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Assessing population size and structure for Andean Condor *Vultur gryphus* in Bolivia using a photographic 'capture-recapture' method

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The Andean Condor *Vultur gryphus* is a globally threatened and declining species. Problems of surveying Andean Condor populations using traditional survey methods are particularly acute in Bolivia, largely because only few roosts are known there. However, similar to other vulture species, Andean Condors aggregate at animal carcasses, and are individually recognizable due to unique morphological characteristics (size and shape of male crests and pattern of wing coloration). This provided us with an opportunity to use a capture-recapture ('sighting-resighting') modelling framework to estimate the size and structure of an Andean Condor population in Bolivia using photographs of individuals taken at observer-established feeding stations. Between July and December 2014, 28 feeding stations were established in five different zones throughout the eastern Andean region of Bolivia, where perched and flying Andean Condors were photographed. Between one and 57 (mean = 20.2 ± 14.6 sd) Andean Condors were recorded visiting each feeding station and we were able to identify 456 different individuals, comprising 134 adult males, 40 sub-adult males, 79 juvenile males, 80 adult females, 30 sub-adult females and 93 juvenile females. Open population capture-recapture models produced population estimates ranging from 52 ± 14 (se) individuals to 678 ± 269 individuals across the five zones, giving a total of 1388 ± 413 sd individuals, which is roughly 20% of the estimated Andean Condor global population. Future trials of this method need to consider explicitly knowledge of Andean Condor movements and home-ranges, habitat preferences when selecting suitable sites as feeding stations, juvenile movements and other behaviours. Sighting-resighting methods have considerable potential to increase the accuracy of surveys of Andean Condors and other bird species with unique individual morphological characteristics.

Keywords: capture–recapture, feeding stations, field photography, Neotropical vultures, sighting-resighting, unique plumage characteristics.

Vultures and condors usually occur at low densities and have vast home-ranges (Gil *et al.* 2014, Lambertucci *et al.* 2014), making them very difficult to survey and monitor. The group is also disproportionally threatened and inherently vulnerable to extinction when compared with other bird groups (Şekercioğlu *et al.* 2004). In fact, 70% of vulture species (16 of 23) are categorized either as Globally Threatened (12 species) or Near Threatened (four species) (BirdLife International 2017). Many vulture species also provide irreplaceable ecological, economic and cultural services, particularly in their role as scavengers (Şekercioğlu 2006, Ogada *et al.* 2012). Thus, population size estimates for these species are of great importance in monitoring programmes or

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population recovery goal setting (Groom 2006, Murn *et al.* 2013).

The Andean Condor *Vultur gryphus* is the largest Neotropical vulture species and has a range extending from northern Colombia to southernmost Argentina and Chile. It inhabits high-elevation montane areas with steep slopes and cliffs, although individuals are occasionally found in other montane habitats or along the Pacific coast (Ferguson-Lees & Christie 2001). The species is listed as Near Threatened based on a suspected population decline throughout its range, probably linked to persecution and incidental poisoning, among other threats (BirdLife International 2017). There are few or no data on Andean Condor populations across much of its range, except for scattered locations along the Andes where its populations have been estimated using point counts (e.g. Lambertucci 2010, Escobar 2013, Naveda-Rodríguez *et al.* 2016), counts at carcasses (e.g. Ríos-Uzeda & Wallace 2007) and moulted feather analysis (e.g. Alcaide *et al.* 2010). Previous studies in Bolivia have estimated its abundance at the regional level (Ríos-Uzeda & Wallace 2007, Méndez *et al.* 2015), but there has been no nationwide population survey to inform appropriate conservation measures for the species in this priority region. Problems surveying Andean Condors are particularly acute in Bolivia, as few roost locations across a vast extent of topographically complex landscapes are known. However, robust population parameters may be derived from capture-recapture frameworks, which are primarily based on the reliable individual identification of the studied animals (based on markings that do not change or disappear during the sampling period), the counting of marked and unmarked animals that are detected during a sampling period and the estimation of a capture probability (Nichols 1992). As field categorization by sex and age in Andean Condors is reasonably straightforward (Ferguson-Lees & Christie 2001) and their unique plumage characteristics and unique crest and dewlap characteristics in adult males show no change throughout periods of at least 3 months and may even extend for years or even the whole life of some individuals (Snyder *et al.* 1987, McGahan 2011), the species can be surveyed using a sighting-resighting approach, as has been done to survey other animal species with individually unique morphological characteristics (Karanth & Nichols 2002, Silver *et al.* 2004).

In this study, we use photographs of individual Andean Condors attracted to strategically sited feeding stations to assess the population size and structure of the species across the eastern Andes of Bolivia, corresponding to the largest portion of the species' range in the country (Balderrama *et al.* 2009). We used a sighting-resighting model to test the suitability of such a set of survey feeding stations to generate population estimates and make recommendations for employing this method for future surveys of this and other bird populations.

METHODS

Study site and feeding station surveys

Surveys were conducted in the eastern Andean region of Bolivia, encompassing the Cordillera Oriental and Sub-Andino physiographical units, where mountain ranges are interspersed with valleys, plateaus, rocky outcrops and sharp montane peaks. The fieldwork was conducted above the treeline, a habitat dominated by sparse *puna*-steppe grassland (Navarro & Maldonado 2002, Ibisch & Mérida 2003, Montes de Oca 2005). Between July and December 2014, 28 equine carcasses (ethically sourced from local farmers) were placed at predetermined feeding stations located randomly throughout the eastern Andes of Bolivia aiming to cover most of the region but also depending on logistical constraints such as agreements and permissions from local communities to conduct surveys (Fig. 1). Feeding stations were located in undisturbed areas on the top of slopes or next to rocky cliffs, and at a distance of ≥ 1 km from the nearest village or main road. A primary observation hide was built 35–100 m from the carcass to permit optimal viewing of perched and flying Andean Condors. A second hide was placed at a suitable location within 100 m of the carcass so that additional observers could focus primarily on photographing flying Condors. Each carcass was monitored daily by two to four observers from 07:00 to 18:00 h until the carcass was completely consumed (consumption time was 3–7 days). Carcasses were placed one after another following the numeration shown in Figure 1. The interval between placing a carcass at the next feeding station was between 1 and 13 days (Table S1).

The breeding season of Andean Condors is variable, taking place mainly between September and December, but it can occur at any time of year in

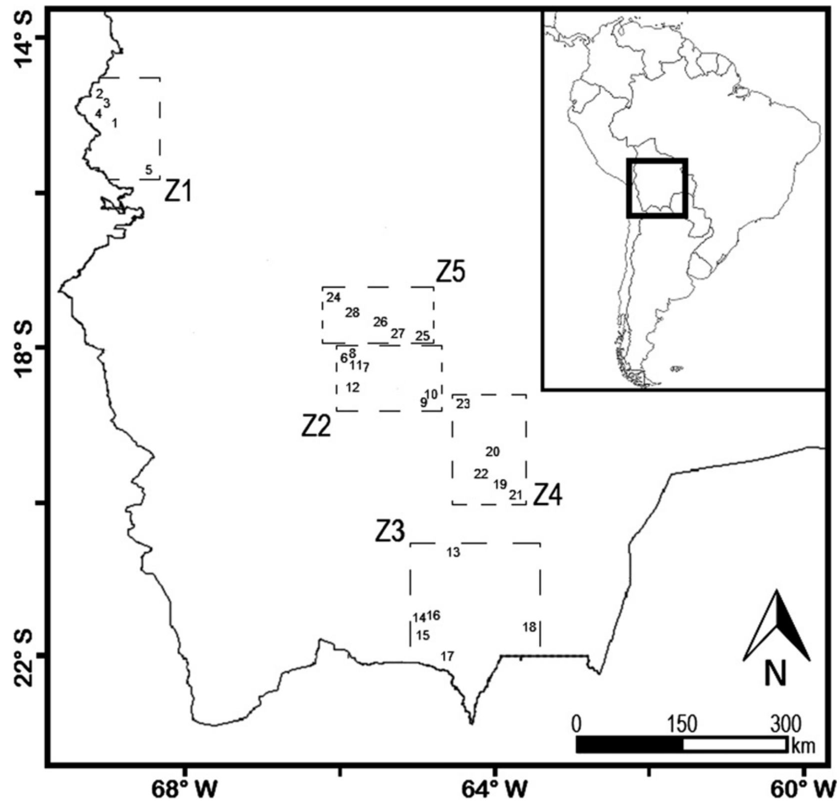

Figure 1. Locations of the 28 survey feeding stations placed in the eastern Andes of Bolivia and within the zones delimited to conduct the 'sight-resight' analysis.

the northern part of the continent (Sáenz-Jiménez *et al.* 2016). Although we could not find any published breeding records of Andean Condors in Bolivia, our own observations suggested that the breeding season of the species in this country takes place mainly between December and March, and thus we assume that our fieldwork was conducted outside the breeding season. Andean Condors show territorial behaviour only during the breeding season, when pairs defend their nest-sites but not their feeding territories (Lambertucci & Mastrantuoni 2008, McGahan 2011).

Identification of individual Condors from photographs

Andean Condors were photographed from the hides using a digital camera mounted on a digiscoping adaptor attached to a spotting scope, plus one or two bridge cameras, giving photographic focal distances of up to 810–1550 mm. All Andean Condors were categorized following the age/sex categories developed by Ríos-Uzeda and Wallace (2007). Adult Andean Condors were identified from side-on profile photographs of perched individuals, by examining the variation in wing covert pattern: specifically, the size, shape and number of the black-and-white markings (Fig. 2). Adult male identification was complemented by examination of crest morphology (size, shape and roughness) and the size and shape of dewlaps (Fig. 2). Individuals in other age/sex categories were identified by examining the variation in primary wing-feather moult patterns and other plumage particularities observable in flying birds, following the approach used by Snyder and Johnson (1985) and Stoynov *et al.* (2015) (Fig. S1).

Population estimates and individual resightings

Andean Condor minimum population size and corresponding population structure were derived from the number of individually identified Condors at all feeding stations. The association between the number of resightings and sex and

Figure 2. Examples of variation in distinctive morphological characteristics of Andean Condors in (a) the crest and dewlap in adult male condors and (b) the extent of black and white covert patterns in adult female Condors.

age categories was determined using a chi-square independence test. For analytical purposes, feeding stations were grouped into zones as follows: feeding stations 1–5 in zone 1, stations 6–12 in zone 2, stations 13–18 in zone 4, stations 19–23 in zone 4 and stations 24–28 in zone 5 (Fig. 1). Within each zone, consecutively surveyed feeding stations were separated into three distance categories: 0–50 km, 51–100 km and > 100 km. Consequently, some of our zones (2, 4 and 5) were located very close to each other, with some feeding stations being closer to feeding stations in a neighbouring zone than to others in the same zone. Thus, it was likely that some Andean Condors could be resighted outside their 'original' zone. However, we decided to restrict the resighting history to within-zone resightings rather than use a spatial capture-recapture approach because there is currently no way to determine empirically an adequate buffer zone or 'habitat mask' around each capture point (the area within one capture point that will have any chance of capturing any individual within the population), as data on Andean Condor movements from our study site are lacking. We used chi-square independence tests to assess the likelihood of resighting Andean Condors at consecutively surveyed feeding stations vs. non-consecutively surveyed feeding stations across the three distance categories (i.e. the number of resightings as a function of distance between feeding stations and whether stations were surveyed consecutively or not).

Population size was estimated by fitting a Jolly–Seber open population model to the individual Condor sighting history of each zone using the R package *RCapture* (Baillargeon & Rivest 2007, Rivest & Baillargeon 2014, R Core Development Team, 2015). We selected this approach based on the assumptions that any Condor in the population, within its own age and sex category, had an equal chance of finding any feeding station and had an equal chance of survival, and because open population 'sighting-resighting' models have proven useful in population estimation for highly mobile animals with large home-ranges (Amstrup *et al.* 2001, McDonald & Amstrup 2001, Holmberg *et al.* 2009, O'Brien & Whitehead 2013). We tested for a trap effect by comparing the Akaike's information criterion (AIC) values from the fitted model, with those from a second model fitted with a homogeneous trap effect (Baillargeon & Rivest 2007). Similar AIC values between the two models would indicate no trap effect, whereas noticeably different AIC values would indicate the presence of a trap effect.

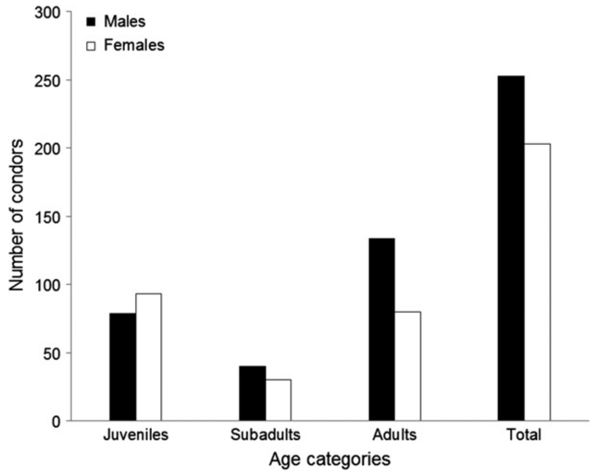

Figure 3. The number of individually identified male and female Andean Condors of different age categories.

RESULTS

Andean Condors were recorded visiting all feeding stations, with the number of Condors counted at each station ranging between one and 57 (mean = 20.2 ± 14.6 sd). We had 566 Condor observations from all feeding stations and were able to identify 456 different individuals (our minimum population size estimate): 134 adult males, 40 sub-adult males, 79 juvenile males, 80 adult females, 30 sub-adult females and 93 juvenile females (Fig. 3). Sub-adult and adult age-classes were dominated by males, whereas more juvenile females were recorded than juvenile males. The open population capture-recapture model produced population estimates for each of the five zones (Table 1), resulting in a cumulative population estimate of 1388 (±413 sd) Andean Condors for the entire study area. The model also indicated that the Andean Condor population was probably highest in zones 3 (678 ± 268 sd individuals) and 2 (320 ± 64 sd individuals). In zone 4, the test for homogeneous trap effect had a much lower AIC value than the fitted model, suggesting that the model with homogeneous trap effect has a much better fit to the data than the fitted model (Table 1). This is in stark contrast to the other four zones, where the AIC values were almost identical between the fitted model and the test for homogeneous trap effect.

Table 1. Andean Condor population size estimates (total number of individuals ± se) based on a Jolly–Seber open population model, and model test for homogeneous trap effect, using the obtained sighting history from the five study site zones in the eastern Andes of Bolivia.

Zone	No. of captured units	Population size estimate (±se)	Fitted model	Test for homogeneous trap effect
1	33	52 ± 14	Deviance = 23.5; df = 23 AIC = 57.6	Deviance = 21.9; df = 22 AIC = 58.0
2	125	320 ± 64	Deviance = 63.4; df = 115 AIC = 138.6	Deviance = 63.3; df = 114 AIC = 140.4
3	117	678 ± 269	Deviance = 13.0; df = 55 AIC = 65.5	Deviance = 13.0; df = 54 AIC = 67.4
4	84	141 ± 22	Deviance = 41.7; df = 23 AIC = 96.2	Deviance = 30.7; df = 22 AIC = 87.3
5	97	197 ± 44	Deviance = 22.4; df = 24 AIC = 64.6	Deviance = 19.7; df = 23 AIC = 63.9

Considering all 566 Andean Condor observations, 110 (19.4%) were resightings, corresponding to 91 individuals (20% of the 456 identified) that were recorded at more than one station. Of these, 17 were adult males, 16 adult females, eight sub-adult males, three sub-adult females, 21 juvenile males and 26 juvenile females; a disproportionate number of these resightings were juveniles ($\chi^2 = 23.4$, df = 5, $P < 0.001$; Fig. 4). Most of the identified Andean Condors ($n = 365$, or 80%) were recorded once, whereas 75 (82.4%) of the 91 resighted individuals were recorded twice, 14 (15.4%) individuals were recorded three times and two individuals were recorded four (1.1%) and five (1.1%) times, respectively. A total of 32 Andean Condors were resighted outside their 'original' zone; 24 were resighted in zone 5 that had been originally sighted in zone 2, four that were resighted in zone 4 had originally been sighted in zone 2, and another four that were resighted in zone 5 had originally been sighted in zone 4. Resightings made within each zone were significantly aggregated at feeding stations that were separated by ≤ 50 km ($\chi^2 = 13.34$, df = 2, $P = 0.001$), but resightings of Andean Condors made throughout the study area were not significantly aggregated in either distance category, or for consecutively surveyed or non-consecutively surveyed feeding stations ($\chi^2 = 1.92$, df = 2, $P = 0.38$; Fig. S2).

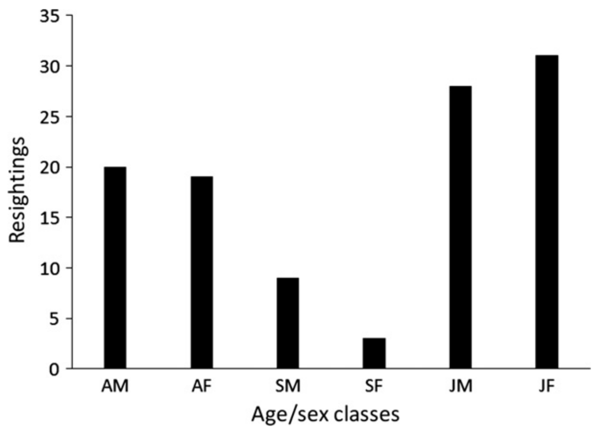

Figure 4. Number of re-sightings in each age/sex class of Andean Condor. AM, adult male, AF, adult female; SM, sub-adult male; SF, sub-adult female; JM, juvenile male; JF, juvenile female.

DISCUSSION

Using carcasses placed at observer-established feeding stations, we were able to attract and identify Andean Condor individuals based on unique morphological characteristics of bare skin (crest and dewlap in adult males) and feather plumage (moult, feather damage and/or coloration of all sex and age groups) (Figs 2 and S1). Although we found coincidences in primary flight feather moulting patterns, the combination of other markings (e.g. damaged feathers) allowed us to differentiate all individuals (Fig. S1). For adult perched Andean Condors, plumage patterns varied in the size, shape and number of the fang-like black-and-white markings that could be distinguished, whereas for adult males, crest marks and shape were unique to each individual (Fig. 2). For flying Andean Condors in the other age and sex classes, primary flight feathers moult and plumage particularities varied in the number and position of missing feathers, the size of growing feathers, the extent of feather damage and the position of damaged feathers (Fig. S1). Detailed research on the timing of Andean Condor moulting will be definitive in determining how long plumage patterns remain as unique natural markings, thus ensuring identification accuracy, as has been documented for California Condors *Gymnogyps californianus* (e.g. Snyder & Johnson 1985). In captive Andean Condors, moulting cycles for flight feathers and wing coverts can last for approximately 2 years, with individuals maintaining invariable plumage for 3–5 months (McGahan 2011). The duration of our surveys might possibly have allowed changes in primary wing-feather moult patterns, leading to violation of one of the model assumptions ('tagging is accurate, no tag loss, no misread tags') for individuals in age/sex categories other than adult males. Future surveys, particularly those longer than used here, might consider the use of N-mixture models (e.g. using the pcountOpen function in R package *unmarked*; Fiske & Chandler 2011) to control for potential changes in moult patterns.

We derived a minimum population size of 456 Andean Condors for the eastern Andes of Bolivia. In contrast, previous photographic studies from the same region estimated minimum population sizes of 78 and 253 individuals in the Apolobamba Mountains, and in the central and southern Andes of Bolivia, respectively (Ríos-Uzeda & Wallace 2007, Méndez *et al.* 2015). Both studies used the numbers and proportion of adult males in the population to extrapolate their estimates, whereas the minimum population size obtained in this study is a direct count of identified Condors in all age and sex classes; such an approach allowed us to omit the high variability of vulture group size at feeding stations that could result in misleading population estimates or perceptions of abundance (Margalida *et al.* 2011).

The population structure of Andean Condors we recorded is similar to those observed by Ríos-Uzeda and Wallace (2007) and Méndez *et al.* (2015) in that the population is slightly skewed towards adult males and immature birds (subadults and juveniles). Sex ratios skewed towards adult males are typical of many threatened species (Donald 2007) and have been reported in other Andean Condor populations (Koenen *et al.* 2000, Sarno *et al.* 2000, Lambertucci 2010). As both parents perform incubation and caring of the chick (Lambertucci & Mastrantuoni 2008), the apparent lack of adult females is unlikely to be related to these roles, but they may be subject to higher mortality rates, a situation that can be exacerbated by disturbance, anthropogenic land transformation and persecution (see Lambertucci *et al.* 2012).

It is noteworthy that in all population estimates for the Bolivian Andes, sub-adult Andean Condors represent the smallest portion of the population (see Ríos-Uzeda & Wallace 2007, Méndez *et al.* 2015, this study). Immature Condors could be experiencing high mortality rates, as they tend to use more disturbed habitats than adults (Donázar *et al.* 1999) and may therefore feed on poisoned baits. Research from the UK has shown that non-breeding Red Kites *Milvus milvus* (aged 1 and 2 years) are more likely to explore the wider landscape to set up their own breeding territory and hence are more likely to come into contact with illegally placed poisoned baits (Smart *et al.* 2010). On the other hand, juvenile male and female Condors are the least dominant when accessing carcasses and may feed on smaller amounts of carrion as a consequence of intraspecific competition (Wallace & Temple 1987, Donázar *et al.* 1999). We found no trap effect (i.e. no 'trap-happy' individuals) in four of our five study zones (Table 1), so the greater number of juvenile resightings across the majority of the study area may be due to juveniles feeding more frequently to satisfy their requirements. However, our models revealed that some Andean Condors may have become 'trap-happy' at zone 4 feeding stations, i.e. some of the identified individuals were more likely to be resighted at zone 4 feeding stations compared with sighting 'new' individuals less familiar with the baited station (Table 1). This could lead to underestimation of the Andean Condor population in this zone. To overcome this, we suggest setting out feeding stations for a number of days before the first survey is undertaken, to allow Andean Condors in the local population to become equally 'trap-happy'. However, careful consideration must be given to the practicalities of doing this over large geographical studies such as this. In addition, the use of covariates to model detectability and abundance (with confidence intervals) at feeding stations could help to determine whether detectability is constant across feeding stations, and identify the feeding stations where lower detection probabilities may lead to inflated overall population estimates.

Our open population model estimate of 1388 (±413 sd) Condors for an area of *c.* 42 000 km^2 is intermediate between previous estimates from Argentina and Ecuador and reveals a decline in population size from south to north. The estimated population size for an area of *c.* 6300 km^2 was 260–332 individuals in northwest Patagonia (Lambertucci 2010), whereas a population of 94–102 in an area of 49 550 km^2 was estimated in Ecuador (Naveda-Rodríguez *et al.* 2016). Andean Condor density estimates (the number of individuals per 100 km^2) also show a similar pattern, decreasing from 4.13 to 5.27 in northwest Patagonia (Lambertucci 2010), to 3.30 in Bolivia (our study) and to 0.19–0.20 for Ecuador (Naveda-Rodríguez *et al.* 2016). Dissimilarities in field procedures and data analysis prevent a more in-depth comparison; however, it is noteworthy that approximately 20% of the estimated Andean Condor global population of 6700 individuals (BirdLife International 2017) occurs in Bolivia, highlighting the importance of the country for the conservation of this species. Suitable habitat for the Andean Condor is not evenly available across our study area and this may explain the variation in population estimates across the five zones (Table 1). Zone 1 (Fig. 1) is located within the narrowest portion of the eastern Andes of Bolivia (Montes de Oca 2005) and represents around one-fifth of the distribution range of the Andean Condor in Bolivia (Balderrama *et al.* 2009), so it is reasonable to expect that the population estimate is lowest in zone 1 and higher in the other four zones situated within the largest portion of the eastern Andes of Bolivia.

The provision of supplementary food at feeding stations ('vulture restaurants') is a common strategy to help reverse declines in wild vulture populations (e.g. Sarrazin *et al.* 1994, Tauler-Ametller *et al.* 2017) where food is the critical limiting factor (Piper *et al.* 1999, Piper 2006). The use of feeding stations and vulture safe zones (e.g. Murn *et al.* 2014) is likely to increase in the future (Deygout *et al.* 2009) given the ongoing threats to vulture populations caused by contaminated carcasses (e.g. Green *et al.* 2004, Oaks *et al.* 2004, Gilbert *et al.* 2007). These conservation measures represent opportunities to conduct photographic sighting-resighting surveys on other vulture species with unique morphological characteristics (e.g. Murn 2012) or for populations with colour-tagged individuals. Assessments of population structure based on plumage patterns have previously been conducted from feeding stations for Egyptian Vulture *Neophron percnopterus* (e.g. Meretsky & Mannan 1999), from long-term transect counts at nesting sites for Oriental White-backed Vulture *Gyps bengalensis* (e.g. Gilbert *et al.* 2006, Arshad *et al.* 2009) and from vantage points situated within critical foraging areas for California Condors (e.g. Snyder & Johnson 1985). Modifications to our method could be applied to populations of other bird species such as macaws and other parrots, which have large home-ranges and feed on ephemeral food sources such as fruiting trees or at clay-licks, using a combination of unique plumage and beak characteristics (e.g. Munn 2006, Usher *et al.* 2016). Future applications of these sighting-resighting methods on any bird species with unique natural markings that congregate to feed will need to give careful consideration to the effective area to be surveyed and to the number and distance between 'feeding stations'. Ideally this should be determined by experimental examination of the area of influence of the primary food resource as bait (e.g. palm nuts for macaws – see Munn 2006, animal carcasses for Andean Condors – see Gómez de Segura *et al.* 2012), along with data on the minimum home-range for the species (e.g. the lower estimate for an Andean Condor is 2700 km^2, Alarcón *et al.* 2013) and the number of home-ranges likely to be surveyed. Information on the home-range size for many of these species is lacking, but evidence from this study suggests that for future Andean Condor studies at least, feeding stations should be no further apart than 100 km, and should be baited and surveyed simultaneously.

In conclusion, we have demonstrated that our photographic sighting-resighting method is a feasible approach for providing reliable estimates of the size and structure of Andean Condor populations. Adopting this method for other Andean Condor populations, for other bird species with unique morphological characteristics (e.g. Bretagnolle *et al.* 1994, Arroyo & Bretagnolle 1999) or for other naturally patterned taxa (e.g. Elgue *et al.* 2014, Dala-Corte *et al.* 2016, Balaguera-Reina *et al.* 2017, Villafañe-Trujillo *et al.* 2018) could lead to the development of specific sex- or age-class conservation measures to help bolster threatened population recovery efforts.

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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. Variation in individual natural markings observable in immature (flying) Condors. All images show damaged wing and tail feathers and patterns of moult in the primary flight feathers.

Figure S2. The number of resightings as a function of distance and time interval (number of days) between subsequently surveyed feeding stations.

Table S1. Total number of Condors observed from each of the 28 survey feeding stations.