efforts to return confiscated live animals of high conservation status back into the wild may have been hampered by the fact that 59% of "Threatened" individuals seized (2010–2014) took place during import rather than upon export (Suppl. material 1). From a technical perspective this can make wild release more challenging as data regarding the country of origin and or site of capture may be lacking (D'Cruze and Macdonald 2015). From a financial perspective, live animals confiscated on import are also more expensive to release due to the extra costs associated with their repatriation (Beck at al. 2007). This may be of particular concern for countries lacking available financial resources as importing countries are currently expected to bear the economic costs of disposal (CITES 2010).

Animal Welfare Implications

From an animal welfare perspective, each of the 64,143 individual live wild animals seized between 2010–2014 will have posed a management issue for the agencies involved. In terms of sheer numbers, it appears that illegally traded reptiles (95% of all live wild vertebrates reported as seized) were a particular challenge during this time period. However, it is important to note that even the species seized in far fewer numbers (e.g. primates) could have proved equally, if not more problematic during confiscation and disposal in this regard (e.g. Farmer 2002; Campbell et al. 2015). In particular, the large proportion of individuals seized during import (43%) are of considerable animal welfare concern as (in addition to suffering experienced during capture and preparation) these animals will have also had their physical and mental states further compromised during illegal shipment after export (Warwick 2014).

Historically, decisions on the disposal of confiscated live animals have been influenced by the perception that returning them to the wild is the optimal solution for animal welfare and conservation (CITES 2010). Although this may be the preferred option, for species of high conservation status and often the welfare of individual animals, a growing body of scientific evidence suggests that such action is not always the most appropriate decision (IUCN 2013). For example, the poorly planned release of confiscated animals into the wild may doom them to a slow, painful death (CITES 2010) and may also threaten the welfare and survival of wild populations by exposing them to disease and genetic pollution (IUCN 2013). Given these risks, and recommendations provided in current guidelines (CITES 2010; IUCN 2013), it is likely that the provision of life time care and euthanasia would have been the preferred options for the majority of wild animals seized between 2010–2014 due to their relatively low conservation status.

Limitations of the CITES Seizure Data

Using seizure records to assess the actual amount of IWT and associated enforcement effort taking place over a given time period is hindered by the fact that not all illegal transactions are seized and not all seizures are recorded officially (Underwood et al. 2013). This is because efforts to control and report on IWT can vary between countries depending on a variety of factors including political will, available resources, levels of corruption (UNODC 2016), the species involved [for example due to difficulties in identifying prohibited taxa (e.g. Zhou et al. 2015c)] and due to real or perceived technical challenges in dealing with confiscated individuals (Underwood et al. 2013).

In particular, poor reporting compliance has already been identified as an on-going issue of concern associated with the CITES trade database (UNEP CITES 2014; D'Cruze and Macdonald 2015). In light of this fact, and also taking the other various factors outlined above into account, it is unlikely that no international illegal trade activity took place in the 128 (70%) countries party to CITES for which no seizure events were reported (Suppl. material 1). Therefore, applying the precautionary principle, it is not unreasonable to treat the total of 64,143 confiscated live wild vertebrates (including the 11,902 live individuals of threatened status) reported in the CITES trade database as a highly conservative figure.

Another specific issue of concern is the fact that CITES does not require Parties to formally record any information regarding the disposal of confiscated live wild animals. This lack of information impedes the monitoring, evaluation and improvement of any disposal decisions taken which could be jeopardizing both animal welfare and the survival of remaining wild populations. As a case in point, currently it is not possible to establish how many seized wild animals have re-entered commercial trade even though this option is only recommended in certain circumstances where "there are no concerns that sale will stimulate further illegal or irregular trade" and "qualified buyers exist" (CITES 2010).

Future recommendations

Our study raises pre-existing concerns that information regarding the actual number of live wild vertebrates seized by CITES Management authorities each year is incomplete. Furthermore, where seizure records do exist, information regarding the ultimate fate of these wild animals is not currently documented in the CITES trade database. To address this issue, we recommended that the relevant Management authorities improve reporting compliance and that CITES strengthens its trade database in continued collaboration other associated national, regional and global data management platforms (UNODC 2016) to include data on the disposal of any live wild animal seizures that are officially recorded (Table 1).

Enforcement agencies must also have the financial resources needed to effectively seize live IWT (Moore et al. 2015), preferably prior to international export. A range

Table 1. Key challenges and management recommendations for the effective seizure and disposal of live animals seized by CITES authorities.

Concern	Continuing Challenge	Recommendation
Legislative and regulatory measures	Non-existent national action plans for effective seizure and disposal of live CITES seizures	Each Party develops a plan of action to be executed following live CITES seizures
	Incomplete understanding of which national agencies are responsible for effective seizure and disposal of live CITES seizures	Each Party identifies (in CITES directory) national agencies with authority to act on disposal of live CITES seizures
National and international law enforcement	National enforcement agencies lack the financial resources for effective seizure and disposal of live CITES seizures	Criminal actors bear the financial costs for disposal of live animal CITES seizures
	National enforcement agencies lack the skilled staff for effective seizure and disposal of live CITES seizures	Each Party provides formal training for staff involved in the seizure and disposal of live CITES seizures
Trade data recording and analysis	Incomplete national CITES WCMC trade database live seizure records	Strengthen existing CITES WCMC international data management platforms
	Non-existent national live disposal records in CITES WCMC trade database	Strengthen CITES WCMC data management platform to include data on disposal of live CITES seizures
Consumer demand reduction	Growing international demand for illegally traded live wild animals	Initiate new international behaviour change focused interventions
	Sustained domestic demand for illegally traded live wild animals	Strengthen existing national behaviour change focused interventions

of potential funding sources is available to cover these costs (e.g. private donations and government allocations) (CITES 2010). However, given its potential to act as a disincentive for IWT, we specifically recommended that countries adopt new and/or strengthen existing legislation in order to charge the criminal actors with the costs associated with the seizure and disposal of confiscated live wild animals (CITES 2010) (Table 1). A formal CITES wildlife policy review could prove useful by identifying specific actions to address any discrepancy between formal compliance (i.e. what is actually required) and real compliance (i.e. what is currently being provided) (CITES 2016).

Conclusion

The two primary legal instruments used to address unsustainable exploitation of wildlife are out-right bans [e.g. the European Union "blanket" ban on the import of captive live birds (BBC 2005)] and conditional allowances permitting limited trade [e.g. (international trade in CITES listed species)] (Dutton et al. 2013). Although both expert and public opinion is often polarised regarding which of these instruments will be most effective for a given wildlife trade issue, the general consensus is that increas-

ing IWT involving live animals sourced both from the wild (e.g. D'Cruze et al. 2015) and captivity (e.g. Nijman and Shepherd 2015) will remain an on-going issue of global animal welfare and conservation concern (e.g. UNODC 2016). Although it will never be possible to detect and seize all live IWT, we call for improved data reporting and enforcement activity, in combination with existing recommendations to increase political will and reduce consumer demand (TRAFFIC 2008; CITES 2010) (Table 1).

Acknowledgements

We gratefully acknowledge the input of Margaret Balaskas, Gemma Carder, Paul Johnson, Mark Jones, Staci McLennan, Chris Newman, Kate Nustedt, and Jessica Wood in the preparation of this manuscript. We would like to thank World Animal Protection for providing funding for this study.

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Supplementary material 1

CITES WCMC Trade database (2010-2014)

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Data type: species data

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