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Assessing the accuracy of plotless density estimators using census counts to refine population estimates of the vultures of Kruger National Park

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Breeding population estimates for three vulture species in Kruger National Park (KNP), South Africa, were made in 2013 using data from aerial censuses and a plotless density estimator (PDE). PDEs are distance-based methods used to assess sparse populations unsuitable for plot-based methods. A correction factor was applied to the 2013 estimates to reflect the difference between the survey counts and the PDE figures. We flew additional censuses across most of KNP and counted all visible nests to assess the 2013 estimates. Survey counts were within 95% confidence limits of corrected PDE estimates for White-backed Vulture *Gyps africanus* (count: 892; estimate: 904 [95% CI ±162]), at the limit of confidence for White-headed Vulture *Trigonoceps occipitalis* (count: 48; estimate: 60 [±13]) and outside confidence limits for Lappet-faced Vulture *Torgos tracheliotos* (count: 44; estimate: 78 [±18]). Uncorrected PDE estimates accurately reflected White-headed and Lappet-faced Vulture nest counts. The clustered patterns of White-backed Vulture nests and dispersed patterns of White-headed and Lappet-faced Vulture nests offer an explanation for these results and means that corrected PDE densities are inaccurate for estimating dispersed nests but accurate for estimating clustered nests. Using PDE methods, aerial surveys over ~35% of KNP are probably sufficient to assess changes in these vulture populations over time. Our results highlight these globally important breeding populations.

Évaluation de la pertinence des estimateurs de densité sans parcelle par recensement pour améliorer l'estimation des populations de vautours du Parc National du Kruger

Résumé: En 2013, dans le Parc National du Kruger (KNP) en Afrique du Sud, des estimations de population de trois espèces de vautours ont été réalisées à l'aide de données obtenues par recensement aérien et d'un estimateur de densité sans parcelle (PDE). Les PDE sont des procédés d'évaluation basés sur la distance utilisés pour l'estimation de populations clairsemées et pour lesquelles les estimateurs fonctionnant sur la base de parcelles ne sont pas pertinents. Un facteur de correction a été appliqué sur les estimations de 2013 pour refléter les différences entre le recensement par comptage et les valeurs du PDE. Nous avons conduit des recensements additionnels à travers la majorité du KNP en comptant tous les nids croisés, afin d'évaluer les estimations de 2013. Les estimations du PDE corrigés sont dans la limite de l'intervalle de confiance à 95 % en ce qui concerne le Vautour africain *Gyps africanus* (comptage : 892; estimation : 904 [95% CI ± 162]), à la limite de l'intervalle de confiance pour le Vautour à tête blanche *Trigonoceps occipitalis* (comptage : 48; estimation : 60 [± 13]) et en dehors de l'intervalle de confiance pour le Vautour oricou *Torgos tracheliotos* (comptage : 44; estimation : 78 [± 18]). Les estimations du PDE non corrigé reflètent fidèlement le décompte des nids du Vautour à tête blanche et du Vautour oricou. La disposition des nids, regroupée chez le Vautour à tête blanche et dispersée chez le Vautour africains et le Vautour oricou, fournit une explication à ces résultats, et montre que les densités par PDE corrigé sont inadaptées pour l'estimation de nids dispersés mais pertinentes pour l'estimation de nids groupés. En utilisant les méthodes par PDE, des observations aériennes sur environ 35 % du KNP sont probablement suffisantes pour évaluer les variations temporelles de population chez ces trois espèces de vautours. Nos résultats soulignent l'importance globale de ces populations nicheuses.

Keywords: aerial survey, Kruger National Park, population estimates, vultures

Introduction

Whilst monitoring threatened or endangered animals does not provide direct conservation benefits to the species of concern, the provision of population estimates is a fundamental part of conservation efforts because without them the impacts of conservation interventions and/or population changes cannot be assessed accurately. Surveys are obviously an essential part of monitoring, but surveying target species that occur across large areas is problematic, particularly when densities are low. Complete counts in these settings can be impractical or prohibitively expensive and in these situations some method of estimation is usually used (Thompson 2004). Estimates for large areas can be derived from samples obtained by surveying smaller areas (Ríos-Uzeda and Wallace 2007; Murn et al. 2016), and the benefits of doing so are clear. Alternatively, where rapid or repeated assessments are required to assess change, indices of abundance from survey methods such as road transects can be used (Herremans and Herremans-Tonnoeyr 2000; Thiollay 2006a; Prakash et al. 2012).

However, such estimations can be contentious (Hayward and Marlow 2014) and an index of change is not always favourable because indices usually rely on the assumption that the index is linked or somehow directly related to the actual abundance (Stephens et al. 2015). Inaccurate indices can have large impacts on subsequent population assessments (Katzner et al. 2011), and so linking them to actual measures of abundance such as breeding populations can improve confidence in their accuracy (Hayward et al. 2015). Any method of population estimation should be validated and calibrated wherever possible, as such estimates are often the basis of national and international policy and regulation (Stephens et al. 2015).

Monitoring changes in African vulture populations has become an important activity because of the threats vultures are facing on the continent along with the rapid decline of most species (Ogada et al. 2016). However, monitoring vulture populations is challenging as they are highly mobile and can cover vast distances during foraging (Phipps et al. 2013). Counting numbers of individual birds that attend feeding events is variable (Pomeroy et al. 2012) and will be affected by spatiotemporal factors, such as carcass availability (Kane et al. 2014), the condition of individual birds (Spiegel et al. 2013), local weather, land use (Murn and Anderson 2008), feeding history, the behaviour of conspecifics (Jackson et al. 2008) or even currently poorly understood factors such as cognitive ability (López-López et al. 2013), among others. Similar reasons for variation in vulture occurrence will affect counts made during road transects (Thiollay 2006a; Virani et al. 2011; Pomeroy et al. 2015), although this method has been used extensively to generate and assess changes in indices of abundance, which have highlighted major declines of vultures (Thiollay 2006b; Virani et al. 2011; Ogada et al. 2016).

In addition to indices of population change, there is a need to determine the actual size of vulture populations because large local or regional populations may provide buffering against general declines or act as source populations for other breeding areas. Achieving this aim, in addition to linking indices with changes in actual vulture populations, can be achieved by monitoring breeding populations. However, although some vulture species are spatially restricted in their breeding distribution (Borello and Borello 2002; Krüger et al. 2014), tree-nesting vultures often occur at low density and may be spread across large areas (Pennycuick 1976; Murn and Holloway 2014) or characterised by clustered patterns (Murn et al. 2002; Bamford et al. 2009). Both situations present challenges for either total counts or estimates made by extrapolation.

Here we examine population estimates for three tree-nesting vulture species (African White-backed Vulture *Gyps africanus* [AWbV], Lappet-faced Vulture *Torgos tracheliotos* [LfV] and White-headed Vulture *Trigonoceps occipitalis* [WhV]) that were made using plotless density estimators (PDEs) in Kruger National Park (Murn et al. 2013) to (1) assess and calibrate the accuracy of the previous estimates from 2013 and (2) assess the utility of the method of surveying limited areas and extrapolating to a larger area.

Methods

Study area and previous population estimates

The study was conducted in Kruger National Park (KNP) in north-eastern South Africa (Figure 1), which covers approximately 20 000 km². In 2011, two areas of KNP were surveyed completely by helicopter: a high nest density (HD) area of ~3 350 km² (approximately 17%) in southern KNP and a low nest density (LD) area of ~3 600 km² (approximately 18%) in northern KNP. Full details of the area definitions, flight routes and survey methods can be found in Murn et al. (2013). Briefly, all active nests of the target species were counted within the survey areas and these data were

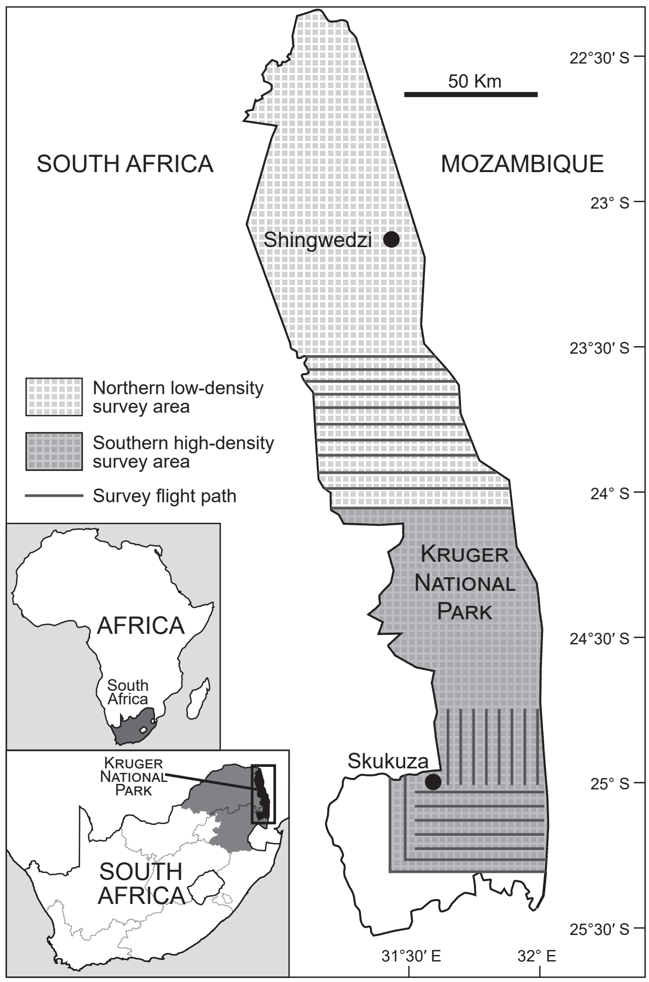

Figure 1: Location of Kruger National Park in South Africa and the northern low-density and southern high-density areas used in the study. Lines show direction of flight survey routes in 2011. Light shading shows the southern high-density and northern low-density areas and the total area covered by aerial surveys

tested for spatial randomness of the nests. To generate breeding population estimates across the whole of KNP, Byth's *T*-square estimator (Byth 1982), a PDE, was used to generate nest densities in the HD and LD survey areas.

Plotless density estimators are distance-based methods of density estimation that were developed to overcome the limitations imposed by sparse populations on plot-based sampling methods (Engeman et al. 1994). *T*-square sampling starts at a random point within a study area, from which the distance to the nearest point of interest (i.e. nest) is measured. Then the distance to that nest's nearest neighbour is measured, but on the opposite side of a plane divided by a perpendicular line running through the first nest. Byth's robust *T*-square estimator TSRB (Byth 1982), which was developed to cope with non-random distributions, generates a density estimate as follows:

$$\text{TSRB} = N^2 \Big/ \left(2\sum_{i=1}^{N} R_i\right)\left(\sqrt{2}\right)\left(\sum_{i=1}^{N} T_i\right)$$

where N is the number of nests, R_i is the distance from the ith random point to the nearest nest and T_i is the distance from the nearest nest to its nearest neighbour.

A correction factor was applied in 2013 to the estimate made using Byth's *T*-square because it was clear that the PDE underestimated both the density and number of nests. This was based on the number of AWbV nests counted during the aerial surveys being much higher than the estimate provided by the subsequent PDE calculations, and so a correction factor was applied that represented the amount by which the PDE figure differed from the survey counts. For the purposes of consistency, the same correction factor that was applied to the AWbV PDE was also applied to the LfV and WhVs.

The corrected densities were then applied to the total size of the high nest density area and the low nest density area across the entire KNP. The population estimate for each area was the product of the estimated density and the size of the area. The HD and LD estimates were added together to generate breeding population estimates for the three species in KNP.

Additional surveys and data comparison

Subsequent to the 2011 aerial surveys, ground surveys and monitoring of nests and nesting areas in KNP continued between 2012 and 2015. During 2014 and 2015, approximately 64 h and 6 800 km of additional survey flights were completed by helicopter across the remaining areas of KNP that were not covered during the 2011 aerial survey. These flights used the same methods and resulted in virtually complete coverage (92%) of the entire KNP across five years (2011–2015). The area in the far south-west of the park was not covered during the aerial surveys as this area is characterised by Lowveld Sour Bushveld and Malelane Mountain Bushveld landscape types (Gertenbach 1983), which are characterised by vegetation communities dominated by *Terminalia sericea* and *Dichrostachys cinerea* or *Combretum epiculatum.* These areas contain limited numbers of acacia trees available for nesting, which are preferred by vultures nesting in KNP (Kemp and Kemp 1975; Deacon 2004; Murn and Holloway 2014). Some survey areas that were known from ground fieldwork to have very low nest densities were double-checked using a fixed-wing aeroplane. All observed nest positions were logged with a hand-held GPS using waypoint and track log functions, plus a PDS/Smartphone running CyberTracker 3.353 software (CyberTracker, Cape Town, South Africa; http://www.cybertracker.org). A nest was only recorded as active if it contained an adult sitting in an incubating position, a chick, an egg or egg remains.

Counts of active nests from all aerial survey years (2011, 2014 and 2015) were pooled and added together for each species. We compared the survey totals to the projected populations for the three vulture species that were generated from the corrected *T*-square density estimates (in Murn et al. 2013). We also compared the survey totals to the population estimates generated by the uncorrected *T*-square PDE.

Results

Table 1 shows the total numbers of nests counted compared with the population estimates that were made in 2013.

The corrected *T*-square estimates from 2013 (essentially census density) were very accurate for AWbV, but inaccurate for LfV and WhV (Table 1). The variations in estimation accuracy were apparent in both the high density (HD) and low density (LD) areas, but the inaccuracy of the corrected *T*-square estimate was most pronounced in the high-density area, where numbers of nests for LfV and WhV were overestimated considerably (Figure 2).

Conversely, the uncorrected *T*-square estimates (not shown in Table 1 or Figure 2) were very inaccurate for AWbV (uncorrected *T*-square estimate 393 [95% CI ±70], survey count 892) but very accurate for LfV (uncorrected *T*-square estimate 49 [95% CI ±11], survey count 44) and WhV (uncorrected *T*-square estimate 51 [95% CI ±11], survey count 48); even the small difference in the actual number of recorded nests for these two species was reflected by the uncorrected *T*-square PDE estimate.

Taking into account the full aerial survey results and the uncorrected *T*-square PDE, the breeding population

Table 1: Numbers of nests of tree-nesting vultures counted by aerial surveys between 2011 and 2015 compared with estimates generated in 2013 in the Kruger National Park, South Africa

	Nests		
	African White-backed Vulture	Lappet-faced Vulture	White-headed Vulture
Total nest counts from aerial surveys	892	44	48
Projected KNP breeding population – corrected *T*-square estimates (Murn et al. 2013)	904 (95% CI ±162)	78 (95% CI ±18)	60 (95% CI ±13)

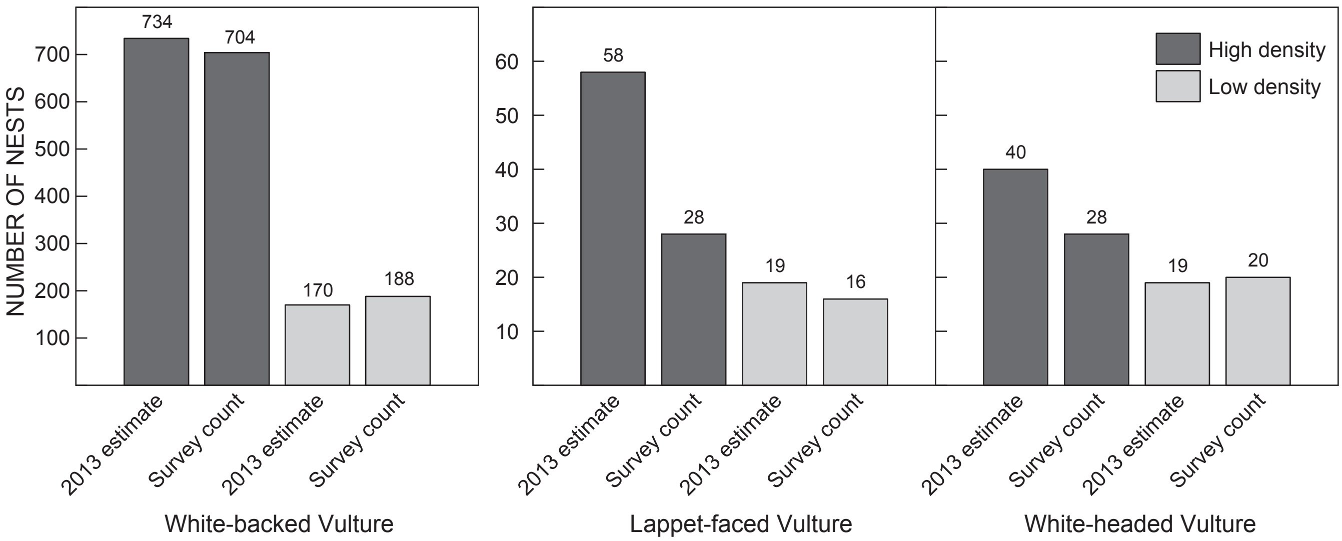

Figure 2: Comparison of survey counts of nests with 2013 estimates for three vulture species in high density (HD) and low density (LD) areas of Kruger National Park, South Africa. See Table 1 for totals of estimates and counts. The 2013 estimates are derived from a corrected *T*-square plotless density estimator

estimate for AWbV in KNP of 904 (95% CI ±162) nests remains unaltered from the 2013 estimate. Using the uncorrected *T*-square PDE, the number of LfV nests is revised to 49 (95% CI ±11) and the number of WhV nests is revised to 51 (95% CI ±11).

Discussion

The aerial survey counts described here enable an objective assessment of our population estimates from 2013; these estimates were made by using Byth's *T*-square PDE to calculate densities in two samples areas of KNP and then extrapolating from the sample areas to KNP as a whole.

The results from the aerial survey counts across the entire KNP highlight that applying a correction factor to the *T*-square PDE was inappropriate for determining the LfV and WhV nest densities, because doing so generated an overestimate of their densities and populations. Conversely, the distribution and pattern of the White-backed Vulture nests confounded the PDE and necessitated the correction factor.

These differences in the accuracy of the *T*-square PDE between the AWbV and the two other species are most likely due to the different spatial pattern of the nests of these species. The clustering pattern of nests (along rivers especially) of the AWbV (Monadjem 2003; Murn et al. 2013) led to underestimation by the *T*-square method, whereas the dispersed and solitary-nesting LfV (Mundy 1982) and WhV (Hustler and Howells 1988; Murn and Holloway 2014) is suited to the method. The spatial characteristics of nests for the three species were investigated and described in 2013 (see Tables 1 and 2 in Murn et al. 2013) and these should have been taken into account when deciding whether or not to apply the correction factor to the 2013 density estimates. The accuracy of population estimates of other species being assessed will also be improved if an analysis of spatial patterns is done prior to determining the appropriate extrapolation methods from surveys of fixed points spread across large areas. Such a method would be applicable to other large tree-nesting raptors, such as Tawny Eagle *Aquila rapax* or African Hawk-eagle *Aquila spilogaster*.

Using pooled nest count totals that were collected over four years could possibly be susceptible to some degree of error, as within breeding areas of AWbVs and also for individual nests of LfVs and WhVs, there is some turnover of nests each year; pairs fail to breed, breeding adults die, territorial pairs do not make a breeding attempt and new nests can be built. Similarly, nests that collapse through the tree canopy or fall out of the nest tree completely will potentially be missed during an aerial survey, but this is a rare occurrence and birds will often rebuild during the same breeding season should a collapse occur (CM unpublished data). Despite this potential for change, twice-yearly ground surveys in 10 different areas of KNP that have been monitored closely since 2008 have not shown major increases or decreases in numbers of nests (CM and AB unpublished data). As a result, we consider the possibility of unrecorded breeding attempts to be low and likely to have negligible impact on the survey totals presented here.

Despite the park-wide survey counts leading to a downward revision of the 2013 population estimates for LfV and WhV, a valuable result is that breeding populations of the three vulture species in KNP can be determined with a high degree of confidence using survey data obtained from only a subset of the park's total area, as was surveyed in 2011 for the 2013 estimates. Using the *T*-square PDE for LfV and WhV and a direct extrapolation from the aerial counts of AWbV nests, these methods of estimation produced results very close to the actual counts. This means that in future, populations of these three species can be monitored by surveying by air the areas covered in 2011 – a southern high-density area of approximately 3 500 km^2 and a similarly-sized northern low-density area. This equates to less than half the total size of KNP (~35%), but incorporates the key vulture breeding areas of open savanna, riverine clusters and low nest density northern plains.

The revised density estimates for LfV and WhV do not significantly alter the comparison of breeding densities of these species in KNP with other reported areas (Table 5 in Murn et al. 2013). The density of breeding LfV in KNP is generally low compared to studies from other areas of southern Africa, such as parts of Zimbabwe (Mundy 1982), Swaziland (Monadjem and Garcelon 2005) and Namibia (Bridgeford and Bridgeford 2003) – though these data are now at least 10 years old or more. The breeding density of WhV is generally consistent across a range of sites and the revised estimates here are almost identical to Hwange National Park in Zimbabwe (Hustler and Howells 1988) and the Serengeti (Pennycuick 1976), but again, these comparative data are old.

This paper revises important baseline parameters that, in combination with population estimates done previously (Murn et al. 2013), can be used for comparison with future estimates from aerial surveys. Given the poor conservation status of most vultures, this is important information. African White-backed Vultures and White-headed Vultures are listed as Critically Endangered, and the Lappet-faced Vulture is Endangered (BirdLife International 2015); KNP and its surrounding areas continue to hold internationally significant populations of these species, which face a variety of threats across other parts of the continent (Ogada et al. 2016). Given that it is now reasonably well-known how far vultures can travel (Phipps et al. 2013; Kendall et al. 2014), and the fact that vultures face an uncertain future outside protected areas, the importance of large breeding populations in national parks such as KNP can only be emphasised further.

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