The relative contribution of camera trap technology and citizen science for estimating survival of an endangered African vulture

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ABSTRACT

Technological advances such as camera traps, and citizen science, coupled with advanced quantitative approaches, can help fill existing knowledge gaps and aid effective conservation.

We combine citizen and camera trap observations to estimate survival of the Endangered lappet-faced vulture, assess the relative contribution of data from camera traps and citizens, as well as impact of loss of individual marks (wing tags), on survival estimates.

We used data from 762 lappet-faced vultures wing tagged as nestlings during 2006–2017 in western Namibia. Observations of wing tagged individuals were provided by citizens or via camera traps. We formulated a multievent capture-mark-recapture model to estimate survival while accounting for probabilities of resighting by citizens and/or camera traps, recovery of dead individuals, and loss of the wing tag.

Survival was relatively high for juveniles (0.79), and increased with age to 0.95. Citizen observations of live and dead birds were low in number. However, when combined with camera trap resightings of live individuals, citizen observations increased the precision of survival estimates of birds older than one year compared to using data from either sources separately. Wing tag loss was high after 5–6 years of tag age. If neglected, tag loss can result in severe underestimation of survival of the older age classes.

Overall, we show that filling ecological knowledge gaps is possible through the efficient use of data provided by different sources, and by applying state-of the art approaches that minimise potential biases, such as those due to tag loss.

1. Introduction

Biodiversity is being lost worldwide at unprecedented rates (IPBES, 2019). Averting the collapse of biodiversity and the associated ecosystem services it supports may still be possible, but increased efforts are required (Ceballos et al., 2015; IPBES, 2019). Conservation efforts can only be effective if adequate basic ecological knowledge of the species and their threats are available (Soulé, 1986; Sutherland et al., 2004). While a recent call strongly highlighted the fundamental value of basic ecological research for conservation (Courchamp et al., 2015), widespread gaps in basic demographic knowledge of species are still pervasive across most taxa (Conde et al., 2019). Critically, adequate information on key demographic parameters, such as birth and death rates, is available from only 1.3% of the world's tetrapod species (Conde et al., 2019). This lack of basic ecological knowledge hinders species conservation policies, which, under urgent and critical circumstances, are often designed and implemented in the dark (Cook et al., 2010).

In recent decades, technologies are revolutionizing the way biodiversity and environmental data are being collected and potentially used for conservation (Pimm et al., 2015). Among such technologies, camera traps are becoming a very common tool in ecology and conservation, and have recently been demonstrated as an effective sampling tool
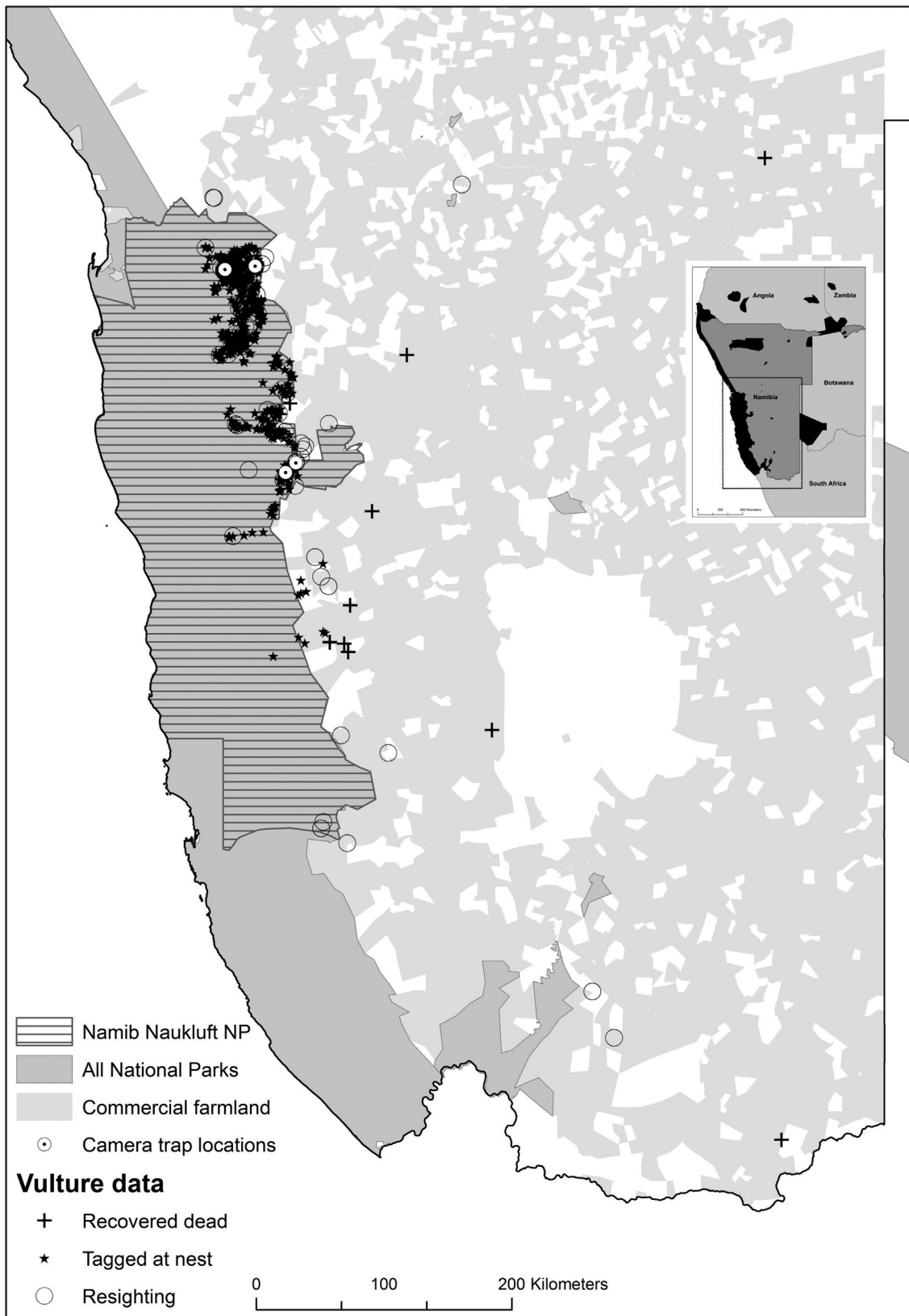
Fig. 1. The distribution of the marked (wing tagged at the nest) and resighted lappet-faced vultures, as well as recoveries of dead vultures, within the study region in Western Namibia. The large map also shows the boundary of the Namib-Naukluft Park, as well as other protected areas and unprotected land dominated by commercial farmland. The inset map shows the location of the study region with respect to Namibia and its neighbouring countries, as well as protected areas.

compared to other methods (Wearn and Glover-Kapfer, 2019). Camera trap projects have been also implemented in synergy with citizen science, whereby observers from anywhere in the world can contribute by classifying camera trap born images placed on web portals (Swanson et al., 2015). However, the most common contribution of citizen science is typically through wildlife observations (Tulloch et al., 2013). The field of ornithology provides an exemplary case of that, with thousands of citizens across the world collecting information. Combined with advanced analytical approaches, the large amount of information derived from technology and citizen science offer unprecedented opportunities to fill the existing gaps in basic ecological knowledge (La Sorte and Somveille, 2020).

Filling such gaps is important particularly for the most imperiled species, such as many Old World vultures. This group of obligate scavengers forms a key functional guild contributing to ecosystems health and functioning (Buechley and Şekercioğlu, 2016). The long lifespan of vultures typically requires relatively long-term field studies until basic ecological knowledge, especially survival, can be robustly quantified (Badia-Boher et al., 2019). Therefore, studying vulture survival in particular is very challenging. At the same time, survival, especially that of adults, is a key demographic parameter driving population trajectories in long-lived species like vultures (Monadjem et al., 2013; Sanz-Aguilar et al., 2015b). For many species, such as the Endangered lappet-faced vulture *Torgos tracheliotos*, survival is totally unknown. This lack of knowledge hinders a holistic assessment of current and future population persistence, thereby compromising our ability to implement conservation interventions targeting key demographic parameters.

To date, not all studies quantifying vulture survival have explicitly accounted for the loss of marks, such as wing (patagial) tags or color rings (but see Badia-Boher et al., 2019; Le Gouar et al., 2008; Lieury et al., 2015), which is known to increase as the marks age. This is unfortunate given the popularity of such marks in projects marking individual vultures of different species, and the importance that survival estimates have in driving population trajectories of such long-lived species (Sanz-Aguilar et al., 2015b).

Here, we combine citizen science opportunistic observations of both alive and dead vultures with systematic recordings from camera traps to estimate, for the first time, the survival of lappet-faced vultures using a multievent capture-mark-recapture modeling framework. We take advantage of an intensive long-term wing tagging program of vulture nestlings in a population inhabiting the Namib-Naukluft Park in Namibia. Most nestlings in the area were fitted with a wing tag and could then be observed by citizens or recorded with camera traps. Specifically, we aim to i) assess the relative contribution of data provided by a citizen science program aimed at reporting live vultures with a wing tag (or dead vultures with at least a metal ring), and the recapture data provided by a more recent camera trap program; ii) quantify the survival rate of lappet-faced vultures by age classes; iii) quantify the potential bias on survival estimates due to ignoring the loss of wing tags.

2. Materials and methods

2.1. Ethics statement

The work was conducted in accordance with all relevant national and international guidelines. The handling and wing tagging of nestlings were carried out by experienced bird ringers holding a valid ringing license approved by the Namibian Ministry of Environment and Tourism, and following the guidelines for ringing provided by SAFRING (http://safring.adu.org.za/).

2.2. Study species and study region

The study took place in the southwestern part of Namibia. The

region is dominated by arid savannah landscapes characterized by sparse woodland, which gives way to progressively more barren land and sandy dune deserts towards the west side until the coast (Mendelsohn et al., 2002). The latter is the dominant landscape present in the Namib-Naukluft Park, the largest protected area in the region (Fig. 1). Unprotected areas in southern Namibia are dominated by commercial livestock farmland, with sheep and goat being the dominant stock bred, with the addition of localized game farming as well as farms focused on ecotourism (Mendelsohn et al., 2002). In these commercial farmland areas, poison use by farmers aimed at eliminating livestock predators, such as jackals and hyenas, is very common (Santangeli et al., 2016). Through the years, this has caused multiple mortalities of vultures, largely attributed to unintentional poisoning (Santangeli et al., 2017).

We focused on the lappet-faced vulture, one of the largest obligate avian scavengers in Africa. The sexes of this species can, to some extent, be differentiated morphologically in the adults (Bamford et al., 2010), but nestlings' sex can only be separated by means of DNA analyses (Mundy et al., 1992). Lappet-faced vultures typically nest on trees in the dry savannah, mostly represented by Acacia (now Vachellia) species (Simmons et al., 2015). The lappet-faced vulture is classified as Endangered by IUCN owing to its rapid and continent-wide population declines that are likely to continue into the future (Ogada et al., 2016; Simmons et al., 2015). The main threats to the species are intentional and unintentional poisoning, habitat degradation and collision mortality with infrastructures (Botha et al., 2017). In Southern Africa, breeding occurs during the Austral winter, with hatching taking place during the middle of the dry season, typically between July and August. The species lays one egg and the nestling period lasts about four months (Mundy et al., 1992). This period coincides with progressively drying conditions in Namibia, which typically exacerbate towards the second half of the nestling period, between September and December (Mendelsohn et al., 2002). In Namibia, it is estimated that there are about 500 breeding pairs of the lappet-faced vulture (Simmons et al., 2015). Of these, the stronghold is concentrated within the Namib-Naukluft Park (Simmons et al., 2015) in the West of the country (Fig. 1).

2.3. Vulture marking

The study was based on the population of lappet-faced vultures that hatched within or near the Namib-Naukluft Park. This breeding population has been monitored since 1991, when efforts to find vulture nests and ring the chicks were initiated. Such efforts increased up to the year 2006, after which efforts have remained largely constant (Santangeli et al., 2018). From 2006, active nests were searched by means of aerial surveys, followed by ground fieldwork whereby all nests detected from the air are visited. Nestlings were fitted with a stainless-steel ring and marked with a wing tag (Santangeli et al., 2018) to aid their subsequent identification. Until the year 2014 a wing tag on only one wing of each individual was placed, but from 2015 a wing tag per each wing was placed. Nestlings were ringed at the age between one month and before fledging, whereas wing tags were placed on nestlings of about 1.5 months of age or older. If during the first nest visit a chick was too small to be ringed and/or tagged with a wing tag, a second visit to that nest was done at a later stage during the breeding season. The whole procedure of ringing and marking with a wing tag typically lasted half an hour or less (Santangeli et al., 2018). The same survey was performed every year from 2006 onwards. The total number of vulture nestlings ringed during the 12 years of study (2006–2017) in the region was 762 individuals.

2.4. Vulture resighting

Resighting data of vultures with a wing tag were obtained from two sources: opportunistic observations from citizens (hereafter citizen

observations), and observations of marked individuals from camera traps (hereafter camera trap observations). Citizen observations consisted largely of sightings made by tourists, park rangers, farmers, birdwatchers and photographers, who typically took pictures or found dead marked individuals. These observations (including species, ring number, coordinates, other ancillary information) were reported to the central administrators of the vulture mark and resighting database managed by Vultures Namibia, the local vulture conservation group. An information campaign was run in the region through the years to make the public aware of the vulture tagging program, and to give guidance on what information to report when a live vulture with a wing tag (or a dead vulture with at least metal ring) was sighted or recovered dead and where to report that information. From the year 2014, a program aimed at resighting vultures with a tag via camera traps was initiated. Camera traps were placed around water points, which are regularly visited by vultures, particularly during the breeding season (e.g. September through January) in the Namib-Naukluft Park. The camera trap project started in 2014 with installation of two cameras at one water point (each camera placed at either side of the water point and facing the water) in the northern part of the Park. In 2015 another single camera trap was installed at a different water point in the same area of the Park. Finally, in 2017 camera traps were installed at two additional water points (two cameras at each water point) located in the central part of the Park (see Fig. 1). The cameras (currently totaling 7, at 4 different locations) have been recording continuously since their installation, taking pictures of any moving animal occurring at and around the water point during day time. All images from the cameras have been manually scanned and inspected to identify tagged vultures, and to read the wing tag number. The information was then directly entered in the database. Live birds have been only resighted through camera traps or citizens when they were carrying a wing tag, that is, no birds having only a metal ring have been resighted alive due to the challenges in reading the metal ring code from distance. However, recoveries of dead birds, among those 762 that were initially wing tagged as nestlings, were based on identification through their metal ring only. In these cases, no information was provided whether the bird was still carrying a wing tag or not. This is because such information was not collected in the field because of omission or because it was impossible owing to only part of the body being left on the place.

2.5. Survival model and model selection

For the survival analyses, we used data from nestlings that hatched between 2006 and 2017 and that were wing tagged, in addition to having a metal ring. We restricted the resighting period for analyses to roughly match the nestling and early fledgling phases of the lappet-faced vultures in the study area, from 1st September to 15th of January. While long, this period maximizes the use of resighting data which are largely concentrated during this dry season of the year. This long encounter period is thus believed to provide a good balance between usage of the available information while assuming zero mortality through this period. The latter is a reasonable assumption, because the long lifespan and high expected survival of the species minimizes the risk of biases due to mortality occurring within the encounter period, which may be the case for short-lived species (O'Brien et al., 2005). For the survival analyses (see below for more details), data have been organized so that the life-history of each individual is represented by a row in the database. Each row starts with the year of birth coded as "1", and progressing from left to right through each successive resighting period in the following years until the year 2018 (the most recent year when resightings are available). We coded differently the resightings coming from citizen observations ("1"), those coming from camera traps ("2"), and those from both citizens and camera traps ("3"). Recoveries of dead individuals were coded as "4". Any other cells where the above did not apply were coded as zeroes, i.e. the bird was not yet born or was not observed. Overall, from the 762 nestlings born and

wing tagged during 2006–2017, a total of 22 live resightings (from 21 live individuals) were reported by citizens, 748 from camera traps (from 386 individuals), and 22 from both methods, whereas 18 birds were recovered dead. As a result of the above, most resighting information is concentrated during the period from 2014 to 2018, when the camera traps were operating. A total of 399 (52% of all 762 wing tagged individuals) were resighted by either method at least once (i.e. in at least one encounter period after their natal year), and 226 (30%) resighted more than once. Mean number of resightings per individual was 1.04 (range: 0–5), with average birds age when last resighted being 5.1 years (range: 1–10; considering only the 399 birds resighted at least once). A total of 153 birds were last resighted at age ≥ 5 years, 108 at age ≥ 6 years, 64 at age ≥ 7 years, 29 at age ≥ 8 years, 10 at age ≥ 9 years, and 1 at the age of 10 years. The above information underscores that there is a substantial number of resightings of birds of 5 years of age or older to allow estimating survival of various age classes.

We used multievent capture-mark-recapture models (Pradel, 2005) to model simultaneously tag loss, survival, resighting and recovery probabilities (Badia-Boher et al., 2019). As goodness-of-fit (GOF) tests for multievent models have not been developed yet, we assessed the GOF for the Jolly Movement multistate model in the software U-CARE 2.3.2 (Choquet et al., 2009a). The overall GOF test was not statistically significant (χ^2 = 19.741, d.f. = 30, p = .923), indicating that no extra parameters were needed to account for heterogeneity in survival or resighting probabilities.

Multievent models include three types of parameters: the initial state parameters that account for the annual proportions of individuals starting at each state; the transition parameters that account for transitions between biological states; and the event parameters that relate the observations encoded in the encounter histories (see above) to the biological parameters. In our case, as wing tags deteriorate with time and can be lost (Monadjem et al., 2013), our model included an unobservable state for live individuals that lost their wing tag. The states considered in our model were: At- bird alive carrying a wing tag; An-bird alive not carrying a wing tag; RD- bird recently dead; and D- bird dead since long time. Note that vultures alive carrying only a metal ring were not resighted and this state was the unobservable state. On the contrary, individuals that have lost the wing tag can be identified by their metal ring if recovered dead. Consequently, the recently dead state is shared by dead individuals carrying wing tags or only metal rings (see further details on the multievent modeling in Appendix 1 – extended methods). Moreover, in order to estimate recovery probabilities, multistate or multievent models require two dead states, a recently dead state in which dead animals can be observable (i.e. recovered) and a long dead state in which animals are not observable (see Badia-Boher et al., 2019; Lebreton et al., 1999).

The Multievent model was implemented in the software *E*-SURGE (Choquet et al., 2009b) that estimates simultaneously the parameters of interest by maximum likelihood, and automatically computes model deviance and AICc (more details of the model specification in Supplementary material Appendix 1 – Extended methods). We started model selection with a general model (Table 1) considering: 1) a linear effect on the logit scale of tag age on tag loss probabilities; 2) variation in survival probabilities as a function of age until age 4; 3) year dependent resighting probabilities by the different methods; and 4) year independent recovery probabilities of dead individuals (Model 1). We set resighting parameters as general as possible and we first modeled tag loss probabilities (Models 1–3). Next, using the above model structure that minimized AICc, we tested if resighting probabilities were equivalent during periods holding the same number of camera sites or cameras per se or constant after 2014 (the year when camera traps started to operate) (Models 4–6). Finally, we modeled survival probabilities as a function of different age structures (yearly differences up to age 2, 3, 4 or 5; similar survival for sub-adults aged 2–3, 2–4 or 3–4, Models 7–12 see details in Table 1). Model selection was based on

Table 1

Modeling the probabilities of tag loss, resighting and survival of lappet-faced vultures in Namibia. Tag loss probabilities were modeled with a linear trend on the logit scale with years since ringing (A), logarithmic trend (A_{log}), exponential trend (A_{exp}), or a constant parameter ("."). Resighting of birds carrying wing tags were modeled as either time dependent (time), as a function of the number of sites with camera traps (N sites), of the number of camera traps (N cam) or as constant after camera trap deployment in 2014 ("."). Recovery probabilities of dead individuals were constant for all models. Survival was modeled as a function of individual age (e.g. a1/a2/≥a3 considered survival of a1 juvenile birds, a2 two years old birds, and /≥a3 birds three years or older; a1/a2–4/≥a5 considered a1 juvenile birds, a2–4 two to four years old birds, and /≥a5 birds five years or older). Np = number of parameters; Dev = deviance; AICc = second-order corrected Akaike's information criterion; ΔAICc = difference in AICc with the model showing lowest AICc (in bold), AICw = Akaike weight.

Model	Tag loss	Survival	Resight	Np	Dev	AICc	ΔAICc	AICw
9	**A**	**a1/≥a2**	**time**	**21**	**3513.37**	**3555.97**	**0.00**	**0.26**
10	A	a1/a2–4/≥a5	time	22	3511.88	3556.54	0.57	0.19
8	A	a1/a2/≥a3	time	22	3512.14	3556.79	0.82	0.17
7	A	a1/a2–3/≥a4	time	22	3512.45	3557.10	1.14	0.14
12	A	a1/a2/a3–4/≥a5	time	23	3511.34	3558.05	2.08	0.09
1	A	a1/a2/a3/≥a4	time	23	3511.95	3558.67	2.70	0.07
2	A_{log}	a1/a2/a3/≥a4	time	23	3513.05	3559.76	3.79	0.04
11	A	a1/a2/a3/a4/≥a5	time	24	3511.23	3560.01	4.04	0.03
4	A	a1/a2/a3/≥a4	N cam	21	3521.50	3564.09	8.13	0
5	A	a1/a2/a3/≥a4	N sites	20	3524.04	3564.58	8.61	0
6	A	a1/a2/a3/≥a4	.	19	3531.37	3569.86	13.90	0
3	.	a1/a2/a3/≥a4	time	22	3581.59	3626.24	70.28	0

Akaike's Information Criterion adjusted for small sample sizes (AICc; Burnham and Anderson, 2002). The model with the lowest AICc was considered the best model fitting the data. Model averaged estimates were calculated by multiplying the real scale estimates provided by program E-Surge by the Akaike weights (AIC_w) of the different competing models and doing the summation for the parameter of interest (Burnham and Anderson, 2002). For obtaining model averaged CI estimates we followed the analytical procedure detailed in Cooch and White (2014).

Next, using the best survival structure found in the previous analysis we aimed to compare survival estimates and the relative contribution of resightings coming from camera traps only, and from citizens only, by running two separate models. The above models were run using data from camera traps only, or from citizens only, in the latter case including both resights and recoveries (results shown in Supplementary Table A1). Finally, in order to estimate the potential bias in survival estimates when tag loss is ignored, we modeled again survival using all the available data but now fixing tag loss to zero.

Validation of the multievent model proposed here to estimate simultaneously survival and tag loss probabilities was performed using simulated data (see details in Supplementary material Appendix 2).

3. Results

3.1. Relative contribution from citizens and camera traps

The resighting part of the model, i.e. resightings obtained from either citizens or camera traps, was best fitted by a function composed of a constant resighting probability for the period before the onset of the camera trap (i.e. before year 2014), and a yearly varying resighting probability during the period when camera traps were operational (2014–2018). Other functions fitting the resighting data yielded suboptimal models based on AICc (Table 1). Before the implementation of camera traps, the probabilities of resighting a live marked vulture by citizen reports were only 0.01 (95%CI = 0.01–0.02). After 2014, when camera traps started to operate, mean resighting probabilities greatly increased, ranging from 0.45 to 0.64 (Supplementary Table A1). The recovery probabilities of dead individuals were estimated at 0.05 (95%CI = 0.03–0.08).

As expected, relative contribution of resighting observations from camera traps dominated the share of all resighting data already from the onset of the camera trap usage in 2014 (Supplementary Table A1). When using only the few resightings from citizens, which also included recoveries of dead birds, the estimated survival was less precise (i.e.

wider 95% CI) and probably biased, as the model was not able to properly separate the estimation of tag loss and survival probabilities (Supplementary Table A1). Conversely, survival estimates derived using only resightings from camera traps broadly aligned to those using both methods combined, but the precision of survival estimates of the older age class was lower when using only camera trap data compared to all data, as shown by the wider 95% CI around the former (Supplementary Table A1).

3.2. Survival estimates and associated biases from ignoring tag loss

Tag loss was best captured by a function that assumed that the probability of losing a tag linearly increases with tag age on the logit scale (see Table 1 and Fig. 2). Tag loss probability was very low, below 10%, for tags of age less than six years, but rapidly increased to reach values of over 80% when tags were ten years old or older (Fig. 2). Models with a logarithmic function were very similar in terms of AICc (Table 1), and provided very similar estimates (results not shown) of tag loss and survival probabilities. We therefore consider only the linear tag loss function to model survival.

The best age structure model for survival included two separate age classes for first year juveniles and older birds (Model 9 in Table 1). However, alternative models were equally supported based on AICc. Thus, we used all models with different survival structure but with same tag loss structure to obtain model averaged estimates of survival for the different age classes (Models 1, 7–12, Table 1; estimates for each of the 7 individual models are shown in Supplementary Table A2). The unbiased survival (i.e. estimated by taking into account tag loss over time) probability estimates increased particularly from the first year of life (0.79, 95% CI: 0.73–0.84) to the second year (0.91, 95% CI: 0.86–0.95; Fig. 2). Survival showed a minor increase to age classes three years and older and reached a mean value of 0.95 (95% CI: 0.85–0.98) for five years old birds and older (Fig. 2). Conversely, not accounting for tag loss by age results in very similar estimates of survival probability for all age classes up to four years as those obtained when tag loss is accounted for (Fig. 2; competing models not accounting for tag loss presented in Supplementary Table A3). However, for the oldest age class of 5 years and older, survival probability was underestimated when tag loss was ignored, with mean 0.74 (95% CI: 0.69–0.78) compared to when tag loss is accounted for in the model (Fig. 2).
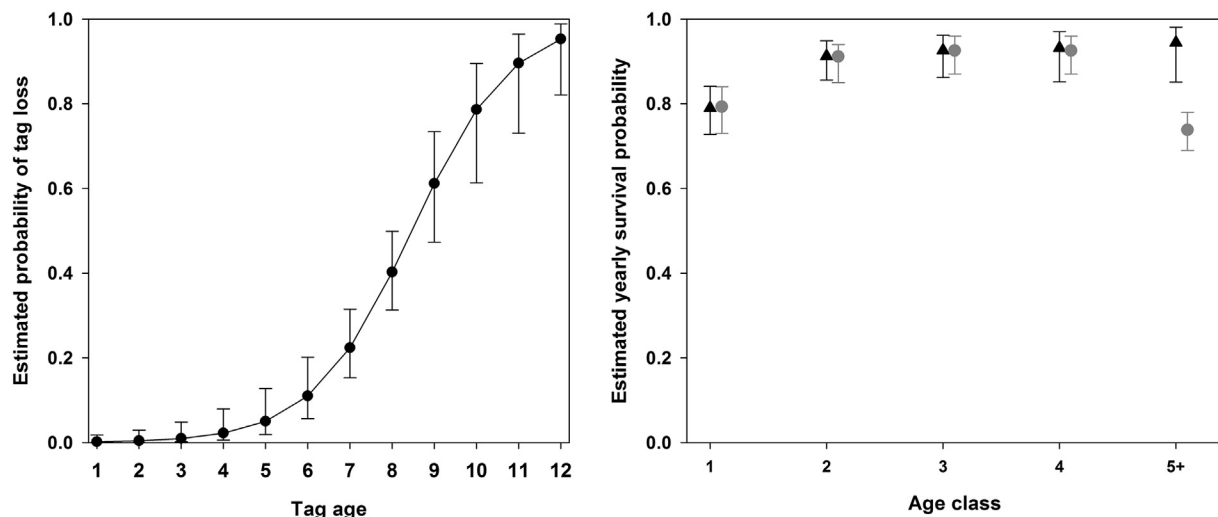
Fig. 2. Estimated probability of tag loss as the tag becomes old (left panel). Estimated yearly survival probability by different age classes (right panel) as derived from models that explicitly accounted for tag loss (black triangles, the unbiased survival estimates), and biased survival probability (grey circles) derived from models not correcting for the loss of tags as they age. Values in each panel depict model averaged estimates with 95% confidence intervals.

4. Discussion

We have shown that camera trap observations, even if based on very few camera trap locations, can, under specific conditions, provide a large amount of resighting observations that dominate the share of total live resightings compared to citizen observations. However, dead recoveries were only reported by citizens, making their contribution useful, as we have shown that survival estimated using both data sources was more precise (i.e. smaller 95% confidence intervals) compared to using either subset of data. Specifically, using only the scarce citizen science data in this case yielded likely unrealistic estimates of survival, highlighting the need to complement these with other sources of resighting information, such as camera traps in this case. Yearly survival estimated based on the combined contribution from camera trap and citizen resightings/recoveries was relatively high across all age classes, stabilizing around 95% for birds of 5 years of age and older. We have shown that the rate of wing tag loss rapidly increases as tags age. Consequently, ignoring tag loss results in a large under-estimation of survival of age classes from five and older.

Opportunistic data can be valuable in improving inference on space use and population size of elusive wildlife in different landscapes (Tenan et al., 2017). Similarly, camera traps were recently reported as an effective tool for wildlife monitoring across a range of environmental conditions and taxonomic groups (Wearn and Glover-Kapfer, 2019). Within the context of the current study, few camera trap locations yielded large amounts of resightings, and largely drove the probability of a tagged vulture being resighted. This may suggest that the contribution of citizen observations was irrelevant in estimating vulture survival. However, as citizen observations came from a large area and also included individuals recovered dead, while in absolute numbers they were very low, they helped alleviate, at least marginally, the spatial bias of data contributed by the localized camera traps (Tenan et al., 2017). Furthermore, citizen science data also increased the precision of survival estimates (Payo-Payo et al., 2018). In open populations, models combining resightings and recoveries, as in this case, allow obtaining real survival estimates when emigration is random (Nichols and Hines, 1993). Moreover, here we assume a constant survival over the period of study. This assumption may not hold for systems under rapid socio-economic and environmental change. However, we believe this is a reasonable assumption in the context of this work whereby the study period is limited, and with limited variation in conditions between and within years in terms of weather and land-use,

which likely also implies relative stability in human-wildlife conflict and possibly poison use, a major threat to vultures in the region (Craig et al., 2019; Santangeli et al., 2017; Santangeli et al., 2016; Santangeli et al., 2019). In the future, as resighting and recovery data will continue to accumulate, it may be possible to quantify potential changes in survival in relation to changes in socio-environmental conditions.

A fundamental bias in these types of capture-mark-recapture studies may stem from the tag being lost, and the animal erroneously considered as dead, resulting in underestimation of survival (Nichols and Hines, 1993). We have shown here that this is the case, especially when only nestlings were wing tagged and survival was estimated for different age classes. The much lower survival of vultures of age five and above resulting from tag loss is a serious issue that should be considered, and duly accounted for, in any such analyses, see good examples of this by Badia-Boher et al. (2019) and Lieury et al. (2015). Wing tagging is often used to track vulture movements and especially their survival (Monadjem et al., 2013; Tavecchia et al., 2012). The estimated loss of wing tags reported here was higher than the loss of metal or color rings reported in other studies (Badia-Boher et al., 2019; Le Gouar et al., 2008), and somewhat confirms anecdotal observations and assumptions on the rate of wing tag loss with age (Monadjem et al., 2013). Given the potential bias induced by tag loss, we urge this issue being explicitly accounted for when assessing survival, particularly of adults, from wing tagged individuals. Tags may also fade and become illegible over time (Monadjem et al., 2013), which in practical terms is the same as the tag being lost. Investigating more durable and easily visible wing tags, e.g. of different materials, would be beneficial, given the popularity of this marking method for vultures. The feasibility of alternative methods than capture-mark-recapture to estimate vulture survival should also be considered in the near future, as they may represent less invasive and rather fast options (Oppel et al., 2016).

The relatively high juvenile survival is likely attributed to the fact that most of the nests are located within or near the boundary of a large protected area, the Namib-Naukluft Park. Juvenile lappet-faced vultures during their first year spend the majority of their time in the natal area (authors unpublished data), which, if located within or around a protected area, may also prevent these birds from falling victim of unintentional poisoning. The latter largely occurs in the commercial farmland areas of South-Eastern Namibia (Santangeli et al., 2016). Moreover, recent findings suggest that the body condition of lappet-faced vultures in Namibia's protected areas improved during drier than average years, likely due to increased ungulate mortality providing

food for vultures (Santangeli et al., 2018). These same environmental drivers may also influence survival, particularly that of juveniles. Further investigations are needed to assess the effect of the above factors on survival as more capture-mark-recapture, as well as tracking data rapidly become available. To this end, we suggest that the current study system could be improved by expanding the spatial coverage of the camera traps, if possible, and/or more widely promoting the sighting and reporting of tagged vultures by citizens. This could be achieved for example by promoting the use of camera traps, or advertising vulture resighting, at the supplementary feeding stations and waterholes that are present through the country, and that are often visited by vultures and wildlife tourists alike, whether in protected areas or private lands. Such expansion of the resighting program should however be coupled with the collection of as accurate as possible information on dead recoveries on the field (e.g. whether dead birds carried the metal ring and/or the wing tag). This information would prove useful in further improving the precision and accuracy of tag loss and survival estimates, and to bring them as close as possible to the real values. While we reported "apparent" survival, we believe that the data and the modeling framework employed here yielded estimates very close to the real values.

In the near future, as the spatio-temporal coverage of the resighting effort expands, it will be possible to address additional specific conservation and research questions that require more data. Among these questions are the potential effects of anthropogenic drivers on survival, yearly variation in survival in relation to yearly environmental change, as well as the benefits and costs of different tagging approaches, e.g. single wing tag versus tag on both wings, as these markings can also have deleterious impacts on birds (Trefry et al., 2013). Moreover, it would be relevant to follow the movement of individual vultures of different ages using biologging technology to understand dispersal patterns. This would, among others, help quantify the impact of potential emigration on the "apparent" survival estimates reported here and evaluate the causes of mortality (Arrondo et al., 2020).

Overall, we have shown that the survival of lappet-faced vultures, especially that of older age classes, in south Namibia is comparable to that of healthy populations of other vulture species (griffon vulture *Gyps fulvus,* cinereous vulture *Aegypius monachus,* Egyptian vulture *Neophron percnopterus,* bearded vulture *Gypaetus barbatus*) in other regions (Arrondo et al., 2020; Sanz-Aguilar et al., 2015a; Mihoub et al., 2014; Schaub et al., 2009; Le Gouar et al., 2008). They also appear similar or slightly higher than the survival values reported for Critically Endangered white-backed vultures *Gyps africanus* or Endangered cape vultures *Gyps coprotheres* in South Africa (Monadjem et al., 2013; Monadjem et al., 2014). These survival values are towards the higher end of the range of values reported for several diurnal raptor species as reviewed by Newton et al. (2016). Interestingly, the estimated adult survival reported here (0.95), which is a largely pristine area devoid of humans, closely matches that of adult griffon vultures (0.96–0.97 for females and males, respectively) and Egyptian vultures (0.95) inhabiting less anthropized regions of Spain (Badia-Boher et al., 2019; Arrondo et al., 2020). Reintroduced and growing populations of griffon and cinereous vultures in France and bearded vultures in Switzerland, show a slightly higher adult survival (0.96–0.98), but also coherent with our estimates (Mihoub et al., 2014; Schaub et al., 2009; Le Gouar et al., 2008). However, juvenile (i.e. first year) survival estimate of lappet-faced vultures in Namibia (0.78) seems slightly lower than the estimates available for healthy populations of European vultures (0.85–0.95) (Badia-Boher et al., 2019; Mihoub et al., 2014; Schaub et al., 2009; Sarrazin et al., 1994). Consequently, a robust evaluation of whether the currently estimated survival can support a viable population of vultures in the area should be carried out, e.g. using population viability analysis, before any conclusions are drawn regarding its fate. This area was recently identified as a major stronghold for the conservation of this threatened species across Africa (Botha et al., 2017). Namibia, as well as many other regions in Southern Africa, represents a

key priority for vulture conservation (Santangeli et al., 2019), but is also afflicted by pervasive threats, such as poisoning (Santangeli et al., 2016). Therefore, it is of crucial importance that monitoring is continued and ideally expanded, to facilitate the updating of key demographic parameters and anticipate potential population declines before it is too late. To this end, the expansion of citizen science and future technological advances will certainly facilitate the accumulation of resighting observations from across wider areas. On a positive note, private citizens focusing on eco-tourism and monitoring local wildlife have recently installed camera traps on their properties in Namibia, which have led to reports of wing tagged vultures. Camera traps are becoming more affordable, and means to process the large amount of images are being rapidly developed (e.g. Falzon et al., 2019; Tabak et al., 2019). This, coupled with the increasing eco-tourism industry in Namibia (Lindsey et al., 2013), and in many other parts of Africa, may represent an opportunity to engage the public and mobilise large amounts of data for monitoring and conservation.

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2020.108593.

Data availability

The data used for the analyses are publicly available in Figshare, DOI: https://doi.org/10.6084/m9.figshare.12083802

Author statement

The authors confirm that the data will be published in figshare upon the article becoming available online in the journal. We have already deposited the data in figshare and included a DOI for them in the manuscript. Other data are already presented in the support material of the paper.

CRediT authorship contribution statement

Andrea Santangeli: Conceptualization, Methodology, Formal analysis, Writing - original draft, Writing - review & editing. **Veli-Matti Pakanen:** Methodology, Formal analysis, Conceptualization, Writing - review & editing. **Peter Bridgeford:** Data curation, Writing - review & editing. **Mark Boorman:** Data curation, Writing - review & editing. **Holger Kolberg:** Data curation, Writing - review & editing. **Ana Sanz-Aguilar:** Methodology, Formal analysis, Conceptualization, Validation, Writing - review & editing.

Declaration of competing interest

The authors declare that they don't have any financial or non-financial conflicts of interest.

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