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The Rufous-thighed Kite *Harpagus diodon* is not an endemic breeder of the Atlantic Forest: lessons to assess Wallacean shortfalls

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The migratory Rufous-thighed Kite *Harpagus diodon* is widely distributed in South America, and a recent spatiotemporal analysis of its distribution that was largely based on citizen science data concluded that it breeds (almost) exclusively in the Atlantic Forest, constituting a 'hidden endemism', and that it is a complete migrant, overwintering in the eastern Amazonian lowlands. However, that study missed key data from large areas that would have resulted in a different biogeographical pattern. Here, we reject the 'hidden endemism' hypothesis and show that the Rufous-thighed Kite is a more widespread breeder. We propose that to uncover Wallacean shortfalls of migratory birds correctly, (1) citizen science data must be integrated with thorough bibliographical searches and specimen examination and (2) life-cycle categories should be critically determined: failing to recognize the importance of these two key issues can undermine the ability of researchers to uncover the true extent of breeding ranges and timing of migration, resulting in erroneous ecogeographical patterns. By proposing and following a set of recommendations, and using previously unpublished and published documented records mostly from the southwestern portion of the distribution of Rufous-thighed Kite, we here show that this species breeds in the Cerrado of eastern Bolivia and is present during the austral spring and summer in the Austral Yungas but largely absent during the austral autumn and winter, mirroring the seasonality of the species in the Atlantic Forest.

Keywords: Austral Yungas, citizen science, Neotropical migration, South America.

'Wallacean shortfalls' refer to the lack of complete knowledge on distributional patterns in nature (Crame 2004). Given the complex and dynamic spatiotemporal patterns of migratory animals, Wallacean shortfalls are likely to be more profound in migratory than in resident species. Until recently, the migratory Rufous-thighed Kite *Harpagus diodon* was considered to be sedentary (Ridgely 1980, Hayes *et al*. 1994, Cabanne & Seipke 2005, Juhant 2011, 2012). A spatiotemporal analysis of its global distribution largely based on citizen science data reached two main conclusions: first, that the species breeds (almost) exclusively in the Atlantic Forest, constituting a 'hidden endemism', and secondly, that it is a complete migrant, overwintering in the eastern Amazonian lowlands (Lees & Martin 2015). Here, we present previously unpublished and published documented records from the southwestern portion of the distribution of Rufous-thighed Kite demonstrating that this species is not an endemic breeder of the Atlantic Forest. We propose guidelines for use of citizen science data, and specifically that to uncover Wallacean shortfalls of migratory birds correctly, researchers must carefully integrate citizen science data with thorough bibliographical searches and specimen examination, and that care must be taken in defining life-cycle categories in order to

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accurately uncover the true extent of breeding ranges and timing of migration. By following this approach, we show that the Rufous-thighed Kite also breeds in the Cerrado of eastern Bolivia, and is present during the austral spring and summer in the Austral Yungas but is largely absent during the austral autumn and winter, mirroring the seasonality of the species in the Atlantic Forest.

METHODS

We assembled a database of records of Rufous-thighed Kite from 1906 to 2014 in the southwestern portion of its distribution in South America, including our unpublished data and data from third parties, literature sources, on-line citizen science initiatives, specimens housed in museums, migration counts, and a systematic raptor foot-survey by M.A.J. in Parque Nacional (PN) Calilegua, Jujuy, Argentina, encompassing 407 h distributed over 60 days in the four seasons (January (7 days), March (8 days), July (25 days), August (5 days) and September (15 days)) from 2004 to 2006 and 2008 (Appendix S1). We also sought records from countries with undocumented reports of the species by contacting specialists (Juan Freile for Ecuador and Oliver Claessens and Jean-Marc Thiollay for French Guiana).

We re-analysed the database of Lees and Martin (2015) with the addition of our data, using both their and our own different life-cycle categories to assess pattern dependence on the categories used (see Appendix S1 for a comparison). Although any life-cycle period delimitation is to some extent arbitrary, boundaries should be set based on meaningful biological data. Admittedly, there will generally be some overlap across the year-cycle (e.g. early breeders can overlap with late migrants in a given area). We thus assigned all records to one of the following life-cycle categories: breeding season (16 October–14 March), non-breeding season (1 May–31 August), southbound migration (1–30 September), northbound migration (1–30 April) and breeding/migration overlap (15–31 March/1–15 October). The breeding and non-breeding seasons were based on data in Wolfe (1938), Davis (1993), Cabanne and Roesler (2007), Jordan *et al.* (2013) and Lees and Martin (2015); northbound and southbound migrations were set at identical durations and were based on Cabanne and Seipke (2005) and Juhant (2012). We allowed uncertainty as to the meaning of records occurring in the 15 days before and after the breeding season by adding a breeding/migration overlap category.

RESULTS

Our record compilation unequivocally shows the regular presence of Rufous-thighed Kites in the lowlands and Austral Yungas of Bolivia and in the Austral Yungas of Argentina during the breeding season (Figs 1 and S1, Appendix S1), including a confirmed breeding record from the western Cerrado in Concepción, Bolivia (Davis 1993). Conversely, there are no documented records from the non-breeding season in these areas (Fig. 1). We provide additional information and a brief analysis of important previous and new records of Rufous-thighed Kites in Bolivia Argentina, Ecuador and French Guiana (see Figs S1 and S2 for documented records and Appendix S2 for details on all records).

The different temporal delimitation of life-cycle periods in the present work and in Lees and Martin (2015) resulted in differences in the amount of data assigned to some categories. Allocation of data to our categories resulted in more breeding season records (551 vs. 442) and notably fewer records on migration (47 vs. 238), and our breeding/migration overlap category accounted for an additional 80 records; no differences occurred in the number of records during the non-breeding season (67 records, see Appendix S1).

Life-cycle differences and the addition of key data resulted in important differences in maps of the seasonal distribution of the Rufous-thighed Kite (Fig. 1). First, our maps show that documented records during the breeding season spread out across the Cerrado and include the Austral Yungas (compare Fig. 1a and Lees & Martin's fig. S1a and fig. 3a). Note that this pattern is recovered regardless of the concept of breeding season used (compare life-cycle categories in Appendix S1). Secondly, numerous documented records of birds previously considered to be on migration are here shown to occur during the breeding/migration overlap, suggesting a potentially larger breeding area (compare Fig. 1c with Lees & Martin's fig. S1d). Thirdly, there are documented records of birds during the breeding season, breeding/migration overlap and in northbound migration in the southwestern portion of the distribution of Rufous-thighed Kites (compare Fig. 1b with Lees & Martin's fig. S1d).

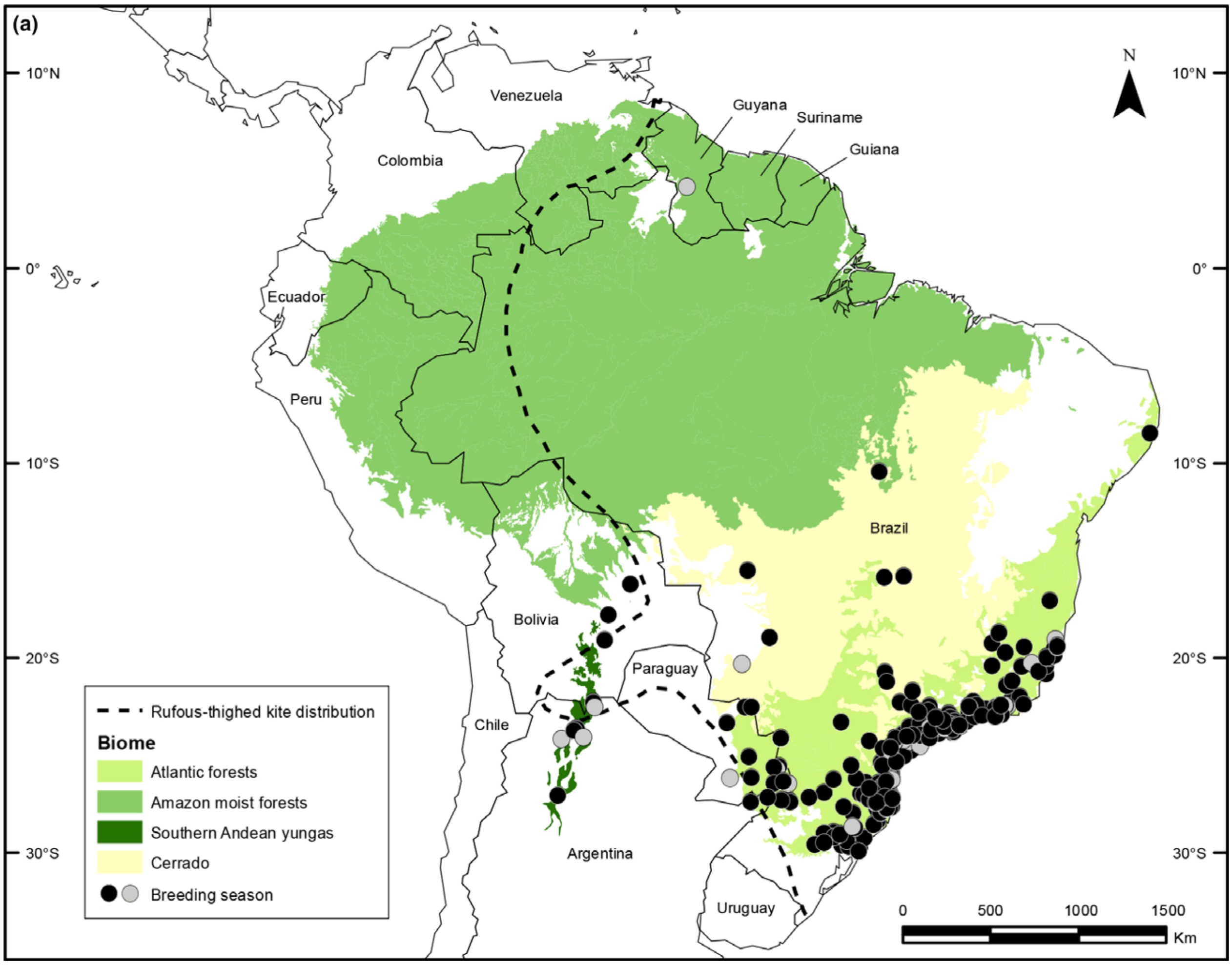

Figure 1. Maps showing documented (black) and undocumented (grey) records of Rufous-thighed Kite *Harpagus diodon* during (a) the breeding season, (b) non-breeding season and (c) southward and northward migration, and breeding/migration overlap. The dashed line represents the western distribution boundary of Rufous-thighed Kite following Ferguson-Lees and Christie (2001). Note the records in eastern Bolivia and in the Austral Yungas of Argentina and Bolivia during the breeding season. See Fig. S1 and Appendix S1 for evidence.

DISCUSSION

Biogeography of the Rufous-thighed Kite

The mainstream literature consistently reports the occurrence of Rufous-thighed Kites in southern Bolivia and northwestern Argentina (Hellmayr & Conover 1949, Brown & Amadon 1968, Short 1975, Blake 1977, Bierregaard 1994, Ferguson-Lees & Christie 2001) and local works have clearly indicated that it is a migrant in these places (Hennessey *et al.* 2003, Cabanne & Seipke 2005, Coconier *et al.* 2007, Juhant 2012). The Rufous-thighed Kite was first considered to be migratory by Mogensen (1930: p. 224), who collected specimens in the Atlantic Forest of Argentina (Appendix S1) and in his routinely overlooked book stated: 'These are certainly migratory birds in Argentina, where they come during the Summer' (our translation). Similarly, literature showing the presence of the Rufous-thighed Kite during the breeding season in the Austral Yungas has existed for over 100 years (Lillo 1909) and coincides with recent reports (Hennessey *et al.* 2003, Coconier *et al.* 2007, and this paper). Lastly, the geographical position of recent records at Concepción between late March and early April by Juhant (2012, see also Appendix S1) is more consistent

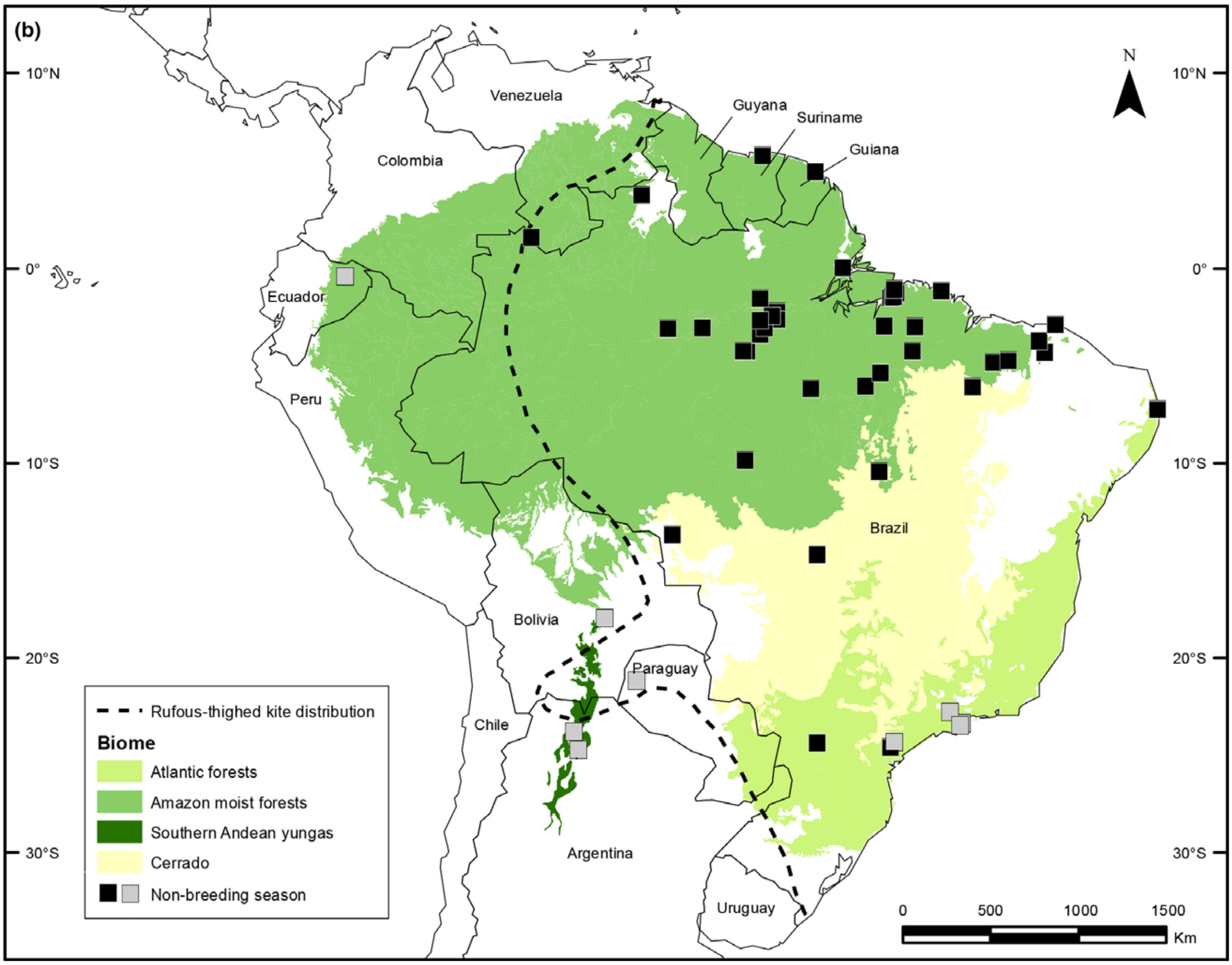

Figure 1b.

with birds migrating northwards from the Austral Yungas foothills (or even from other nearby breeding localities in Cerrado habitat) than with birds migrating westwards from the Atlantic Forest (Fig. 1). Despite these data, the species was either reported directly as an endemic breeder of the Atlantic Forest by Lees and Martin (2015: p. 103 and 111) or as 'a breeding endemic of the Atlantic Forest and pockets of forest of similar vegetative physiognomy in the adjacent Cerrado biome' (p. 108). Unfortunately, published records mentioned in the present work that provided evidence against the 'hidden endemism hypothesis' were overlooked or not discussed in detail by Lees and Martin (2015) (see Supporting Information Appendices S1 and S2 for details).

We conclude that there is no evidence that the Rufous-thighed Kite is an endemic breeder of the Atlantic Forest. Instead, there is at least one confirmed breeding record in the lowland Cerrado of eastern Bolivia, and the regular presence of adults and pairs in the Austral Yungas between October and early April strongly indicates that the species also breeds in this region simultaneously with the timing of confirmed breeding records from the Atlantic Forest (see Appendix S2). Our data also refute possible alternative hypotheses such as considering the Rufous-thighed Kite a vagrant in the Austral Yungas (there are regular records of presumed pairs and groups during the breeding season), and that records in the Austral Yungas during the austral spring and summer may be explained by the persistence of overwintering individuals (there are no documented records from the austral autumn–winter in the Austral Yungas). The essential bits of information necessary to reach

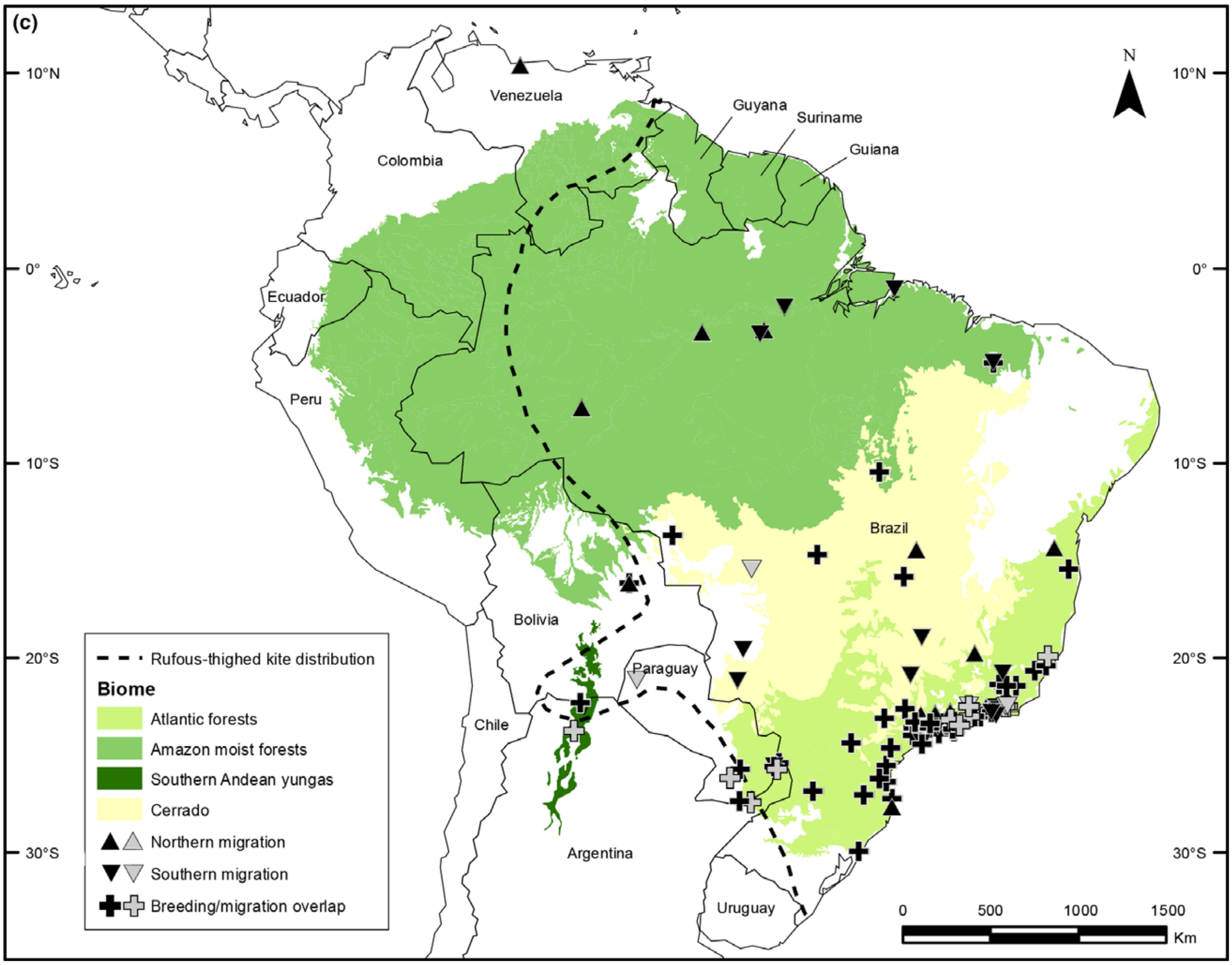

Figure 1c.

these conclusions have been widely available in the literature, and we have here supplemented these with more data to support our arguments. We submit that a more careful consideration of available information prior to the acceptance of a 'readily apparent pattern' of distribution by Lees and Martin (2015) would have resulted in conclusions coincidental with ours.

Periods to study the seasonality of the Rufous-thighed Kite should be established based on moments when a given behaviour is thought to predominate or be widespread at the population level (see Methods). The categories used by Lees and Martin (2015) to segregate records in life-cycle periods (breeding, migration and non-breeding seasons) appear artificial and may introduce biases by narrowing the time span of records belonging to possible breeders and widening the migration period. Although breeding records span October–April (see Lees and Martin's (2015) fig. S2 and appendix S1b), the breeding period (*sensu* Lees & Martin 2015) is restricted to November–February, and their migration period encompassing parts of the austral autumn (March–April) and austral spring (September–October) overlaps extensively with moments when breeding is known to occur (Wolfe 1938, Lees & Martin 2015, Appendix S1).

Taking into consideration cases falling close to the limits of time intervals is crucial to understanding the migration of any species. If not, the emerging pattern might be a product of the chosen categories more than of the underlying biology of the birds. For instance, the breeding female from late October in the eastern Bolivian lowlands (Davis 1993, Fig. S1, Appendix S1) and several breeding records from October, March and April in the Atlantic Forest would have been considered mere migrants if based only on presence data using Lees and Martin's (2015) categories. This suggests that other data from these dates (and other crucial dates with widely overlapping phenologies) need to be filtered with great care given the potential for erroneous conclusions. Supporting this view, the vast majority of records during migration (*sensu* Lees & Martin 2015) occur well within the known breeding period and within the breeding area, which suggests that those authors' migration category might have been too broadly defined (Appendix S1). Our 'migration/breeding overlap' category appears to result in an improvement, in the face of the lack of more precise data, as it provides a buffer of uncertainty at moments in which bird records seem to have fairly even chances of being engaged in any of these activities. Finally, the highly informative figure S1 of Lees and Martin (2015) exhibits problems stemming mostly from database issues readily apparent in their appendix S1a (see enumeration of some such problems in Appendix S3).

To summarize, our analyses clearly indicate that the Rufous-thighed Kite is a widespread breeder in the Atlantic Forest, Cerrado (although possibly patchily distributed) and most likely also in the Austral Yungas of tropical and subtropical South America, with seasonal movements probably throughout its distribution (but see Appendix S2 for discussion of the situation for French Guiana). The Yungas and the Atlantic Forest have long been known to share numerous closely related taxa thought to be identical at the species or subspecies level, some of which also occur in forest patches in Cerrado (Nores 1992, 1994, Silva 1994). However, their avifaunas as a whole are markedly different and both have large numbers of endemic birds (Stattersfield *et al.* 1998). The recognition that Rufous-thighed Kites are present during the breeding season in the Austral Yungas and that they nest across the Cerrado and the Atlantic Forest demands different biogeographical explanations than those accounting for the existence of endemic birds. Now that this pattern is clear (although still imperfectly delineated), fruitful phylogeographical and ecological studies are needed to deepen our knowledge of the biogeography of this forest raptor.

Assessing Wallacean shortfalls

The digital era and citizen science portals have multiplied the evidence available to reconstruct distribution patterns and migratory routes. Citizen science resources will play an important role in clarifying the distribution and movements of birds. This may be especially true for the Neotropical avifauna, which harbours nearly one-third of the birds of the world, all displaying a myriad of lifestyles. Despite the importance of citizen science initiatives, they may not be not sufficient to provide accurate spatiotemporal distributions of all bird species (Dickinson *et al.* 2010, Kamp *et al.* 2016). Solving long-standing Wallacean shortfalls will generally require special searches of data from poorly surveyed areas by all means, and definition of life-cycle categories based on known biological parameters of the study subjects (Remsen 2001). Missing key data may alter conclusions substantially, unintentionally leading to a different sort of Wallacean shortfall.

We propose the following eight recommendations that should help researchers develop critical assessments of spatiotemporal distributions of avian species when using citizen science data:

1. *Follow Lees et al.'s (2014) recommendations.* Lees *et al.* (2014) proposed several valuable measures to guarantee rigorous bird inventories. Application of these measures to single-species distributional analyses should result in methodologically and biologically robust results.
2. *Do not abuse databases.* Even in the 21st century, researchers must unite patchy information from disparate sources to elucidate distributional patterns, and although digitalization of bird collections saves time and money, it remains fundamental for researchers to examine specimens and accompanying labels. As museums improve the digitalization of their collections, including digital pictures of specimens and labels, this task will be simplified. Text-only museum databases should not be used as sources of ready-to-use data but rather as time-saving tools: data should be quality-checked by researchers. This should also include contacting museum curators or collection managers in search of specimens that may have not been databased.
3. *Contact local museums.* Local museums may harbour a wealth of information from areas

not well represented in large international museums. If the distribution of an organism is suspected to include a little-sampled area, it is important to contact these institutions looking for important specimens that may help fill gaps in our knowledge.

4. *Contact local researchers and experienced observers*. Value local knowledge. Neotropical ornithology is a burgeoning field, and numerous excellent ornithologists and students are active in most countries. Local researchers and experienced observers who may have important data from poorly surveyed areas should be contacted.
5. *Read the relevant literature*. Distributional data are spread out in many different sources. The grey literature (i.e. unpublished reports and publications of restricted circulation such as local bulletins and magazines) frequently contains interesting but overlooked records. Any distributional work should strive to find those. If you cannot find them, contact local researchers (see above). Papers in international journals are frequently taken as standard references, and thus they need to provide accurate mapping and relevant sources of information. If dealing with migratory species, make sure to read key references describing seasonality at single localities and to understand migratory systems known to exist in the region of interest.
6. *Study biogeographical patterns*. Other organisms may have distributional patterns similar to that of your study subject. Being aware of these patterns may help you refine, better understand or suspect shortfalls in your distributional analysis. Although large-scale maps may be misleading, do not ignore large areas traditionally mapped as part of the distribution of your subject; instead, go in-depth to uncover on which data they were based.
7. *Try to reject your preferred working hypotheses and question the robustness of your data*. Global distribution analyses will require an effort to describe accurately the distribution in terms of space and time. Be sure to achieve good quality data to allow for robust conclusions at the chosen work scale. A global analysis that fails to obtain available data from a wide portion of the distribution of an organism will mislead researchers, conservationists and policy makers. The same applies to the time dimension, whether when analysing seasonal distribution, changes in historical distributions or recent geographical expansions or retractions. A pattern may be apparent in your data because you have failed to generate/find data capable of rejecting it. Adding more data from nearby or densely sampled localities and/or dates describing the same basic distribution pattern is good because it helps to consolidate it. However, this entails a danger of making you think that you have good enough data when this might not be the case, if you missed the few but crucial records that help uncover a different pattern. Good hypothetical-deductive science works by attempting to reject hypotheses. Your aim should be to reject your preferred hypotheses by looking for records from areas and dates that would have the potential to reject them. Often, these records may not be available in citizen-science databases (see above).
8. *Critically assess life-cycle periods*. Check whether the assignment of records to categories is robust, and test how sensitive your results are to categories defined with different criteria. This may be especially important for little-known species whose biology is imperfectly known (see Biogeography of the Rufous-thighed Kite above).

By following these recommendations, we were able to assess critically the Wallacean shortfall of the Rufous-thighed Kite, and expand on and correct some of the key conclusions put forward by Lees and Martin (2015). For example, by following recommendation no. 4, we consulted observers who submitted their Rufous-thighed Kite observations to eBird and researchers known to work in key places. This resulted in a wealth of documented records from poorly sampled areas (Appendix S1). We have shown that these recommendations can be important tools to assess Wallacean shortfalls and hope they serve other researchers working to clarify the distribution of birds.

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Harrington commented on an early draft. Juan Freile and Quillen Vidoz answered our information requests promptly. We are very thankful to Alex Lees and Rob Martin for gently sharing their impressive database and for the respectful exchange of opinions on the distribution of Rufous-thighed Kites. Alex Jahn, Rebecca Kimball, José A. Sánchez-Zapata and an anonymous reviewer provided thoughtful reviews that improved our work. The members of the ECOSON (E. Depino, I. Holzmann, F. Gandoy, G. Mangini and G. Núñez) provided useful suggestions and criticism. This is Hawk Mountain Sanctuary contribution to conservation science number 299.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Figure S1. Photographs documenting records of Rufous-thighed Kite *Harpagus diodon* demonstrating that the species breeds in Bolivia and occurs in the Austral Yungas foothills of Argentina and Bolivia during the breeding season.

Figure S2. Adult Rufous-thighed Kite *Harpagus diodon* that represents the only documented record of the species in French Guiana. La Carapa, Macouria, French Guiana, between 20 June and 4 July 2014, Jonathan Amirat.

Appendix S1. Full database with records of Rufous-thighed Kite *Harpagus diodon* used in Lees and Martin (2015) and in the present paper. See Figure S1 and text for evidence.

Appendix S2. Details on new and previously published records of Rufous-thighed Kite *Harpagus diodon* in Bolivia and Argentina, and in Ecuador and French Guiana.

Appendix S3. Enumeration of some problems in figure S1 of Lees and Martin (2015).