Variability in size of groups in communal roosts: influence of age-class, abundance of individuals and roosting site

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Abstract. Many birds roost communally but their patterns of use of communal roosts is generally poorly known. For conservation purposes, and to better understand communal roosting generally, it is important to know the factors that influence the size of groups at roosts. I studied the effect of age-class, number of individuals and roosting site on the patterns of variation in the size of communally roosting groups of Andean Condors (*Vultur gryphus*). I fitted a variance–mean relationship (Taylor's Power Law, TPL) to the number of individuals that roosted daily at seven communal roosts, and made temporal (in each roost) and spatial (among roosts) comparisons of the relationship. The abundance of individuals at a roost fitted the TPL well, both temporally and spatially. The variation in the abundance of individuals was significantly influenced by the roosting site selected, independent of the effect of the mean number of individuals. Moreover, the effect of roosting site on the variability of abundance of individuals was stronger than the effect of age-class. Accordingly, I highlight the importance of the roosting site in modulating variation in the size of groups of communally roosting individuals. This understanding of the patterns of variation in the use of communal roosts could aid in determining the importance of sites for the conservation of a species.

Introduction

A number of species of bird are known to roost communally (e.g. Ward and Zahavi 1973; Eiserer 1984). Such communal roosting can potentially provide benefits to individuals, including, for example, information about conspecifics, thermoregulatory advantages, avoidance of predation and increases in foraging efficiency (Ward and Zahavi 1973; Morrison and Caccamise 1990; Beauchamp 1999). However, in contrast, communal roosting may also be disadvantageous, for example, in increasing conspicuousness to predators, or by increasing parasitic infections, commuting costs and competition, and, where birds roost at several levels, increasing the deterioration of plumage when the droppings of birds perched higher at the roost fall onto individuals roosting below them (Yom-Tov 1979; Eiserer 1984; Beauchamp 1999). Roosting sites with stable and suitable conditions may be used repeatedly but where the environmental conditions of potential roosting sites vary greatly, a species may choose a new location every roosting period (Eiserer 1984). Despite the potential theoretical importance of congregations of individuals at roosts, there have been few studies examining variation in the abundance of individuals using communal roosts and the influence of the roosting site selected on this variability (Rabenold 1987; McVey *et al.* 2008; Olea and Mateo-Tomás 2009).

The relationship between the mean density or abundance of an organism and the variance of the mean is a major focus of studies investigating spatio-temporal patterns in population densities (Anderson *et al.* 1982; Gaston and McArdle 1994; Landres *et al.* 1999; Ballantyne IV and Kerkhoff 2007). The dependence of population variability on mean density needs to be considered when comparing variation among species and also within populations (McArdle *et al.* 1990). Spatio-temporal variation in the abundance of individuals of a species can be useful in clarifying the general patterns of variation in different areas and enabling comparisons between populations (Gaston and McArdle 1994). Repetition of surveys in space and time provides an estimate of this variability. Subsequently, the mean abundance of individuals in a place and its variability could be used to characterise a specific site (e.g. a communal roost) and to provide the basis for comparable estimations.

The description of the variance–mean relationship can allow the prediction of the variation in the dynamics of populations (Maurer and Taper 2002). A well-documented general pattern in ecology is the variance–mean relationship known as Taylor's Power Law (TPL; Taylor 1961), which has been determined for several animal populations (Taylor 1961, 1986; Taylor and Woiwod 1980; Maurer and Taper 2002). In general, the use of power laws permit the study of ecological systems, even if there are few data on the demography and the dynamics of a species, and can also be used in determining conservation strategies (Marquet *et al.* 2005). In particular, the exponent of the TPL can be used to assess the stability of a place (Ballantyne and Kerkhoff 2007). Although the existence of a relationship between the mean number of individuals and its variance is known, this relationship can vary among species (Taylor 1961; Taylor and Woiwod 1980) and there is little information on the variables that can influence such variation within a species. Here, I suggest that testing the

variance–mean relationship for a population moving between different sites can provide key information on the grouping patterns of a species. In turn, this information can be useful in classifying places based on the patterns of variability in abundances of the individuals that use them.

I analysed the dynamics of the use of communal roosts by the Andean Condor (*Vultur gryphus*) to test for spatio-temporal patterns in the variability of the number of individuals (hereafter 'abundance') at a roost. I tested the influence of the abundance of individuals, their age-class and the roosting site selected, on the patterns of variability in the group at each roost. These variables can be important when selecting areas for conservation (Lambertucci *et al*. 2008). I looked for the slope of the relationship between mean abundance of individuals and its variance for daily communal roosting Condors, including temporal (for each roost) and spatial (among roosts) comparisons. I investigated whether the slope of this relationship for Condors using communal roosts agrees with the TPL, and tested whether the specific site used to roost influenced the patterns of use of the roosts. For this purpose, I analysed the daily size of the group formed in seven different Condor roosts. Finally, I separated the individuals into two age-classes (adults and immatures), to identify possible differences in the patterns of use of communal roosts by each cohort.

Material and methods

Study species

The Andean Condor is classified as near threatened worldwide (BirdLife International 2013) and is subject to a range of threats that differ over its distributional range (e.g. Speziale *et al*. 2008; Carrete *et al*. 2010; Lambertucci *et al*. 2011, 2012). The species roosts and rests communally on ledges of high cliffs, in groups of varying size (Donázar and Feijóo 2002; Lambertucci *et al*. 2008). Birds roost and rest communally throughout the year (Donázar and Feijóo 2002; Lambertucci *et al*. 2008), but, although they roost communally, Andean Condors breed solitarily, sometimes hundreds to thousands of metres away from communal roosting sites (Ferguson-Lees and Christie 2001; Lambertucci *et al*. 2008; Lambertucci and Speziale 2009), laying a single egg every second year; fledglings remain in their natal area throughout the first year (Ferguson-Lees and Christie 2001; Lambertucci and Mastrantuoni 2008). The roosting sites used by birds vary through the year but there are few details of this temporal variation (Donázar and Feijóo 2002; Kusch 2004; Lambertucci *et al*. 2008; Lambertucci 2010). The biology of this species allows for the study of the possible influences of the roosting site selected without the possible complicating effect of breeding.

Study area and surveys

I studied communal roosts over ~2500 km^2 of the Andean Precordillera (foothills) and Cordillera of north-western Patagonia, Argentina (40°30′–41°30′S, 71°W). The mean distance between communal roosts was 8.9 km (range 2–22 km; see Lambertucci 2010). The study area is a heterogeneous landscape, encompassing a mosaic of woodlands and shrub steppe, with a cool-temperate climate.

I selected seven large (>10 birds) communal Condor roosts, which best represented population numbers within the study area (Lambertucci 2010): Cuyín Manzano (CM), Condorerita (Co),

Buitrera (Bu), Chaqueñita (CH), Fragua Chica (FC), Fragua Grande (FG) and Fragua Roca (FR). Two or three trained observers visited each communal roost every day, counting the numbers of birds present from observation points >300 m from the cliffs. Each survey at a communal roosting site, consisted of two counts: the first at dusk and a second at first light the next morning to verify the first count; the count was dated as that of the first count. I always used the maximum number of individuals observed per count either from the last or the first census of the day. When more than one roost was surveyed per day, counts were done simultaneously (for sites surveyed in the same year) to avoid counting the same bird more than once. Counts were made in all seasons at each roost, with a maximum 70 daily counts per roost per season. A total of 2166 counts was completed: 546 counts at CM (counts conducted 1999–2001); 623 counts at Co (1999–2001); 205 counts at Bu (2007); 201 counts at CH (2006); and 197 counts at each of FC, FG and FR (all 2006). I considered austral summer as January–March, autumn April–June, winter July–September and spring October–December. For each communal roost we recorded the number of Condors present in a communal roost. Condors were classified into two age-classes: immatures (<6 years old) and adults (≥6 years old). Adults are black with a white collar and pure-white upperwing-coverts contrasting strongly with the rest of the wing whereas immature birds are brown-grey overall, including the upperwing-coverts, and may or may not have a white collar (Ferguson-Lees and Christie 2001; Lambertucci *et al*. 2008).

Statistical analyses

Taylor's Power Law ($V = ax^b$) proposes a tendency for the variance in abundance (V) to increase with mean abundance (x) in samples of biological populations. The slope (b) of the regression of the log-variance against the log-mean is expected to lie between 1 and 2 (Taylor 1961, 1986). I analysed the strength of the spatio-temporal variance–mean abundance relationship of a roost and tested for the positive slope predicted by the TPL, plotting the log-transformed variance as a function of the log-transformed mean abundance. Data were pooled across days in a season (using a minimum of 30 daily censuses) to estimate the mean abundance and to calculate the variance in a given period. This allowed a considerable number of observations for the estimation of each mean and variance, and more than one estimation per season. A linear regression analysis was applied on log-transformed data to estimate $b = (\log V - \log a)/\log x$. I tested for differences in the slopes and the effect of the roosting site and age-class on the variance–mean relationship at a temporal scale using general linear models (GLM) on log-transformed data. For age-classes, I considered the total number of immatures and adults in surveys conducted at two sites (CM and Co) at the same time. There were no differences in the variance–mean relationship of a communal roost between years (in all cases $P > 0.1$) so I pooled the data between years.

Finally, I also analysed the data at a pure spatial scale to test if a variance–mean relationship between the seven communal roosts fitted the TPL well. Firstly I calculated the variance–mean relationship for each communal roost separately. For this I averaged the daily abundance of individuals observed over the complete series of data and calculated the mean and the variance

in the use of a roost. Then, I performed a linear regression analysis on log-transformed data to estimate the variance– mean relationship.

Results

The slopes of the estimated variance–mean relationships at each roost were between 1.09 and 1.97, which is within the range predicted by TPL (i.e. 1–2; Fig. 1). At each roost, the daily variability in the abundance of Condors increased in those sampling periods with higher abundance of individuals (all R^2 0.84, $P<0.01$). Considering each roost, the variability in mean daily abundance increased in months with higher abundance (Fig. 1). In general, for a similar mean abundance, variances were higher in some roosts than in others, denoting differences in their patterns of use (Fig. 1).

The slopes of the variance–mean relationship did not differ strongly among roosting sites ($F_{Roost \times Mean: 6,39} = 0.50$, $P=0.085$). However, there is a significant effect of roosting site on the variability in abundance that is independent of the effect of the mean abundance ($F_{Roost: 6,39} = 0.98$, $P=0.004$; $F_{Mean: 1,39} = 11.80, P<0.001$). From the patterns of use observed I could group the communal roosting sites with similar patterns of use (Table 1). Based on the variance–mean relationships I found three different groups of roosts (Table 1): (1) the most used and most numerically variable (CM, Co, Bu), (2) those with intermediate levels of use and variability (CH, FC, FG), and (3) the least used (FR).

The effect of age-class on the variation in abundance was less pronounced than the effect of roosting site (Fig. 2). The slope of the variance–mean relationship tended to be higher for adults than for immatures but the effect could have been influenced by the higher abundances of adults compared to immatures ($F_{Age: 1,18} = 5.94, P = 0.025; F_{Mean: 1,18} = 253.74, P<0.001; F_{Age \times Mean: 1,18} = 4.26, P = 0.054$; Fig. 2).

Finally, the pure spatial variance–mean relationships estimated by applying a linear regression between the communal roosts also fitted well to a TPL, with a slope (b) of 1.38 ($R^2 = 0.87$, $P<0.01$; Fig. 3). This again showed that the seven roosting sites fell into three groups: (1) four sites that were the most used and
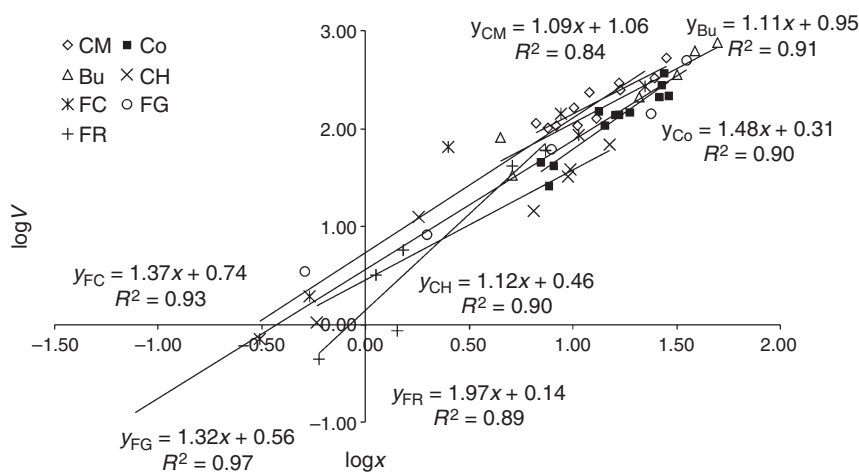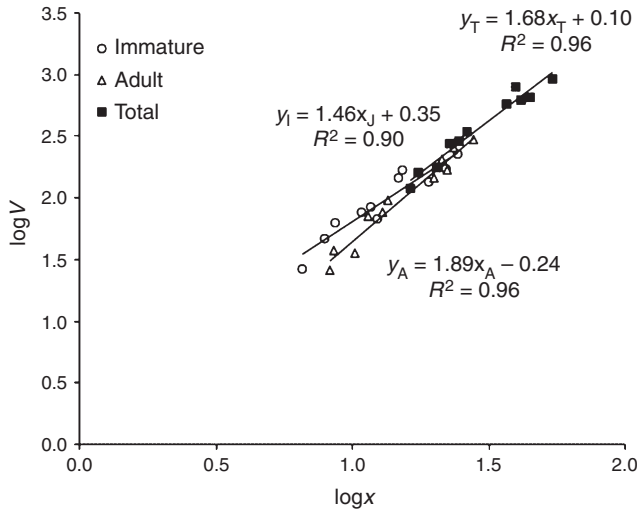

Fig. 1. Relationship between the logarithm of the mean number of Condors (log$x$) and its variance (log$V$) in seven communal roosts (all cases $P<0.01$). Each point is the mean number of individuals from ≥ 30 daily counts over the duration of the study. The number of estimations (points) per roosting site is: CM = 11, Co = 12, Bu = 6, CH = 6, FC = 6, FG = 6, FR = 6 (for names of sites, see Table 1).
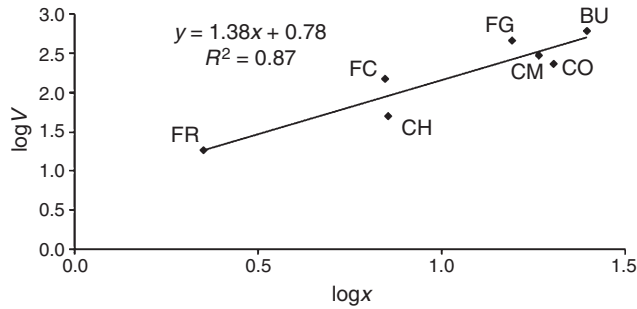
Table 1.   Comparison of communal roosts based on the variability of their use by Andean Condors

Roosting sites: CM, Cuyín Manzano; Co, Condorerita; Bu, Buitrera; CH, Chaqueñita; FC, Fragua Chica; FG, Fragua Grande; FR, Fragua Roca. Figures are significance values (Tukey test) of the comparison between communal roosts; those in bold are significant at $P<0.05$. The similar roosts that group together are indicated with asterisks (***) in the column for each of the three groups

Roost	Communal roost							Groups of similar roosting sites		
	CM	Co	Bu	CH	FC	FG	FR	1	2	3
CM									***	
Co	0.362								***	
Bu	0.995	0.222							***	
CH	**<0.001**	**<0.001**	**<0.001**					***		
FC	**<0.001**	**<0.001**	**<0.001**	0.579				***		
FG	**<0.001**	**<0.001**	**<0.001**	0.999	0.364			***		
FR	**<0.001**	**<0.001**	**<0.001**	**0.003**	**<0.001**	**0.008**				***

Fig. 2. Relationship between the logarithm of the mean number of adult (triangles), immature (circles) or all Condors (squares) ($\log x$) and the variance of the mean ($\log V$) from simultaneous counts at two communal roosts (Cuyín Manzano (CM), Condorerita (Co)) (for all regression equations $P < 0.01$). The variance–mean is based on the total number of Condors at the two roosts combined. Each point represents the mean daily abundance averaged for each season.

Fig. 3. Relationship between the logarithm of the mean number of Condors ($\log x$) and its variance ($\log V$) at the seven communal roosts (CM, Cuyín Manzano; Co, Condorerita; Bu, Buitrera; CH, Chaqueñita; FC, Fragua Chica; FG, Fragua Grande; FR, Fragua Roca). Each point corresponds to the mean daily count of individuals over all surveys out each communal roosting site and its variance (see Methods).

most numerically variable (CM, CO, BU and FG); (2) two roosts with intermediate values (CH and FC) and (3) one roost with low mean use and variability (FR) (Fig. 3). Thus, it is possible to use the variance–mean relationship to classify roosting sites according to the use of each without any further data on the roosts.

Discussion

The present study confirms that the slope of the relationship between the mean and the variance in the abundances of a bird in a communal roost agrees with that proposed by Taylor (1961), for both spatio-temporal comparisons and spatial comparisons alone. In all the roosts examined, the slope fell between 1 and 2 as proposed by the theory (Taylor 1961; Taylor *et al.* 1980). From a

biological perspective, a TPL with a slope <2 indicates that more abundant populations (in this case groups of roosting individuals) are less variable than would be expected by their statistical properties (Taylor and Taylor 1977; Taylor *et al.* 1980; Taylor and Woiwod 1980). Thus, *b* is an index of congregation (Taylor 1961), with a lower *b* indicating lower levels of congregation. Based on this power law, it was possible to identify three groups of communal roosting sites of Andean Condors. In contrast, the variability in the abundance of roosting Condors was influenced by the roosting site independently of the influence of mean Condor abundance. Interestingly, the individuals that move between the communal roosts are part of the same population (Alcaide *et al.* 2010; Lambertucci 2010; S. A. Lambertucci, unpubl. data). Thus, they may be changing their patterns of congregation, depending on the abundance of individuals at a roosting site and on the roosting site used.

The positive variance–mean relationship I found was consistent both temporally (in each roost) and spatially (across roosts). Andean Condors congregated differently depending on the place at which they chose to roost. Selection of a communal roost may be based on factors such as the safety of the site and the ease of taking off or landing (Thompson *et al.* 1990; Donázar and Feijóo 2002; Lambertucci *et al.* 2008). As expected, the spatial pattern in the use of roosting sites suggests that the mean daily variability in the abundance of Condors was greatest in those roosts that had the higher abundances of Condors (Taylor 1961, McArdle *et al.* 1990; Gaston and McArdle 1994). However, the effect of the differences in the abundance is not the only factor affecting the variability in the use of roosts, since the site selected was also important.

Considering age, at the same levels of abundance at a roost, immature birds were generally more variable than adults in use of roosts. This may be a result of behavioural differences between adults and immatures, as immature birds tend to disperse widely in search of food or breeding opportunities, as has been documented in other species (Greenwood and Harvey 1982; Meretsky *et al.* 2000). Although some roosting sites may be used more by immatures or by adults, both age-classes occur together at communal roosts (Lambertucci 2010). It is likely that each communal roost has characteristics that make them more attractive to the different ages. Moreover, the presence and variability in abundance of individuals at each roost might also be affected by other aspects of their natural history, for example, in the period of post-fledging dispersal immature birds tend to congregate (Ward and Zahavi 1973; Eiserer 1984; Lambertucci 2010).

This study focussed only on the patterns of variation in use of communal roosts as a way to characterise those sites and to evaluate the effect of the roosting site on this variation in use. The three groups of roosts identified may indicate ecological and behavioural needs of the species and environmental conditions (Ward and Zahavi 1973; Eiserer 1984; Beauchamp 1999). They may also indicate characteristics of the roosts, for example the size of the ledge, its aspect, number of shelves and accessibility for predators, although this remains to be tested (Lambertucci *et al.* 2008, S. A. Lambertucci, unpubl. data). It may also be important to consider the accessibility of roosts, because the flight-range of the Condors is limited by available resources to fly (e.g. thermals) and the size and weight of the birds (Pennycuick and Scholey 1984; Shepard *et al.* 2011). Other factors, such as weather and

behavioural interactions, are also likely to influence differences in the use of roosts (Rabenold 1987; Blanco and Tella 1999; Olea and Mateo-Tomás 2009).

I suggest future studies should analyse the characteristics of the roosts to understand better the patterns of selection of those places and the use of different types of roost in relation to their environmental characteristics, and to establish a range of important sites for the conservation of the species under different conditions (e.g. roosts constantly used, used sporadically, used only by one sex, used as a refuge, etc.). Importantly, the variability in the use of those places can have conservation implications in the demography of the species. Then, habitats or places that allow the maintenance of the variability should be considered for conservation (Reed *et al.* 2003), particularly for a species such as the Andean Condor that breeds solitarily but roosts in large groups (Lambertucci *et al.* 2008). Therefore, connecting the mathematical properties of TPL (slope b) with the use of roosting sites (season-specific, age-specific, etc.) or with characteristics of the roosting site (geomorphology, topography, climate) may be a promising tool in the study of roosting dynamics, as well as in the population monitoring of communally roosting birds.

In summary, I found recognisable spatio-temporal patterns in the variability of the abundance of individuals using different roosting sites. I showed that the variability in the abundances of roosting Condors is influenced by the roosting site independent of the mean abundance of Condors. The variance–mean relationship allowed the analysis of the influence of age and roosting site on the congregation of individuals. It may also allow the prediction of stability in the abundance of a specific site. This characteristic could be useful for classifying sites according to the variability of their use. Understanding the value of each roost based on the variation in its patterns of use could aid in the development of sound conservation strategies by providing a tool to determine priorities for the conservation management of important roosting sites for a species.

Acknowledgements

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