

## Declining Rates of Species Described per Taxonomist: Slowdown of Progress or a Side-effect of Improved Quality in Taxonomy?

GEORGE SANGSTER<sup>1,2,\*</sup> AND JOLANDA A. LUKSENBURG<sup>3</sup>

<sup>1</sup>Department of Bioinformatics and Genetics, Swedish Museum of Natural History, P.O. Box 50007, SE-104 05 Stockholm, Sweden; <sup>2</sup>Department of Zoology, Stockholm University, SE-106 91 Stockholm, Sweden; and <sup>3</sup>Department of Environmental Science and Policy, George Mason University, 4400 University Drive, Fairfax, Virginia 22030 4444, USA

\*Correspondence to be sent to: Department of Bioinformatics and Genetics, Swedish Museum of Natural History, P.O. Box 50007, SE-104 05 Stockholm, Sweden; E-mail: g.sangster@planet.nl.

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Even after more than 250 years of descriptive taxonomy, it is clear that there are many more species than have been described so far (e.g., [May 1988](#); [Stork 1993](#)). A major concern for biology is that the capacity of the taxonomic workforce is insufficient to document the missing species within a reasonable time ([Wheeler and Cracraft 1997](#); [Wheeler et al. 2004](#)). This concern is reflected in recent opinion papers that argued that taxonomy is in a state of crisis ([Agnarsson and Kuntner 2007](#)), that the profession is endangered ([Pearson et al. 2011](#)) and that taxonomists are an endangered race ([Wägele et al. 2011](#)). For long-term taxonomic capacity planning, two major empirical issues are important: the total number of missing species, and the pace at which these can be documented by taxonomists. Both issues require detailed study and careful evaluation.

Given the pressure of time resulting from the ongoing extinction crisis, it is important that as many species are adequately documented as soon as possible. Efficiency is therefore an important but largely overlooked aspect of taxonomy. Several recent studies have presented evidence that in a wide range of organisms the number of newly described species continues to increase, in some cases even exponentially, but that the number of taxonomists producing these descriptions has increased even faster ([Pimm et al. 2010](#); [Joppa et al. 2011a](#); [Costello et al. 2012](#); [Tancoigne and Dubois 2013](#)). Consequently, numbers of species described per taxonomist have decreased. In three of these studies, this was interpreted by the authors as an effect of a diminishing pool of missing species which makes it harder to discover any new ones ([Pimm et al. 2010](#); [Joppa et al. 2011a](#); [Costello et al. 2012](#); see also [Costello et al. 2013](#)). Although these studies rejected the idea that the number of taxonomists is declining, they nevertheless implied that the output per taxonomist is declining.

Both [Joppa et al. \(2011b\)](#) and [Costello et al. \(2012\)](#) predicted numbers of undescribed species based on

the assumption that long-term declines in the number of species described per taxonomist are caused by a declining pool of undiscovered species. Using this approach, [Costello et al. \(2012\)](#) were led to conclude that there were only 1.8–2.0 million species on Earth. This number is remarkably low given that about 1.9 million species have already been described ([Chapman 2009](#)) and thus suggests that only few species remain to be discovered. Furthermore, their estimate contrasts starkly with those others, including [Mora et al. \(2011](#); 8.7 million species on Earth), [Chapman \(2009](#); 10 million species) and [Grimaldi and Engel \(2005](#); 4 million species of insects alone).

Surprisingly, neither [Joppa et al. \(2011a\)](#) nor [Costello et al. \(2012, 2013\)](#) evaluated the possibility that trends in the number of authors of taxonomic descriptions have not so much to do with the *discovery* of species but rather with the scientific *documentation* of newly proposed species. In this article, we examine the possibility that the increased number of authors involved in descriptions is not primarily an effect of a declining pool of undescribed species but rather represents a side effect of a drive towards increased quality of taxonomic descriptions. During the last few decades, taxonomy has transformed into an independent science that regards taxa as scientific hypotheses that are subject to falsification, and thus require detailed documentation. If increased numbers of authors involved in descriptions are a result of higher standards in taxonomy, one would expect that taxonomic descriptions (i) have become more elaborate in recent decades (e.g., are based on more specimens and characters, include more information and illustrations), and (ii) take more time to complete (i.e., there is a longer interval between discovery and description). Importantly, if the increased authorship of new species is reflected in higher-quality descriptions, and if better descriptions require fewer revisions by other taxonomists, then the net result may be an *increase* of efficiency.

There are surprisingly few studies that have measured the quality of species descriptions, and, to our knowledge, none that have assessed the relationship between quality and revision. In a study of dinosaur descriptions, [Benton \(2008\)](#) found that the type material of new species has become more complete since the 1950s. For birds, it has been claimed that the quality of descriptions has declined ([LeCroy and Vuilleumier 1992](#)) but this claim has been challenged ([Collar 1999](#)) and neither of these views were supported by quantitative data.

In addition, we examine the relative importance of descriptions and revisions in taxonomic progress. The importance of revisionary taxonomy is well known among taxonomists (e.g., [Wheeler and Cracraft 1997](#); [Raczkowski and Wenzel 2007](#)) but often fails to be appreciated by others, including macroecologists and biodiversity scientists. [Pimm et al. \(2010\)](#), [Joppa et al. \(2011a\)](#), and [Costello et al. \(2012\)](#) based their conclusions on description dates and original authorship of taxa that are currently recognized as species (i.e., after revision by subsequent taxonomists). This approach confounds descriptive and revisionary taxonomy, and does not accurately reflect either type of taxonomy. Importantly, description is not enough. Even if all species have been described (i.e., *named*), this does not necessarily mean that all species have been correctly delimited and properly documented. If past taxonomic activity has been biased against cryptic species ([Blackburn and Gaston 1995](#); [Bickford et al. 2007](#)), or towards lumping distinctive taxa in widespread polytypic species ([Sangster 2009](#)), the total number of species may still be greatly underestimated.

This study focuses on birds because birds are often considered to be the taxonomically most mature group of animals (e.g., [Mayr 1982](#); [Price 1996](#)). If a diminishing pool of missing species limits taxonomic progress, one might expect this limitation to be most severe in the best-studied groups, including birds.

## METHODS

The quality of species descriptions was studied in 481 extant bird taxa that were originally described as species in the period 1935–2009. These represent all species described during this period. Type descriptions published between 1935 and 1990 were identified using two partially overlapping datasets, the Peters Checklist ([Peters 1937–1951](#); [Mayr and Greenway 1960, 1962](#); [Mayr and Paynter 1964](#); [Paynter 1967–1970](#); [Mayr and Cottrell 1979](#); [Traylor 1979](#); [Mayr and Cottrell 1986](#)) and a series of inventories of new species descriptions ([Zimmer and Mayr 1943](#); [Mayr 1957, 1971](#); [Mayr and Vuilleumier 1983](#); [Vuilleumier and Mayr 1987](#); [Vuilleumier et al. 1992](#); [Bahr 1995](#)). Type descriptions published from 1991 up to and including 2009 were located in the zoological literature and using *Zoological Record* (BIOSIS), *Web of Science* (Thomson Scientific), and *Recent Ornithological Literature*. Descriptions of species likely or known to be extinct

at the time of publication, introductions of new names for previously described species, and nomenclaturally unavailable names were excluded.

Seven measures of quality were studied: (i) the number of pages devoted to descriptions of new species, (ii) the number of specimens of the new species, (iii) the number of character states differentiating the new species from its most similar or most closely related species (as identified in the original description), (iv) the number of taxa to which the new species was compared, (v) the inclusion of an illustration (photograph or artwork) of the new species, (vi) the inclusion of a map of the range or collecting localities of the new species, and (vii) the inclusion of a sonagram (audiospectrogram) of the vocalizations of the new species. In addition, the number of pages per taxonomist was calculated by dividing the total number of pages per description by the number of authors of each description. The number of pages was measured in units of 0.25 pages; title, authorship, author affiliations, abstract, illustrations, maps, sonagrams, acknowledgements, and references were excluded. If multiple species were described in a single publication, the number of pages was divided by the number of new species described. The number of character states was the sum of all morphological, behavioural, acoustic, and ecological differences. If taxa also differed in any molecular analysis, this was treated as a single difference for each locus included in the study. Mitochondrial sequences, microsatellites, and allozyme analyses were each counted as single characters.

The relationship between the quality of species descriptions and the proportion of newly proposed species that have been revised was studied using a dataset that included all 414 species described in the period 1935–1999. A cutoff date of 31 December 1999 was used to allow time for revision. Two categories of revision were compared: (i) unrevised species: valid species which are placed in the same genus as in the original description, and (ii) revised species: taxa originally described as species but which are now considered either invalid taxa, subspecies, or valid species in a different genus than in the original description. The current status of species was determined using the *Zoonomen* database ([Peterson 2012](#)). Well-documented revisions not yet incorporated in the *Zoonomen* database at the time of writing were included in the study: *Lophura hatinhensis* (synonym of *L. edwardsi*, [Hennache et al. 2012](#)), *Myrmeciza disjuncta* (now *Aprositornis disjuncta*, [Isler et al. 2013](#)), *Hypositta perdita* (synonym of *Oxylabes madagascariensis*, [Fjeldsâ et al. 2013](#)), *Miraфра sidamoensis* (now *Heteromiraфра archeri sidamoensis*, [Spottiswoode et al. 2013](#)), *Cettia carolinae* (now *Horornis carolinae*, [Alström et al. 2011](#)), *Cisticola dorsti* (synonym of *C. guinea*, [Dowsett-Lemaire et al. 2005](#)), and *Dendroica angelae* (now *Setophaga angelae*, [Lovette et al. 2010](#)).

We used both univariate (Mann–Whitney *U* test, Fisher's Exact Test) and multivariate (regression) analyses to assess the relationship between the quality of species descriptions and the proportion

TABLE 1. Temporal trends in measures of quality in species descriptions of birds (1935–2009)

	Best-fitting line	Spearman's rho	P-value	<i>t</i>
Pages (number)	0.117x–227.055	0.879	<0.001	13.63
Specimens (number)	0.073x–136.679	0.514	<0.001	2.53
Characters (number)	0.063x–117.752	0.718	<0.001	8.54
Taxa compared (number)	0.058x–110.170	0.522	<0.001	3.17
Illustration (proportion)	0.014x–26.243	0.795	<0.001	11.55
Map (proportion)	0.012x–23.919	0.793	<0.001	11.93
Sonagram (proportion)	0.009x–18.495	0.789	<0.001	10.18
Pages per taxonomist (number)	0.032x–60.100	0.520	<0.001	4.45

Notes: Yearly means ( $n=75$ ) were used as data points.

of newly proposed species that have been revised. Multivariate analyses were performed with Regression with Empirical Variable Selection (REVS, Goodenough et al. 2012), a method which avoids well-known problems associated with full and stepwise regression methods (e.g., Whittingham et al. 2006; Hegyi and Garamszegi 2011). REVS uses branch-and-bound all-subsets regression to quantify the amount of empirical support for each independent variable, and then calculates multiple linear regression models. The Akaike Information Criterion (AIC) was used to compare models and identify the best model. Analyses were performed in R version 2.15 (R Development Core Team 2011) with the LEAPS package (Lumley 2009), and a script modified from Goodenough et al. (2012).

The time between the initial discovery of a species and its formal description was assessed in all bird taxa that were described as species in the period 1935–2009. Species were excluded from the dataset if the year of discovery could not be determined from the type descriptions.

The relative impact of descriptions and revisions on the number of recognized bird species was determined by comparing the number of validly described new species of birds and the total number of species estimated or recognized in 18 classifications of Recent birds published between 1946 and 2012 (Mayr 1946; Mayr and Amadon 1951; Storer 1960, 1971; Edwards 1974; Moroney et al. 1975; Gruson 1976; van Tyne and Berger 1976; Bock and Farrand 1980; Sibley and Monroe 1990, 1993; Sibley 1996; Clements 2000; Dickinson 2003; Perrins 2003; Clements 2007; Gill and Donsker 2011; Peterson 2012).

## RESULTS AND DISCUSSION

### *Quality and Efficiency*

All seven measures of quality were significantly and positively related to the year of description ( $P < 0.001$ , Table 1). The mean number of pages devoted to a description, which is an indication of the amount of taxonomic information presented, has increased > 8-fold, from about one in 1935–1939 to more than eight in 2005–2009 (Fig. 1a). The numbers of specimens (Fig. 1b), characters (Fig. 1c) and taxa compared (Fig. 1d), each more than doubled during the study period. The

proportion of descriptions with an illustration of the new species increased from 15% to 90% during the study period (Fig. 1e), those with a range map increased from less than 20% before 1970 to more than 80% during the 1990s and 2000s (Fig. 1f), and those with one or more sonagrams increased from close to zero before 1970 to more than 50% in 1995–2009 (Fig. 1g). The number of pages produced per taxonomist almost doubled during the study period (Fig. 1h).

There was a significant positive relationship between the quality of descriptions and the probability that no subsequent revision was made. Univariate analyses show that species taxa proposed during 1935–1999 that were subsequently revised (i.e., are now considered either invalid taxa, subspecies or members of another genus) were described using significantly fewer pages, specimens and characters, were compared to fewer species, were less often illustrated, and their descriptions less often included maps and sonagrams than valid species that have remained in their original genus (Fig. 2).

More powerful multivariate analysis of species taxa proposed during 1935–1999 confirmed the relationship between quality and revision (Table 2). The best model identified by REVS was highly significant ( $F_{5,397} = 16.54$ ;  $P < 0.001$ ; adjusted  $R^2 = 0.162$ ). This model included five variables that were positively related to the probability that a taxon was not revised. There was a significant positive effect of year of description on the probability that a taxon was not revised, independent of the quality variables. This may indicate that the taxonomic status of some of the more recently described species requires revision. This is not surprising given that there was less time to revise more recently described species than those that have been described earlier. To determine whether the observed relationship between the quality of descriptions and the probability of subsequent revision is an artifact of incomplete revision of recent descriptions, the dataset was subdivided into five sets, each spanning 13 years, and the analysis was repeated for each set. The positive relationship between the quality of descriptions and the probability that no subsequent revision was made, was observed in each of these periods, although most comparisons were no longer significant due to smaller sample sizes (Fig. S1). Thus, the observed relationship between quality and revision

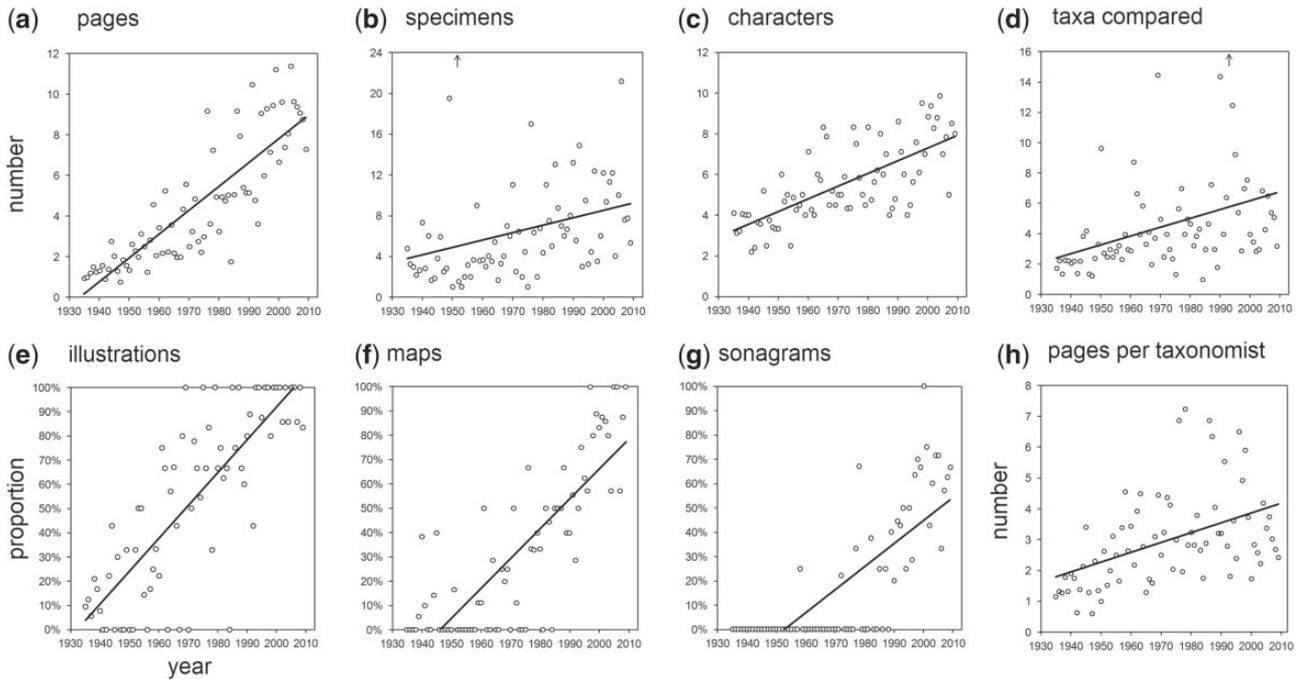


FIGURE 1. Temporal trends in measures of taxonomic quality (1935–2009), expressed as yearly means ( $n=75$ ): a) number of pages per description, b) number of specimens per new species, c) number of character state differences per new species, d) number of taxa to which the new species has been compared, e) proportion of descriptions in which a new species is illustrated, f) proportion of descriptions illustrated with a map, g) proportion of descriptions in which vocalizations are illustrated with sonograms, h) number of pages per description per taxonomist. Two outliers in figures b and d are indicated by an arrow.

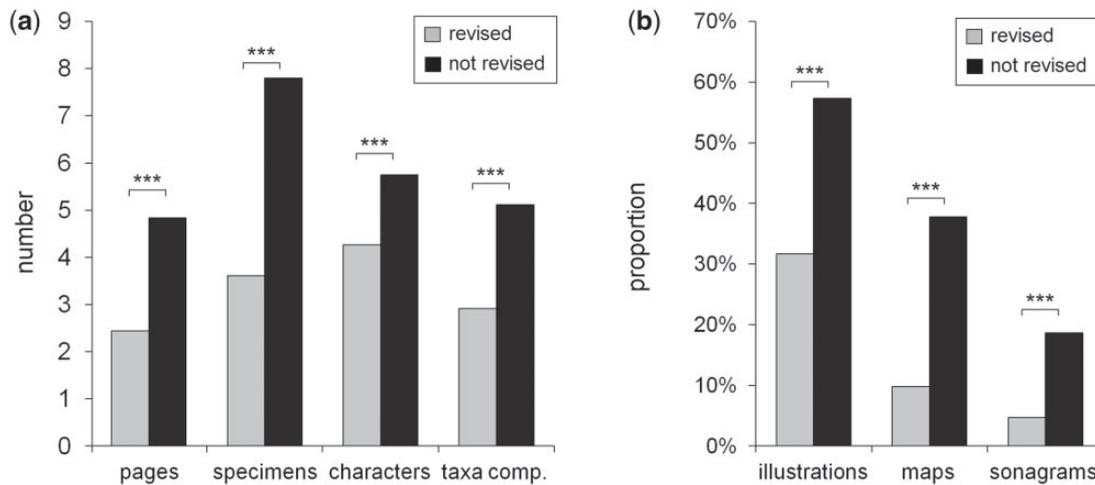


FIGURE 2. Relationship between quality of original descriptions of species (1935–1999) and subsequent revision ( $n=414$ ). Significance levels ( $***P < 0.001$ ) are based on Mann–Whitney  $U$  test (a, pages, specimens, characters, taxa compared) and Fisher’s Exact Test (b, illustrations, maps, sonograms).

cannot be explained by incomplete revision of recent descriptions.

The time between initial discovery and formal publication of new species showed a strong and significant increase during the study period (Fig. 3a; Spearman’s  $\rho=0.652$ ;  $P < 0.001$ ;  $t=6.99$ ). Species taxa proposed in the late 1930s were typically described about 1 year after their discovery, whereas the mean interval

between discovery and description had increased to about 6 years by the late 2000s.

These results show that taxonomic descriptions have become more elaborate and that the amount of information (i.e., number of pages) produced per taxonomist has increased. Because the increase in the number of authors per description coincides with a strong overall increase in quality, increased authorship

TABLE 2. Regression analysis of the effect of seven measures of quality and year of description on the probability that a newly described species is not revised ( $n=403$  bird species described from 1935–1999)

Predictive variable	Estimate $\pm$ SE	$t$	$P$ -value	AIC	$\delta$ AIC
Year (continuous)	0.004 $\pm$ 0.001	3.089	0.002	–603.7	19.9
Map (no/yes)	0.201 $\pm$ 0.065	3.092	0.002	–615.5	8.1
Specimens (continuous)	0.005 $\pm$ 0.002	2.366	0.018	–619.0	4.7
Taxa compared (continuous)	0.009 $\pm$ 0.004	2.077	0.038	–622.0	1.7
Characters (continuous)	0.013 $\pm$ 0.007	1.917	0.056	–623.7	0
Pages (continuous)	–	–	–	–622.4	1.3
Sonagram (no/yes)	–	–	–	–620.5	3.2
Illustration (no/yes)	–	–	–	–618.5	5.2
Intercept	–7.730 $\pm$ 2.584	–2.992	0.003		

Notes: AIC values are those of increasingly complex models, with parameters entered from top to bottom. Thus, the AIC value of “Year” relates to the model with only “Year” being entered, the second to the model with both “Year” and “Map,” and so on. The model with the first five variables entered was optimal (as shown by AIC). Differences from the optimal model are indicated by delta AIC ( $\delta$ AIC) values.

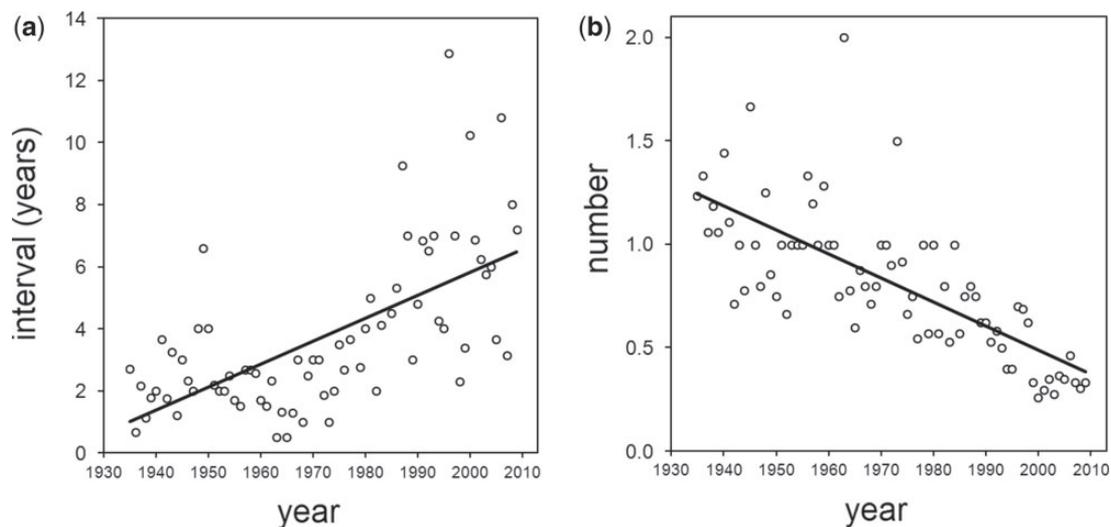


FIGURE 3. Temporal trends in a) the time between the discovery of a new species and its formal scientific description, and b) the number of species described per taxonomist per year (1935–2009), expressed as yearly means ( $n=75$ ).

cannot simply be attributed to a declining pool of missing species. Based on the results of the present study, we suggest that the primary force driving the decline of the number of species described per taxonomist is a drive towards higher quality. The trend towards more elaborate studies reflects a transition in taxonomy from naming taxa (which in a strict sense requires only a few lines of text) to a science, in which the existence of new taxa and their properties are presented as hypotheses that require documentation and testing (Haszprunar 2011; Sluys 2013). The increased interval between discovery and description during the study period is consistent with this trend. Elaborate, well-researched descriptions typically take more time, and require more authors, than the brief descriptions often published in previous decades.

The results of this study further show why elaborate descriptions of new species are important for taxonomy. Elaborate descriptions less often required revision by subsequent taxonomists, and may therefore be regarded as more efficient, than less elaborate descriptions.

Because the quality of descriptions has increased since the 1930s (Fig. 1), and a significant positive relation exists between quality and the probability that no revision is needed (Fig. 2, Table 2), it is likely that efficiency in taxonomy has increased likewise.

The findings of this study offer a different perspective on progress in taxonomy than those of Joppa et al. (2011a) and Costello et al. (2012). Whereas these authors attributed the drop in the numbers of species described per taxonomist to the (supposed) difficulties of finding any new species, our study shows that (at least in birds) this drop is best seen as a side-effect of a trend towards higher-quality descriptions, and that this trend translates into fewer subsequent revisions.

#### No Slowdown of Progress

The pool of “missing” species is often equated with *undescribed* species (e.g., Joppa et al. 2011a; Costello et al. 2012). However, this pool also contains *misclassified*

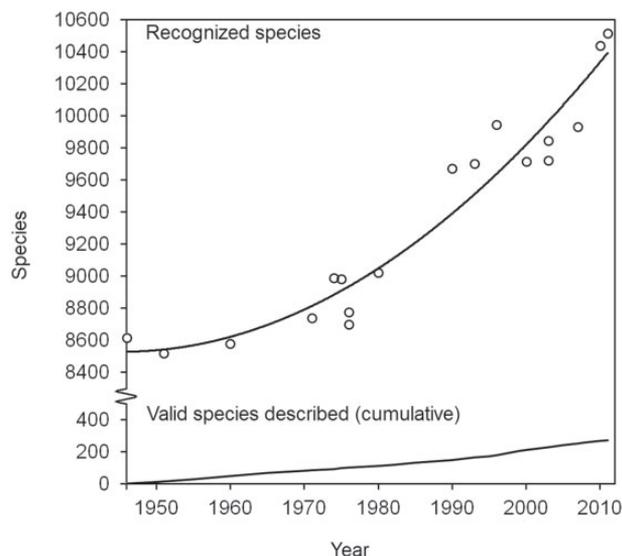


FIGURE 4. Trends of the total number of recognized species of Recent birds (based on 18 estimates and classifications) and newly described valid species of birds (1946–2011). Note that the number of recognized species increases much faster than the number of newly described valid species. A second-order trendline was added to illustrate the trend of the number of recognized species.

species: named species that remain hidden because these are incorrectly considered as invalid taxa or as subspecies of another species. Previously named species that are currently misclassified must be “rediscovered” by taxonomic revision. Between 1946 and early 2012, the number of recognized bird species increased from 8616 to 10,511 (Fig. 4). During the same period, 266 valid species were described, which represent 14.0% of the total increase of 1895 species, or roughly one in seven species. Since 1946, the rate of increase of the total number of species was exponential ( $y = 0.431x^2 + 0.652x$ ) whereas the increase in newly described valid species was linear ( $y = 3.968x$ ) (Fig. 4).

This underscores that in avian taxonomy, revision is a much more important source of newly recognized species than descriptions of previously unnamed species (Fig. 4). Consequently, progress in avian taxonomy is not limited by a diminishing pool of undescribed species. Importantly, there is no evidence of a slowdown of taxonomic progress (Fig. 4). This result is not unexpected given that in the first half of the twentieth century there was a very strong bias toward lumping distinctive bird species into large polytypic species (Haffer 1992) and this bias is only slowly undone by modern revisions (Sangster 2009).

Species limits in many groups of birds have not been revisited in recent decades using modern techniques, modern data and explicit taxonomic criteria. As a consequence, numerous species of birds remain inadequately documented by current standards. It is therefore not surprising that many “species” of birds, including those not yet formally revised, have been shown to comprise multiple diagnosable taxa

(Garrido et al. 1997; Navarro-Sigüenza and Peterson 2004; Peterson 2007; Isler et al. 2007), multiple reproductively isolated taxa (Knox 1990; Alström and Olsson 1999; König 1991; Martens et al. 2004) and multiple phylogeographically distinct subunits (Honey-Escandon et al. 2008; Lohman et al. 2010; Deiner et al. 2011; Milá et al. 2012; Irestedt et al. 2013). This suggests that the actual number of bird species may be much higher than presently recognized. Clearly, even in relatively well-known groups such as birds the pool of missing species is likely very large, and is not limiting taxonomic research.

## CONCLUSIONS

Declines in the number of species described per taxonomist do not indicate a diminishing pool of undescribed species but are better explained by a widespread drive among taxonomists towards higher-quality descriptions. Taxonomists have good reasons for this, because more elaborate descriptions require fewer subsequent revisions. The findings of this study and the lack of evidence that increasing numbers of authors involved in descriptions are driven by a diminishing pool of undescribed species, suggest that trends in the number of species described per author should not be used to estimate total numbers of species. Furthermore, because numbers of recognized species of birds are increasing exponentially it is incorrect to suggest that species inventories of birds, let alone of all animals, are “nearly complete.” The drive towards better descriptions and the strong increase of species numbers long after their initial descriptions, underscore the fundamentally analytic and iterative nature of taxonomy (Yeates et al. 2011; Sluys 2013; de Carvalho et al. 2014), aspects often overlooked by biodiversity scientists and other end-users of taxonomy. Broader appreciation of the scientific nature of taxonomy, and of the limitations of nomenclatural databases, will help to acquire a better understanding of the diversity of life.

## SUPPLEMENTARY MATERIAL

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.m4g2n>

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## REFERENCES

- Agnarsson I., Kuntner M. 2007. Taxonomy in a changing world: seeking solutions for a science in crisis. *Syst. Biol.* 56:531–539.
- Alström P., Höhna S., Gelang M., Ericson P.G.P., Olsson U. 2011. Non-monophyly and intricate morphological evolution within the avian family Cettiidae revealed by multilocus analysis of a taxonomically densely sampled dataset. *BMC Evol. Biol.* 11:352.
- Alström P., Olsson U. 1999. The Golden-spectacled Warbler: a complex of sibling species, including a previously undescribed species. *Ibis* 141:545–568.
- Bahr N. 1995. Additions to the list of new species of birds described from 1981 to 1990. *Bull. Br. Ornithol. Club* 115:114–116.
- Benton M.J. 2008. Fossil quality and naming dinosaurs. *Biol. Lett.* 4:729–732.
- Bickford D., Lohman D.J., Sodhi N.S., Ng P.K.L., Meier R., Winker K., Ingram K.K., Das I. 2007. Cryptic species as a window on diversity and conservation. *Trends Ecol. Evol.* 22:148–155.
- Blackburn T.M., Gaston K.J. 1995. What determines the probability of discovering a species?: a study of South American oscine passerines. *J. Biogeogr.* 22:7–14.
- Bock W.J., Farrand J. 1980. The number of species and genera of recent birds: a contribution to comparative systematics. *Am. Mus. Novit.* 2703:1–29.
- Chapman A.D. 2009. Numbers of living species in Australia and the world. 2nd ed. Canberra: Australian Government, Department of Environment, Water, Heritage and Arts.
- Clements J.F. 2000. *Birds of the world, a checklist*. Vista: Ibis Publishing Company.
- Clements J.F. 2007. *The Clements checklist of birds of the world*. 6th ed. Ithaca: Cornell University Press.
- Collar N.J. 1999. New species, high standards and the case of *Laniarius liberatus*. *Ibis* 141:358–367.
- Costello M.J., Wilson S., Houlding B. 2012. Predicting total global species richness using rates of species description and estimates of taxonomic effort. *Syst. Biol.* 61:871–883.
- Costello M.J., Wilson S., Houlding B. 2013. More taxonomists describing significantly fewer species per unit effort may indicate that most species have been discovered. *Syst. Biol.* 62:616–624.
- De Carvalho M.R., Ebach M.C., Williams D.M., Nihei S.S., Trefaut Rodrigues M., Grant T., Silveira L.F., Zaher H., Gill A.C., Schelly R.C., Sparks J.S., Bockmann F.A., Séret B., Ho, H.-C., Grande L., Rieppel O., Dubois A., Ohler A., Faivovich J., Assis L.C.S., Wheeler Q.D., Goldstein P.Z., de Almeida E.A.B., Valdecasas A.G., Nelson G. 2014. Does counting species count as taxonomy? On misrepresenting systematics, yet again. *Cladistics* 30:322–329.
- Deiner K., Lemmon A.R., Mack A.L., Fleischer R.C., Dumbacher, J.P. 2011. A passerine bird's evolution corroborates the geologic history of the island of New Guinea. *PLoS One* 6(5):e19479.
- Dickinson E.C., editor. 2003. *The Howard and Moore complete checklist of the birds of the world*. 3rd ed. London: Christopher Helm.
- Dowsett-Lemaire F., Borrow N., Dowsett R.J. 2005. *Cisticola dorsti* (Dorst's Cisticola) and *C. ruficeps guinea* are conspecific. *Bull. Br. Ornithol. Club* 125:305–313.
- Edwards E.P. 1974. *A coded list of birds of the world*. Sweet Briar, VA: Edwards.
- Fjeldså J., Mayr G., Jönsson K., Irestedt M. 2013. On the true identity of Bluntshli's Vanga *Hypositta perdit* Peters, 1996, a presumed extinct species of Vangidae. *Bull. Br. Ornithol. Club* 133:72–75.
- Garrido O.H., Parkes K.C., Reynard G.B., Kirkconnell A., Sutton R. 1997. Taxonomy of the Stripe-headed Tanager, genus *Spindalis* (Aves: Thraupidae) of the West Indies. *Wilson Bull.* 109:561–594.
- Gill F., Donsker D. 2011. *IOC World Bird Names* (version 2.8.3). Available from: <http://www.worldbirdnames.org/> (last accessed March 30, 2011).
- Goodenough A.E., Hart A.G., Stafford R. 2012. Regression with empirical variable selection: description of a new method and application to ecological datasets. *PLoS One* 7(3):e34338.
- Grimaldi D., Engel M.S. 2005. *Evolution of the insects*. Cambridge, UK: Cambridge University Press.
- Gruson E.S. 1976. *Checklist of the world's birds*. New York: Quadrangle.
- Haffer J. 1992. The history of species concepts and species limits in ornithology. *Bull. Br. Ornithol. Club Centenary Suppl.* 112A:107–158.
- Haszprunar G. 2011. Species delimitations – not 'only descriptive'. *Org. Div. Evol.* 11:249–252.
- Hegyi G., Garamszegi L.Z. 2011. Using information theory as a substitute for stepwise regression in ecology and behavior. *Behav. Ecol. Sociobiol.* 65:69–76.
- Hennache A., Mahood S.P., Eames J.C., Randi E. 2012. *Lophura hatinhensis* is an invalid taxon. *Forktail* 28:129–135.
- Honey-Escandon M., Hernandez-Banos B.E., Navarro-Siguenza A.G., Benitez-Diaz H., Peterson A.T. 2008. Phylogeographic patterns of differentiation in the Acorn Woodpecker. *Wilson J. Ornithol.* 120:478–493.
- Irestedt M., Fabre P.-H., Batalha-Filho H., Jönsson K.A., Roselaar C.S., Sangster G., Ericson P.G.P. 2013. The spatio-temporal colonization and diversification across the Indo-Pacific by a 'great speciator' (Aves, *Erythropitta erythrogaster*). *Proc. R. Soc. B* 280:20130309
- Isler M.L., Bravo G.A., Brumfield R.T. 2013. Taxonomic revision of *Myrmeciza* (Aves: Passeriformes: Thamnophilidae) into 12 genera based on phylogenetic, morphological, behavioral, and ecological data. *Zootaxa* 3717:469–497.
- Isler M.L., Isler P.R., Whitney B.M. 2007. Species limits in antbirds (Thamnophilidae): the Warbling Antbird (*Hypocnemis cantator*) complex. *Auk* 124:11–28.
- Joppa L.N., Roberts D.L., Pimm S.L. 2011a. The population ecology and social behaviour of taxonomists. *Trends Ecol. Evol.* 26:551–553.
- Joppa L.N., Roberts D.L., Pimm S.L. 2011b. How many species of flowering plants are there? *Proc. R. Soc. B* 278:554–559.
- Knox A.G. 1990. The sympatric breeding of Common and Scottish Crossbills *Loxia curvirostra* and *Loxia scotica*, and the evolution of Crossbills. *Ibis* 132:454–466.
- König C. 1991. Zur Taxonomie und Ökologie der Sperlingskäuze (*Glaucidium* spp.) des Andenraumes. *Ökol. Vögel* 13:15–76.
- LeCroy M., Vuilleumier, F. 1992. Guidelines for the description of new species in ornithology. *Bull. Br. Ornithol. Club* 112A:191–198.
- Lohman D.J., Ingram K.G., Prawiradilaga D.M., Winker K., Sheldon F.H., Moyle R.G., Ng P.K.L., Ong P.S., Wang L.K., Braile T.M., Astuti D., Meier R. 2010. Cryptic genetic diversity in "widespread" Southeast Asian bird species suggests that Philippine avian endemism is gravely underestimated. *Biol. Conserv.* 143:1885–1890.
- Lovette I.J., Pérez-Emán J.L., Sullivan J.P., Banks R.C., Fiorentino I., Córdoba-Córdoba S., Echeverry-Galvis M., Barker F.K., Burns K.J., Klicka J., Lanyon S.M., Bermingham E. 2010. A comprehensive multilocus phylogeny for the wood-warblers and a revised classification of the Parulidae (Aves). *Mol. Phylog. Evol.* 57:753–770.
- Lumley T. 2009. Package 'LEAPS': Regression subset selection. Available from: <http://cran.r-project.org/web/packages/leaps/leaps.pdf> (last accessed August 22, 2014).
- Martens J., Tietze D.T., Eck S., Veith M. 2004. Radiation and species limits in the Asian Pallas's warbler complex (*Phylloscopus proregulus* s.l.). *J. Ornithol.* 145:206–222.
- May R.M. 1988. How many species are there on earth? *Science* 241:1441–1449.
- Mayr E. 1946. The number of species of birds. *Auk* 63:64–69
- Mayr E. 1957. New species of birds described from 1941–1955. *J. Ornithol.* 98:22–35.
- Mayr E. 1971. New species of birds described from 1956–1965. *J. Ornithol.* 112:302–316.
- Mayr E. 1982. *The growth of biological thought*. Cambridge: Harvard University Press.
- Mayr E., Amadon, D. 1951. A classification of recent birds. *Am. Mus. Novit.* 1496:1–42.
- Mayr E., Cottrell, G.W., editors. 1979. *Check-list of birds of the world*. Vol. 1. 2nd ed. Cambridge: Museum of Comparative Zoology.
- Mayr E., Cottrell, G.W., editors. 1986. *Check-list of birds of the world*. Vol. 11. Cambridge: Museum of Comparative Zoology.
- Mayr E., Greenway, J.C., editors. 1960. *Check-list of birds of the world*. Vol. 9. Cambridge: Museum of Comparative Zoology.
- Mayr E., Greenway, J.C., editors. 1962. *Check-list of birds of the world*. Vol. 15. Cambridge: Museum of Comparative Zoology.

- Mayr E., Paynter, R.A., editors. 1964. Check-list of birds of the world. Vol. 10. Cambridge: Museum of Comparative Zoology.
- Mayr E., Vuilleumier, F. 1983. New species of birds described from 1966–1975. *J. Ornithol.* 124:217–232.
- Milá B., Tavares E.S., Muñoz Saldaña A., Karubian J., Smith T.B., Baker A.J. 2012. A Trans-Amazonian screening of mtDNA reveals deep intraspecific divergence in forest birds and suggests a vast underestimation of species diversity. *PLoS One* 7(7):e40541.
- Mora C., Tittensor D.P., Adl S., Simpson A.G.B., Worm B. 2011. How many species are there on Earth and in the ocean? *PLoS Biol* 9:e1001127.
- Moroney J.J., Bock W.J., Farrand J. 1975. Reference List of the Birds of the World. New York: American Museum of Natural History.
- Navarro-Sigüenza A.G., Peterson A.T. 2004. An alternative species taxonomy of the birds of Mexico. *Biota Neotropica* 4(2):1–32.
- Paynter R.A., editor. 1967–1970. Check-list of birds of the world. Vol. 12–14. Cambridge: Museum of Comparative Zoology.
- Pearson D.L., Hamilton A.L., Erwin T.L. 2011. Recovery plan for the endangered taxonomy profession. *BioScience* 61:58–63.
- Perrins C.M., editor. 2003. New encyclopedia of birds. Oxford: Oxford University Press.
- Peters J.L. 1937–1951. Check-list of birds of the world. Vols 3–7. Cambridge: Museum of Comparative Zoology.
- Peterson A.R. 2012. Zoonomen database. Available from: <http://www.zoonomen.net> (last accessed October 22, 2013).
- Peterson A.T. 2007. Geographic variation in size and coloration in the *Turdus poliocephalus* complex: a first review of species limits. *Publ. Univ. Kansas Nat. Hist. Mus.* 40:1–17.
- Pimm S.L., Jenkins C.N., Joppa L.N., Roberts D.L., Russell G.H. 2010. How many endangered species remain to be discovered in Brazil? *Nat. Conserv.* 8:71–77.
- Price T.D. 1996. Exploding species. *Trends Ecol. Evol.* 11 :314–315.
- R Development Core Team 2011. R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing.
- Raczkowski J.M., Wenzel J.W. 2007. Biodiversity studies and their foundation in taxonomic scholarship. *BioScience* 57:974–979.
- Sangster G. 2009. Increasing numbers of bird species result from taxonomic progress, not taxonomic inflation. *Proc. R. Soc. B.* 276:3185–3191
- Sibley C.G. 1996. Birds of the world. [CD-ROM] Version 2.0. Cincinnati: Thayer Birding Software.
- Sibley C.G., Monroe B.L. 1990. Distribution and taxonomy of birds of the world. New Haven: Yale University Press.
- Sibley C.G., Monroe B.L. 1993. A supplement to distribution and taxonomy of birds of the world. New Haven: Yale University Press.
- Sluys R. 2013. The unappreciated, fundamentally analytical nature of taxonomy and the implications for the inventory of biodiversity. *Biodiv. Conserv.* 22:1095–1105.
- Spottiswoode C.N., Olsson U., Mills M.S.L., Cohen C., Francis J.E., Toye N., Hoddinott D., Dagne A., Wood C., Donald P.F., Collar N.J., Alström P. 2013. Rediscovery of a long-lost lark reveals the conspecificity of endangered *Heteromira* populations in the Horn of Africa. *J. Ornithol.* 134:813–825.
- Storer R.W. 1960. The classification of birds. In: Marshall A.J., editor. *Biology and comparative physiology of birds*. Vol. 1. New York: Academic Press. p. 57–93
- Storer R.W. 1971. Classification of birds. *Avian Biol.* 1:1–18.
- Stork N. 1993. How many species are there? *Biodiv. Conserv.* 2:215–232.
- Tancoigne E., Dubois A. 2013. Taxonomy: no decline, but inertia. *Cladistics* 29:567–570.
- Traylor M.A., editor. 1979. Check-list of birds of the world. Vol. 8. Cambridge: Museum of Comparative Zoology.
- Van Tyne J., Berger A.J. 1976. Fundamentals of ornithology. 2nd ed. New York: J. Wiley and Sons.
- Vuilleumier F., LeCroy M., Mayr E. 1992. New species of birds described from 1981 to 1990. *Bull. Br. Ornithol. Club Centenary Suppl.* 112:267–309.
- Vuilleumier F., Mayr E. 1987. New species of birds described from 1976 to 1980. *J. Ornithol.* 128:137–150.
- Wägele H., Klusmann-Kolb A., Kuhlmann M., Haszprunar G., Lindberg D., Koch A., Wägele J.W. 2011. The taxonomist – an endangered race. A practical proposal for its survival. *Front. Zool.* 8:25.
- Wheeler Q.D., Cracraft J. 1997. Taxonomic preparedness: are we ready to meet the biodiversity challenge? In: Reaka-Kudla M.L., Wilson D.E., Wilson E.O., editors. *Biodiversity II*. Washington: Joseph Henry Press. p. 435–446.
- Wheeler Q.D., Raven P.H., Wilson E.O. 2004. Taxonomy: impediment or expedient? *Science* 303:285.
- Whittingham M.J., Stephens P.A., Bradbury R.B., Freckleton R.P. 2006. Why do we still use stepwise modelling in ecology and behaviour? *J. Anim. Ecol.* 75: 1182–1189.
- Yeates D.K., Seago A., Nelson L., Cameron S.L., Joseph L., Trueman J.W. 2011. Integrative taxonomy, or iterative taxonomy? *Syst. Entomol.* 36:209–217.
- Zimmer J.T., Mayr E. 1943. New species of birds described from 1938 to 1941. *Auk* 60:249–262.