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REVIEW

Integrating vulture social behavior into conservation practice

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ABSTRACT
Vultures are one of the most threatened bird groups globally. Although many of the threats faced by vultures have been identified, the impact of human activities on the social life of vultures has received little attention. In this paper, we emphasize the need to integrate vulture sociality into conservation practice. First, we summarize current knowledge on vulture social behavior, and the evolutionary and ecological roots of their breeding systems. We describe the existence of contrasting gradients in social foraging strategies and hierarchical social structures among colonial and territorial breeders associated with species (and population) reliance on carrion differing in size and predictability. We also highlight the potential role of vulture gatherings in maintaining population-level social structures and for mate-finding given high mate-selectivity. Next, based on this social framework, we discuss the impact of human activities on social foraging, territory structures, resource partitioning processes, and mating dynamics. However, little is known about how disruptions of social habits may have contributed to vulture population declines and/or may impede their recovery. Lastly, we provide directions for future research on vulture socio-ecology that may improve current conservation efforts. We encourage researchers and wildlife managers to pay more attention to natural carrion diversity underlying vulture social system diversity, especially when implementing supplementary feeding programs, and to consider the complex mating and settlement dynamics in reintroduction programs. Overall, we stress that understanding the complex social life of vultures is critical to harmonize their conservation with anthropogenic activities.

Keywords: anthropogenic impacts, breeding systems, conservation, social behavior, socio-ecology, vultures

LAY SUMMARY

- Although many of the threats faced by vultures have been identified, the impact of human activities on the social life of vultures has received little attention.
- We provide a comprehensive review of current knowledge of vulture social behavior and the evolutionary and ecological roots of their social systems.
- Within this social framework, we discuss aspects as diverse as vulture breeding and mating systems, foraging techniques, social hierarchies, territorial and gathering behavior, and interspecific interactions.
- Overall, we stress that advancing our socio-ecological understanding of the rich social life of vultures is critical to harmonize their conservation in this rapidly changing world.

Integrando el comportamiento social de los buitres en la práctica de la conservación

RESUMEN
Los buitres constituyen uno de los grupos de aves más amenazados a nivel global. Aunque muchas de las amenazas a las que se enfrentan han sido identificadas, el impacto de las actividades humanas en la vida social de los buitres ha recibido muy poca atención. En esta revisión, hacemos hincapié en la necesidad de integrar los aspectos sociales de los buitres en la práctica de la conservación. Primero, sintetizamos el conocimiento actual sobre el comportamiento social de los buitres, así como en las raíces evolutivas y ecológicas de sus sistemas reproductivos.

Describimos los gradientes existentes en las estrategias de forrajeo social y las estructuras sociales jerárquicas entre reproductores coloniales y territoriales, los cuales se relacionan con la dependencia de las distintas especies (y poblaciones) hacia carroñas de distinto tamaño y predictibilidad. También resaltamos el papel potencial de los agrupamientos de buitres en el mantenimiento de las estructuras sociales a nivel de población, además de en el emparejamiento, dado el alto grado de selectividad a la hora de buscar pareja. Basándonos en este marco social, discutimos el impacto de las actividades humanas en la búsqueda social de alimento, las estructuras de los territorios, los procesos de segregación de los recursos y la dinámica de los emparejamientos, si bien se conoce muy poco sobre cómo las perturbaciones de los hábitos sociales pueden haber contribuido al declive de las poblaciones de buitres o impedir su recuperación. Finalmente, aportamos ideas para estudios futuros sobre la socioecología de los buitres que podrían ayudar maximizar el rendimiento de los actuales esfuerzos de conservación. Animamos a los investigadores y gestores del medio natural a prestar más atención a potenciar la diversidad del recurso carroña, sobre la que se asienta la diversidad de los sistemas sociales de los buitres, especialmente a la hora de implementar programas de alimentación suplementaria. Además, los programas de reintroducción deberían considerar las complejas dinámicas de emparejamiento y asentamiento. En general, nuestra revisión destaca la importancia de entender mejor la complejidad de la vida social de los buitres para así armonizar su conservación con las actividades humanas.

Palabras clave: Buitres, sistemas reproductivos, socioecología, comportamiento social, impactos humanos, conservación

INTRODUCTION

Vultures are the only obligate scavengers among terrestrial vertebrates, comprising 23 species of 2 independent phylogenetic lineages: New World vultures (Cathartidae, 7 species) and Old World vultures (Accipitridae, 16 species; Ferguson-Lees and Christie 2010). They constitute one of the most threatened groups of birds worldwide (Buechley and Şekercioğlu 2016); most vulture species have experienced dramatic declines on a global scale (with the exception of some New World species; Ogada et al. 2012). Vultures play a crucial role in ecosystem functioning and stability (DeVault et al. 2016), and the reduction in their numbers has substantial ecological, social, and economic implications related to regulatory and cultural ecosystem services (Becker et al. 2005, Markandya et al. 2008, Margalida and Colomer 2012, Morales-Reyes et al. 2015, DeVault et al. 2016). Although the anthropogenic causes of their declines have been extensively discussed in several recent reviews (Ogada et al. 2012, 2016a, Buechley and Şekercioğlu 2016), the impact of human activities on the social life of vultures remains largely overlooked.

Vultures are highly social animals with a diverse range of breeding systems both within and among species, ranging from strict territoriality to various forms of social breeding (Ferguson-Lees and Christie 2010). Their degree of sociality also varies widely irrespective of breeding system, with some species showing permanent forms of group living, whereas others have much more fluid social systems characterized by fission–fusion dynamics linked to food bonanzas, communal roosting, and other social gatherings (Donázar 1993). Despite this fascinating complexity, significant gaps remain in our knowledge regarding many basic aspects of their ecology, social life, and the ecological factors underlying their breeding systems. Given the steep drop in vulture numbers worldwide, an urgent need exists to establish the functional links between their behavioral ecology and conservation (Caro 2007, Blumstein and Fernández-Juricic 2010, Berger-Tal et al. 2011).

We have 3 aims. First, we provide a comprehensive review of current knowledge of vulture social behavior and the evolutionary and ecological roots of their social systems. We highlight current gaps in knowledge about vulture socio-ecology and social system diversity. Variation in vulture social systems are defined by species differences in (1) social organization regarding breeding systems, (2) foraging and social information-use strategies, (3) communal roosts and other social gatherings, (4) hierarchical social structure associated with foraging and food exploitation, and (5) mating and parental care systems. Second, based on this framework, we describe species-specific consequences for vulture social systems of human activities (poisoning, poaching, habitat destruction and modification), showing that anthropogenic influences on the social dynamics of local vulture populations may be substantial and affect a wide range of population processes. Third, we propose directions for future research and provide examples of conservation problems where knowledge about vulture social biology could be particularly beneficial. Overall, we wish to stress that increased awareness of the complex social life of vultures is of critical importance for more effective management and conservation of different vulture species.

THE SOCIO-ECOLOGY OF VULTURES: THE STATE OF THE ART

Despite vultures being a small group of birds, they display outstanding socio-ecological diversity. However, the types of vulture social behaviors and their functions remain poorly described in the scientific literature. Below we synthesize the current knowledge about the different components of the social habits of vultures. For this purpose, we used the Web of Science to conduct a systematic review (Haddaway et al. 2015) of English language scientific articles published before December 2019. Our search string included the following terms in the title: "vulture AND social*" (n = 19 papers found), "vulture AND breed*" (n = 116), "vulture AND forag*" (n = 26), "vulture AND roost*" (n = 32), and "vulture AND parental" (n = 4). We repeated these searches changing "vulture" to "condor", as researchers studying condors rarely use the term vulture, and obtained 25 additional articles. Then, we refined the final number of articles used by reading the title and, if needed, the abstract and full content. We excluded articles that did not explicitly deal with any social aspect. Then, we followed a "snowball" procedure, identifying additional relevant literature from the reference lists of the previously selected articles. Finally, we also consulted several monographs on vultures (Wilbur and Jackson 1983, Mundy et al. 1992, Donázar 1993, Snyder and Snyder 2000, Houston 2001, Dobado and Arenas 2012), raptors (Newton 1979, Del Hoyo et al. 1994, Ferguson-Lees and Christie 2010), and birds (Newton 1998).

Social and Non-social Breeding Habits

According to patterns of aggregation and spacing of nesting sites, vulture breeding habits can be broadly categorized into 4 groups: (1) territorial, (2) solitary, (3) loose colonial, and (4) cohesive colonial (Table 1). The distinction between territorial and solitary breeding species depends on whether they defend a foraging area or their nesting site against conspecifics (Donázar 1993), although this question remains poorly quantified and understood for most species. Considerable differences may also exist in distances between nest and degrees of territorial defense between and within populations of the same species (Donázar 1993, Fargallo et al. 1998, Anderson 1999, Martinez and Blanco 2002). Loose colonial breeding is characterized by relatively small and patchy breeding aggregations, most commonly in trees. Nest spacing in these species can be highly variable, sometimes including different nests within the same tree. Cohesive colonial *Gyps* species may form large breeding aggregations of hundreds of nests, usually on cliffs.

Foraging and Social Information-Use Strategies

Different vulture species evolved distinct physio-morphological adaptations (e.g., body size, beak shape, olfactory sense, soaring capacity) for the exploitation of carcasses differing in size and predictability (Hertel 1994, Ruxton and Houston 2004). Often, these adaptations are related to complex patterns of interspecific resource partitioning and facilitation in so-called "vulture guilds", whereby small-bodied species may detect/signal the presence of carrion and large-bodied species may facilitate access to carcasses by tearing open skin with their powerful beaks (Africa: Kruuk 1967, König 1983, Kendall et al. 2012; Americas: Wallace and Temple 1987a, Houston 1988, Lemon 1991; Europe: Cortés-Avizanda et al. 2012, Moreno-Opo et al. 2016, 2020). Facilitative interactions also occur among vultures and facultative scavengers such as other raptors, corvids, and large mammalian carnivores (Kane et al. 2014, Moleón et al. 2014a). A notable exception is the frugivorous Palm-Nut Vulture (*Gypohierax angolensis*), which does not rely exclusively on carrion to survive (Carneiro et al. 2017).

There are 2 main foraging strategies in vultures: solitary, when individuals or pairs forage alone, and loosely to highly dispersed groups, in which individuals observe the behavior of other individuals to find food (Giraldeau and Caraco 2000). Foraging strategies and breeding habits are closely associated, and ultimately linked to species-specific specializations for carrion differing in size, density, and predictability (Table 1). For example, colonial *Gyps* vultures feed almost exclusively on (individually) indefensible food resources (mainly wild ungulate [Mundy et al. 1992, Houston 2001] and livestock carcasses [Donázar 1993, Parra and Tellería 2004, Xirouchakis 2005]), and they rely heavily on social information for finding food (Jackson et al. 2008, Deygout et al. 2010, Dermody et al. 2011, Cortés-Avizanda et al. 2014). This contrasts with the majority of territorial and solitary breeding vulture species, which exploit a mixture of small/medium-sized and large carcasses (Old World vultures: Hiraldo 1976, König 1983, Ceballos and Donázar 1990, Margalida et al. 2009, 2012, Karimov and Guliyev 2017; New World vultures: Coleman and Fraser 1987, Hiraldo et al. 1991, Kelly et al. 2007), with small-bodied species also relying on carrion pieces of large carcasses left by more powerful vultures. The detection and consumption of small- and medium-sized carcasses typically does not require complex social strategies and can be performed by solitary individuals, in part because of the often higher densities of these carrion items (DeVault et al. 2003), but also given specific morphological adaptations (e.g., eye size and wing-loading in Lappet-faced Vultures [*Torgos tracheliotos*] [Spiegel et al. 2013]; olfactory sense in species from the genus *Cathartes*: Turkey Vultures [*C. aura*] [Houston 1986, Grigg et al. 2017], Lesser Yellow-headed Vultures [*C. burrovianus*] [Houston 1988], and Greater Yellow-headed Vultures [*C. melambrotus*] [Gomez et al. 1994]). Although Andean Condors (*Vultur gryphus*) and California Condors (*Gymnogyps californianus*) forage and breed solitarily, they feed mostly on large carcasses

TABLE 1. Overview of the breeding systems and foraging strategies of Old and New World vultures. Status refers to the International Union for Conservation of Nature (IUCN) Red List Categories (LC = Least Concern, NT = Near Threatened, E = Endangered, CR = Critically Endangered). Endangered and Critically Endangered species are shown in bold. Differences in breeding systems are based upon patterns of aggregation and spacing of nesting sites and degrees in territorial defense: territorial (T), solitary (S), colonial (C), and loose colonial (LC). All references deal with studies describing nesting habits/parental care behaviors. Foraging strategy refers to levels of social foraging, based on the most commonly observed food-searching habits of the species. Foraging in loose groups (LG) implies the extensive use of conspecifics to locate (large) ungulate carcasses, while solitary foragers (S) are facultative social foragers that search for food alone or in couples and that rely on a mixture of small/medium and large carrion resources. Species differences in levels of sociality are indicated by roosting communally ([c]) and tendency to associate in social groups (* = species that frequently form groups of up to 50 individuals; ** = gregarious species often seen in large groups of more than 100 individuals [based on historical abundance]). As a general rule, colonial and loose colonial breeders rely more on social information, whereas territorial/solitary breeding species tend to forage solitarily or in couples. See text for more details.

Old World vultures

Species	Region	Status	Mating system	Foraging strategy
Gypaetinae				
Gypohierax angolensis	Africa	LC	T	S[c]
Gypaetus barbatus	Eurasia and Africa	NT	T[1,2,3]	S
Neophron percnopterus	Eurasia and Africa	EN	T[4]	S[c**]
Aegypiinae				
Sarcogyps calvus	Asia	CR	T[5,6,7]	S
Trigonoceps occipitalis	Africa	CR	T[8]	S
Aegypius monachus	Eurasia	NT	S/LC[9]	S/LG[c]
Torgos tracheliotos	Africa	EN	T[10,11]	S[c*]
Necrosyrtes monachus	Africa	CR	LC	S/LG[c**]
Gyps africanus	Africa	CR	LC[12]	LG[c**]
Gyps tenuirostris	Asia	CR	S/LC	LG[c**]
Gyps rueppelli	Africa	CR	C/LC	LG[c*]
Gyps coprotheres	Africa	EN	C[13]	LG[c**]
Gyps fulvus	Eurasia	LC	C[14,15]	LG[c**]
Gyps himalayensis	Asia	NT	LC	LG[c*]
Gyps indicus	Asia	CR	C/LC[16]	LG[c**]
Gyps bengalensis	Asia	CR	C[17,18]	LG[c,**]

New World vultures

Species	Region	Status	Mating system	Foraging strategy
Cathartidae				
Vultur gryphus	South America	NT	S[19]	S[c*]
Gymnogyps californianus	North America	CR	S[20]	S[c*]
Sarcoramphus papa	South America	LC	S[21,22]	S[c]
Coragyps atratus	Americas	LC	S[23]	S/LG[c**]
Cathartes aura	Americas	LC	S[24]	S[c**]
Cathartes burrovianus	South America	LC	S?	S
Cathartes melambrotus	South America	LC	S?	S

References: 1 = Margalida and Bertran (2000), 2 = Margalida and Bertran (2005), 3 = Bassi et al. (2017), 4 = Etxebarria et al. (2019), 5 = Dhakal et al. (2014), 6 = Bhusal and Paudel (2016), 7 = Manandhar et al. (2019), 8 = Murn and Holloway (2014), 9 = Dobado and Arenas (2012), 10 = Mundy et al. (1992), 11 = Shobrak (1996), 12 = Maphalala, and Monadjem (2017), 13 = Robertson (1986b), 14 = Donázar (1993), 15 = Xirouchakis and Mylonas (2007), 16 = Manchiryala and Medicheti (2014), 17 = Venkitachalam et al. (2013), 18 = Thakur (2015), 19 = Lambertucci and Mastrantuoni (2008), 20 = Snyder and Snyder (2000), 21 = Ramo and Busto (1988), 22 = Schlee (1995), 23 = Buckley (2020), 24 = Rollack et al. (2013).

(Lambertucci et al. 2009), including those of marine mammals such as whales (Chamberlain et al. 2005, Lambertucci et al. 2018). The dietary breadth of these huge scavengers can neverthless be diverse, as 22.5% of carrion taxa consumed by Andean Condors may be European hare (Ballejo et al. 2018), whereas a variety of large and medium-sized mammals has been reported in the diet of the California Condor (Collins et al. 2000).

Given the difficulty of observing vultures in the wild, solitary food searching and social feeding habits in general remain poorly quantified (but see Byrnes et al. 2019 and Holland et al. 2019 for studies on sympatric Black Vultures [*Coragyps atratus*] and Turkey Vultures). Most vultures are opportunistic foragers that are attracted to large carcasses or food bonanzas by local enhancement (i.e. to other feeding vultures; Cortés-Avizanda et al. 2014). However, the presence of large groupings at carcasses may bias the perceived importance of this resource type, especially taking into consideration the often high levels of competition that limit individual food intake rates. In territorial/solitary breeding species, the choice between solitary food-searching vs. collective feeding may depend not only on the availability of small/medium carrion resources (Cortés-Avizanda et al. 2011), but also on individual traits such as sex, age, social rank, and territorial status (van Overveld et al. 2018).

Communal Roosting and Other Social Gatherings

Floaters, especially immature birds, of most species are gregarious, resulting in an intense pre-breeding social life with continuous interactions of variable intensity and nature (e.g., aggressive, cohesive, and sexual) depending on context (Newton 1979, Donázar 1993). However, once recruited into the reproductive population, territorial species generally adopt a more solitary lifestyle when roosting and foraging (Newton 1979, Donázar 1993, Ferguson-Lees and Christie 2010). Year-round, solitary living is nevertheless rare, and individuals of all species eventually converge into aggregations of varying size (i.e. so-called “open” groups where individuals come and go at different rates, similar to many corvids; see Boucherie et al. 2019), depending on environmental and individual conditions (age and breeding status), and the overall abundance of each particular vulture species.

While communal night roosting is a key element of the social organization of the majority of vulture species, this behavior seems absent in some territorial species (e.g., Bearded Vultures [*Gypaetus barbatus*], Red-headed Vultures [*Sarcogyps calvus*], White-headed Vultures [*Trigonoceps occipitalis*]; Table 1). Past studies have mainly focused on these gatherings as centers of information for food exploitation (Ward and Zahavi 1973). In some species, it has been claimed that roosts facilitate foraging (e.g., Griffon Vultures [*Gyps fulvus*] and Black Vultures, both of which form loose foraging groups), either through information transfer (Rabenold 1987a, Buckley 1997, Harel et al. 2017) or by facilitating the formation of foraging groups (Buckley 1996, Dermody et al. 2011). Such benefits may not apply to other species, such as Turkey Vultures (Prior and Weatherhead 1991, 2004, Buckley 1997), which tend to be more solitary foragers (owing to their well-developed sense of smell), although they regularly (although not exclusively) roost in mixed flocks with Black Vultures (Holland et al. 2019).

Nocturnal communal roost sites are nowadays often situated close to anthropogenic and highly predictable food resources, such as garbage dumps and feeding stations (Table 2). This suggests an important underlying role of roosts as a food insurance strategy aimed at reducing the time energy of movements to obtain food resources. In the majority of species, communal roosts are also characterized by strong seasonal social dynamics, whereby the composition of the roost varies according to territorial status and/or age class (immature vs. adult), migratory status, and the presence of newly fledged birds (Table 2). Roosts may therefore serve an important function as centers of social information (c.f. Bijleveld et al. 2010), where individuals update social information on conspecifics, search for mates, and newly born birds become integrated into the local population (see Blanco and Tella 1999 for an example on social corvids).

Evidence suggests that gatherings around carcasses may also function as meeting places for social purposes. For example, observations of individually marked Griffon Vultures revealed that some individuals may visit carcasses on consecutive days, even when they are satiated from their first visit, as assessed by their full crop (Acha et al. 1998). Mundy et al. (1992) suggested that Lappet-faced Vultures feed on small prey, and attend large animal carcasses mainly for social interaction. Canarian Egyptian Vultures (*Neophron percnopterus majorensis*) aggregate in large numbers at supplementary feeding stations, especially outside the breeding season. At these gatherings, individuals display a wide range of affiliative and agonistic behaviors not linked to food exploitation (van Overveld et al. 2020). Gatherings with a specific socializing function have also been reported for Egyptian Vultures living in Socotra (Yemen) (Porter and Quiroz 2010, Porter and Suleiman 2012). Many vulture species also form large gatherings after feeding, often near water sources, but the possible social functions of these gatherings have been largely unstudied. However, Sauer (1973) provided a detailed description of the behavior of Lappet-faced Vultures and Cape Vultures (*Gyps coprotheres*) at diurnal gatherings in Namibia and suggested they constitute an important function as meeting places, where vultures gather for "social contact, rest and maintenance performance". Diurnal gatherings may not necessarily be restricted to resting or foraging places as, for example, Griffon Vultures may perform extensive group soaring above their colonies, especially during the pre-breeding period (T. van Overveld et al. personal observation; see also Xirouchakis and Mylonas 2007).

Social Hierarchies

Social hierarchies within vulture guilds have been well studied, showing species-specific dominance ranks depending on body size with additional effects of age (immature vs. adult) and sex within species (Old World vultures: König 1983, Moreno-Opo et al. 2020; New World vultures: Wallace and Temple 1987a, Houston 1988). Social hierarchies at the individual level have only been studied in Egyptian Vultures, where social structure is governed by sex- and age-dependent relationships, in which the slightly larger females are dominant over males, and non-territorial and young individuals of both sexes have a lower social position that increases with age (van Overveld et al. 2018, 2020). The social systems of territorial breeders seem to be characterized by either female or male dominance, depending on the degree of sexual size-dimorphism (e.g., male dominance in Andean Condors [Donázar et al. 1999, Marinero et al. 2018], female dominance in Egyptian and Bearded Vultures [Negro et al. 1999, van Overveld et al. 2020]). Competitive interactions during feeding in territorial/solitarily breeding species are often characterized by relatively few or low-level physical fights (e.g., Egyptian Vultures [van Overveld et al. 2020], Figure 1A; Turkey Vultures [Lemon 1991, Prior and Weatherhead 1991]), or by aggression directed to specific individuals in larger bodied species (e.g., Bearded Vultures [Moreno-Opo et al. 2020], Figure 1B; Cinereous Vultures [*Aegypius monachus*] [Moreno-Opo et al. 2020]; Lappet-faced Vultures [Bamford et al. 2010]). Several territorial species evolved ritualized dominance displays to diffuse aggression (e.g., "duels" in Egyptian and Bearded Vultures, whereby birds parade face-to-face and erect head feathers; van Overveld et al. 2020), or the "threatening march" by Cinereous Vultures (Moreno-Opo et al. 2020) and Lappet-Faced Vultures (König, 1983), and/or specific traits indicative of contest ability (e.g., flushing of the face: color changes caused by increased blood flow through vascularized skin; Andean Condors [Marinero et al. 2018]; Lappet-faced Vultures [Bamford et al. 2010]; Hooded Vultures [*Necrosyrtes monachus*] [Negro et al. 2006]), or, as in Bearded Vultures, by a marked expansion of the scleral ring during intraspecific encounters (e.g., fights) or when the birds feel threatened (e.g., when handled) (Negro et al. 1999). Black Vultures are an exception to these patterns. Although this species shows solitary breeding, their collective foraging habits resemble that of a colonial breeding species (see below, Figure 1C). They are renowned for displaying high levels of inter- and intraspecific aggressiveness during food exploitation, despite being relatively small (Buckley 2020), allowing them to outcompete larger species, including Andean Condors (Carrete et al. 2010). In Black Vultures, it has been also claimed that feeding groups may consist of coalitions composed of family members, and even kin from other families, which provide each other with social support in contests over food (Rabenold 1986, Parker et al. 1995).

In *Gyps* spp., feeding interactions are characterized by extensive physical fighting or pecking among conspecifics (Figure 1D). Their threat displays and ornaments are generally less elaborate, although not absent, including vascular skin on wing patches and various dominance poses (e.g., wing-spreading; T. van Overveld et al. personal observation). In colonial species, in general, social hierarchy at carcasses seems to be shaped by 3 factors: hunger, size, and age, with the hungriest, largest, and most experienced individuals having advantage against conspecifics (Donázar 1993, Bosè and Sarrazin 2007, Bosè et al. 2012, Moreno-Opo et al. 2020). However, there are strong differences in aggressiveness among species during food exploitation (Hille et al. 2016; J.A. Sánchez-Zapata personal observation).

Despite the scarcity of detailed work on intraspecific agonistic relationships, studies point towards a gradient in hierarchical social structure, with a strong hierarchal lifestyle typifying territorial species. However, subtle differences may exist in the nature and patterning of social relationships among territorial breeders. For example, Canarian Egyptian Vultures frequently engage in socializing activities outside a pair-living context (through non-reciprocal allopreening), sometimes including members of the same sex and unrelated adults and immatures (van Overveld et al. 2020). Although the function of this behavior is not yet clear, this type of allopreening behavior is absent in the closely related, but more solitary, Bearded Vulture (A. Margalida personal observation). Allopreening is also commonly observed in other social vulture species such as the Black Vulture (Rabenold 1986) and Andean Condor (McGahan, 2011). In Turkey Vultures, dominance status may vary according to migratory status, with wintering individuals being dominant over residents (Kirk and Houston 1995). This indicates not only that local hierarchical social structures may temporally change, but also that baseline levels of individual aggressiveness can vary among populations of the same species. Hierarchical social structures in Turkey Vultures also seem more pronounced compared to Black Vultures (Prior and Weatherhead 1991), pointing towards additional differences in social

TABLE 2. Overview of studies on nocturnal and diurnal gatherings in vultures. In the majority of species, gatherings are characterized by strong seasonal social dynamics (i.e. increases in group size outside the reproductive period). Age-specific roosts (where adults and immatures roost at different locations) are reported for Andean Condors only. Note that nocturnal roosts are nearly always located close to predictable food resources and/or linked to transhumance, while diurnal gatherings are formed at food resources and near water ponds. Also, note that dominance interactions are not restricted to gatherings at food resources, but also at diurnal resting sites and nocturnal roosts. Evidence for social information transfer on food locations is reported for 2 species (*Gyps fulvus* and *Coragyps atratus*).

Species	Gathering type	Seasonal dynamics	Environmental factors	Social interactions
Neophron percnopterus	Nocturnal	Breeding,[1] migration [1]	refuse dump,[2,3] livestock (farms),[2] feeding station [a]	age/dominance-specific roosting place [a]
	Diurnal	Breeding [4]	feeding station,[4] food bonanzas,[5] waterponds [5]	dominance displays, copulations allopreening (mate-seeking, pair-bonding) [4,5]
Gyps fulvus	Nocturnal	Breeding [6,7]	feeding station,[8] livestock (transhumance) [6,7,9]	foraging information transfer [8]
	Diurnal		feeding station [8,10]	Observing [8,10 b]
Torgos tracheliotos	Diurnal		waterponds,[11] carcasses [12]	dominance displays,[11,12] pair-bonding [11]
Necrosyrtes monachus	Nocturnal	Breeding [13]	Slaughterhouses [13,14]	
Gyps coprotheres	Diurnal		waterponds [11]	dominance displays (low) [10]
Vultur gryphus	Nocturnal	age-specific [15,16]	weather (thermals, cold stress),[17,18,19] livestock (farms, transhumance)[16]	age/dominance-specific roosting place [18]
Sarcoramphus papa	Diurnal		waterponds [20]	
Cathartes aura	Nocturnal [c]	Breeding [21]	predation [22,23]	age/dominance-specific roosting place [23]
Coragyps atratus	Nocturnal	Breeding [24]	refuse dump [25]	family-association,[24,26] dominance displays [27] information transfer [28,29,30]

References: 1 = Ceballos and Donázar (1990), 2 = Donázar et al. (1996), 3 = Margalida and Boudet (2003), 4 = van Overveld et al. (2020), 5 = Porter and Suleiman (2012), 6 = Xirouchakis and Mylonas (2004), 7 = Xirouchakis (2007), 8 = Harel et al. (2017), 9 = Olea and Mateo-Tomás (2009), 10 = Acha et al. (1998), 11 = Sauer (1973), 12 = Bamford et al. (2010), 13 = Mullié et al. (2017), 14 = Ssemmanda et al. (2005), 15 = Lambertucci et al. (2008), 16 = Lambertucci (2013), 17 = Lambertucci (2010), 18 = Lambertucci and Ruggiero (2013), 19 = Donázar and Feijóo (2002), 20 = Baker and Whitacre (1996), 21 = Mcvey et al. (2008), 22 = Buckley (1998), 23 = Evans and Sordahl (2009), 24 = Rabenold (1986), 25 = Novaes and Cintra (2013), 26 = Parker et al. (1995), 27 = Rabenold (1987a), 28 = Rabenold (1987b), 29 = Buckley (1996), 30 = Buckley 1997 (no data from actual roosting behavior).

[a] Personal communication T. van Overveld and J. A. Donázar.

[b] Personal observation G. Blanco.

[c] No evidence for foraging information transfer at Turkey Vulture roosts (Buckley 1997, Prior and Weatherhead 2004).

FIGURE 1. Examples of group foraging for vultures with different social systems. (**A**) Egyptian Vultures (*Neophron percnopterus*) are territorial breeders but aggregate in large numbers at abundant food resources and roosts, especially outside the breeding season. Their group foraging is characterized by strong hierarchical relationships with few physical fights (photograph courtesy of T. van Overveld). (**B**) Bearded Vultures (*Gypaetus barbatus*) display year-round territoriality and forage and roost solitarily (or in couples). Intra- and interspecific encounters at food resources are characterized by aggressive fights between specific individuals, in this case 2 immatures (photograph courtesy of A. Margalida). (**C**) Black Vultures (*Coragyps atratus*) are solitary breeders and renowned for displaying high levels of intraspecific aggressiveness during food exploitation, despite being relatively small. Group foraging resembles that of colonial breeding species (photograph courtesy of M. de la Riva). (**D**) Colonial Griffon Vultures (*Gyps fulvus*) rely on large, individually indefensible carcasses and group foraging is characterized by extensive fighting (photograph courtesy of M. de la Riva).

organization between these 2 sympatric species (Byrne et al. 2019, Holland et al. 2019).

Mating Behavior and Parental Care

Vultures typically form life-long relationships, in which pair formation is associated with complex, ritualized courtship displays including acrobatic flights (plunges and twists, and so-called "tandem-flights"), dancing behaviors, and ritualized head movements (Del Hoyo et al. 1994, Ferguson-Lees and Christie 2010). The presence of elaborate head ornamentation in territorial breeding species (e.g., colorful facial skins and structures such as bulbs and wrinkles), while largely absent in colonial breeders, indicates some fundamental differences in the role of traits reflecting individual quality (e.g., health [Negro et al. 2002, Blanco et al. 2013], social status [see above]), in species defending territories and/or exhibiting more solitary foraging strategies. Age- and sex-dependent patterns of breeding recruitment and pairing also differ between territorial and colonial species. For instance, in colonial *Gyps* vultures, individuals with subadult plumage can form an appreciable proportion of the breeding populations (Mundy et al. 1992, Blanco et al. 1997), especially females (Blanco and Martínez 1996). However, breeding before acquiring full adult plumage is highly exceptional in Egyptian, Bearded, and other territorial vultures (Mundy et al. 1992, Donázar 1993).

After mating, pairs maintain strong pair bonds, as shown by extensive, sometimes year-round, allopreening sessions displayed by most species. Frequent observations of copulations outside the fertile period, even after chicks have hatched (e.g., Egyptian Vultures: Donázar et al. 1994, Cugnasse 2000; Bearded Vultures: Bertran and Margalida 1999; White-headed Vultures: Murn and Holloway 2014; California Condors: Mee et al. 2004; Griffon Vultures:

Xirouchakis and Mylonas 2007; Cape Vultures: Robertson 1986), may point towards an additional pair-bonding function of this behavior. The existence of tight pair bonds is further illustrated by observations of pairs foraging together and/or arriving at carcasses simultaneously, especially in territorial/solitary breeding species (e.g., King Vultures [*Sarcoramphus papa*] [Wallace and Temple 1987a, Haenn et al. 2014]; Lappet-faced Vultures [Mundy et al. 1992]; Red-headed Vultures [Bhusal and Paudel 2016], Egyptian and Cinereous Vultures [T. van Overveld, G. Blanco personal observation]). Strong pair bonds are typical for bird species with high levels of parental cooperation during breeding (Kenny et al. 2017). Most studies show that both sexes contribute to parental tasks (Table 1), although some subtle differences may exist with higher contributions of males to territorial defense (Bearded Vultures: Margalida and Bertran 2005) or chick-feeding (Andean Condors: Lambertucci and Mastrantuoni 2008), and females to incubation (Egyptian Vultures: Etxebarria et al. 2019). Long development times of nestling vultures, together with prolonged periods of post-fledging care, may lead to biannual breeding patterns in some species (e.g., California Condors: Snyder and Snyder 2000).

While social monogamy and biparental care of offspring is the most common mating and care strategy in vulture breeding systems, in some territorial species breeding strategies can be remarkably diverse. For example, Bearded Vultures in the Spanish Pyrenees frequently form polyandrous trios (Heredia and Donázar 1990, Carrete et al. 2006a; see also Krüger 2007 for an example of a polyandrous trio in South Africa) or even quartets (Margalida et al. 1997), and polygynous trios are also occasionally reported (Fasce and Fasce 2011, Gil et al. 2017). Polyandrous trios have also been observed in Egyptian Vultures in mainland Spain (Tella 1993). Canarian Egyptian Vultures may regularly form both polyandrous and polygynous trios (T.van Overveld, M. de la Riva, J.A. Donázar personal observation). Polygynous trios have also occasionally been recorded in other species, such as Cinereous Vultures (Dobado and Arenas 2012). Although evidence suggests that trio formation is linked to high population densities in Bearded Vultures (Carrete et al. 2006a), the causes and consequences of these alternative reproductive tactics in vultures are generally poorly understood. High levels of sexual conflicts among males in polyandrous trios often may lead to reduced reproductive output (Carrete et al. 2006a, Bertran et al. 2009). Males in polyandrous trios regularly engage in homosexual behaviors (male-male mountings, often followed by allopreening; Bertran and Margalida 2003), while females occasionally display reverse-mountings (Bertran and Margalida 2006). These observations again point towards an important social bonding function of copulations, in this case conflict management promoting cooperation (Bertran et al. 2009).

ANTHROPOGENIC IMPACTS ON VULTURE SOCIAL DYNAMICS

Disruptions of Social Foraging

Low vulture population densities caused by human persecution may cause social disturbance by affecting overall levels of social cohesion in populations, so that individuals become less well connected (Sih et al. 2009). A decrease in interaction patterns may be particularly harmful for species that rely heavily on social information use during foraging, for example, in colonial species such as *Gyps* spp. (Table 1), but potentially also affect the social foraging dynamics of pre-breeding territorial and solitary species, which usually show more social habits than adults. Some modeling studies have shown the potential for Allee effects reducing foraging efficiency in colonial breeders (Jackson et al. 2008, Dermody et al. 2011).

In addition, negative effects of population density declines on social foraging may be exacerbated by changes in population phenotypic composition (Farine et al. 2015) through the disappearance of keystone individuals (e.g., old, dominant birds with extensive social and environmental knowledge; Sih et al. 2009) or by changes in the distribution of behavioral phenotypes (e.g., "personality" types differing in exploration and risk-taking tendencies; Réale et al. 2007, Spiegel et al. 2017). Selective mortality among older birds and/or more explorative individuals may create perturbations in social foraging by affecting producer–scrounger relationships (i.e. "producers" search for food themselves or rely on previously acquired information, while "scroungers" follow others to collect food resources; Vickery et al. 1991) and/or social learning processes, resulting in the loss of knowledge about food locations and/or novel food resources (Brakes et al. 2019). As many vulture species also importantly rely on interspecific information to locate carcasses, any changes in the abundance of species with a "finding/producing" role (small-bodied vultures and facultative avian and mammalian scavengers), could have reverberating effects on carcass detection rates.

Changes in Food Exploitation Patterns

Apart from disruptions in social foraging dynamics, recent sanitary legislation aimed at removing livestock (Donázar et al. 2009a) and big game carcasses (Margalida and Moleón 2016) are forcing vultures to increasingly rely on predictable and clumped food resources of anthropogenic origin, such as landfills and supplementary feeding stations (Donázar et al. 2009b, Margalida et al. 2010, Plaza and Lambertucci 2017, Henriques et al. 2018). Such locations exert a variety of species-specific pressures, depending on species' traits (e.g., the degree of social foraging, competitive skills) and patterns of abundance, distribution, and predictability and nature of food resources. Although anthropogenic feeding locations have been part of the foraging environment for *Gyps* spp. for centuries (Moleón et al. 2014b; see also Roller MaMing et al. 2016 for the ancient practice of "sky burials"), an increased dependency on feeding stations may create a more disadvantageous foraging scenario for smaller, competitively inferior species. In particular, the high predictability of food supply at fixed feeding points diminishes the important role of arrival time characteristic for intra-guild feeding processes at unpredictable large carcasses (e.g., "finder's advantage" for small species/solitary foragers [Kendall et al. 2013]; see also Cortés-Avizanda et al. 2016 for an extensive discussion of this topic). Alternatively, reductions in population densities of "key-stone" hide-tearers (eagles, large-bodied vultures), may have reverberating effects on carrion consumption patterns by smaller bodied species, for instance, by forcing them to feed on carcasses at a later stage of decomposition, and possibly, lower carrion quality (Parmenter and MacMahon 2009). Lastly, artificially large aggregations occurring repeatedly at the same feeding sites, sometimes reaching up to thousands of individuals in Griffon Vultures in Spain (Acha et al. 1998; J.A. Donázar, M. de la Riva personal observation), may increase parasite and disease transmission, both intra- and interspecifically, as well as exposure to pharmaceuticals (Margalida et al. 2014, Pitarch et al. 2017, Blanco 2018).

The social impact and/or adaptive strategies associated with the exploitation of landfills, or human waste in general, tend to be less clear and highly species- and context-specific. Some evidence suggest landfills are used mainly by inexperienced birds or subdominant individuals in Andean Condors (Pavez et al. 2019), which differs from the use of feeding stations by dominant birds in Canarian Egyptian Vultures (van Overveld et al. 2018). While feeding at rubbish may increase the risk of infections and poisoning (Plaza and Lambertucci 2018, Plaza et al. 2019), and promote the consumption of junk (Houston et al. 2007), some species such as Black Vultures seem to benefit from the increased presence of anthropogenic resources (de Araujo et al. 2018, Plaza and Lambertucci 2018). Hooded Vultures are human commensals in several parts of western Africa, where they forage and breed in loose groups near towns and cities, whereas in southern Africa the species displays a more solitary way of living and inhabits dense forests (Anderson 1999, Thompson et al. 2020). Egyptian Vultures living on the island of Socotra also still provide a key regulating service by disposing of organic waste produced in towns (Porter and Suleiman 2012, Gangoso et al. 2013). However, strong population declines in other parts of its range have been accompanied by a highly secretive lifestyle.

Changes in the composition of facultative scavenger communities and the ratio of facultative to obligate scavengers can also impact vulture foraging and competitive social interactions (Moleón et al. 2014a). Strong population declines of apex predators globally (Stier et al. 2016) may have important cascading effects on food supply and carcass signaling to vultures (Moleón et al. 2014a), with potential strong impacts on grouping behaviors and individual (e.g., experience-dependent) foraging success that need scientific attention. Reductions in group size in crowd-foraging *Gyps* spp. may lower their ability to compete with mammalian scavengers such as spotted hyenas (*Crocuta crocuta*) and feral dogs (*Canis familiaris*) (Butler and du Toit 2002).

Perturbations of Social Structures

Changes in the predictability of food resources may lead to an overall intensification of inter- and intraspecific social competition, affecting overall ranking dynamics within populations. However, such effects should be particularly pronounced in territorial species displaying a strong hierarchical way of living. If resources differing in predictability also differ in quality (i.e. low-quality garbage dumps vs. high-quality carcasses at feeding station or farms; see above), large interindividual differences in competitive abilities or changes in the strength of social interactions may give rise to asymmetric patterns of individual, age- and/or sex-specific mortality within populations (Hernández and Margalida 2009, Sanz-Aguilar et al. 2017). Furthermore, changes in competitive regimes, combined with the frequent disappearance of individuals (through human persecution) may create unstable dominance structures, possibly leading to elevated stress levels linked to rearrangements of hierarchical relationships (see Sapolsky 2005 for an example on social primates).

Changes in resource distribution through the presence of supplementary feeding stations and landfills may influence the quality of territories in the vicinity of these patches (Liberatori and Penteriani 2001, Tauler-Ametller et al. 2017), and lead to status-dependent settlement patterns (van Overveld et al. 2018). Since predictable food resources may be more valuable to the dominant sex, this may lead to complex situations in which females perceive the value of territories differently compared to males, with consequences for mating dynamics. However, although breeding close to predictable feeding patches may confer important advantages regarding a reduction in food-searching costs during chick-rearing (e.g., Liberatori and Penteriani 2001), it has been shown to have a negative effect on the reproductive output of Bearded Vultures, possibly because territory owners may suffer from increased conflicts with birds visiting feeding sites (Carrete et al. 2006b). Predictable feeding patches may potentially also lead to changes in local population structures by influencing dispersal tendencies, as has often been suggested to be the case for the strong philopatric behavior of Bearded Vultures in the Spanish Pyrenees (but see Margalida et al. 2016, 2017a).

Lastly, limited attention has been given to the integration of captive-bred individuals within local population social structures. Captive-reared young are highly sensitive to human behavioral imprint (Schlee 1995, Meretsky et al. 2000), which may lead to undesired human-orientated behaviors (see Walter et al. 2010 for examples in the early stages of the California Condor reintroduction project). Feeding stations may act as important release sites for captive-reared young where the presence of many other wild birds may promote the development of social skills (Wallace and Temple 1987b, Walters et al. 2010). However, little is known about the social position of reintroduced young (or adults) in wild groupings (Utt et al. 2008) and how social factors shape explorative movements following introduction.

Mating Problems

Despite the scarcity of information on vulture mating behavior in the wild, the complex pairing behavior of vultures is a well-known issue in captive breeding programs, which typically experience low-matching rates in forced pairing settings (Antor et al. 2007). Low pair-matching rates have required that some breeding programs, such as that of the Cinereous Vulture, develop specific "dating aviaries" where individuals can choose their own mate in the hope of improving pairing success (Vulture Conservation Foundation; https://www.4vultures.org/2019/02/14/dating-the-cinereous-vulture-way-helping-captive-birds-find-love/). Mating problems also seem to play an important role during reintroduction projects, which typically require the release of a high number of individuals to create self-sustaining breeding populations, despite the presence of many mature nonbreeders (Schaub et al. 2009). In the wild, demographic imbalance due to human-related mortality could reduce the probabilities of finding optimal mates, especially in territorial vulture species.

DIRECTIONS FOR THE FUTURE

As we have outlined in this review, current anthropogenic influences on the social dynamics of vulture populations can be substantial and affect a wide range of processes that affect population dynamics. Despite the marked diversity in vulture social behaviors, variation in vulture social system diversity has been rarely integrated into vulture conservation practice. Below we highlight fundamental scientific knowledge gaps and future research questions that should be addressed for evidence-based conservation of vultures and their eco-sociological integrity.

Disruptions of Social Breeding and Foraging

Understanding the social consequences of low population sizes is of particular relevance for understanding the foraging dynamics of many *Gyps* spp. living in Asia and Africa, with 5 out of 8 species being critically endangered and some populations being almost completely wiped out, mainly due to intentional (Ogada et al. 2016b) and unintentional poisoning (Green et al. 2004). Unfortunately, little is known about how disruptions in social breeding and foraging have further contributed to their declines, or may slow down population recovery. In particular, a lack of understanding exists about the extent to which reductions in colony sizes have affected specific advantages associated with colonial breeding (e.g., information transfer, reduced predation and mate-finding; Evans et al. 2016, Angulo et al. 2018), and its potential negative consequences on reproductive output (but see Pfeiffer et al. 2016). Furthermore, sparse published information is available on fine-scale differences in feeding habits, social structures, and behavioral differences among different species of this genus. It remains therefore largely unknown whether population declines are more pronounced in cohesive or loose colonial breeders and the extent to which this may be linked to differences in social information-use strategies, foraging preferences, and competitive skills. Such information would also be of particular relevance for an effective implementation of supplementary feeding programs in these regions (Hille et al. 2016). Close monitoring of the recovery of these species may provide valuable opportunities for improvement of knowledge on recolonization processes by colonial species (Mateo-Tomás and Olea 2011), as well as links between population size and population resilience and stability. Research on social foraging skills should also integrate the role of facultative scavengers that may naturally provide carrion or information about carrion to vultures and with which vultures interact at carcasses (Moleón et al. 2014a).

Vulture Supplementary Feeding Programs

While feeding stations are used as an almost universal tool to support local vulture populations (Europe: Donázar et al. 2009; Asia: Gilbert et al. 2007; Africa: Mundy et al. 1992, Piper et al. 2005; and, to a lesser extent, the Americas: Wallace and Temple 1987b, Walters et al. 2010), the guidelines for the management of feeding sites seem still largely based on ecological rather than social criteria (e.g., carrion availability, physiographic features, intra-guild processes; Cortés-Avizanda et al. 2010, 2016, Moreno-Opo et al. 2015a). However, although a careful consideration of the number of feeding sites, their location, and predictability of food supplies may help to mimic the natural dynamics of food supply, it seems unavoidable that such sites will mainly benefit colonial *Gyps* spp. Those species are accustomed to feed on large, indefensible carrion quantities, and (semi-) predictable resources associated with human farming activities have been part of their resource environment for centuries. Moreover, even if smaller, less competitive species may benefit from the leftovers provided by larger species, it is questionable whether this would compensate for reductions in small and medium-sized natural carrion types, of which their diet is essentially composed. Furthermore, little is known about the relative use of natural food vs. surplus food (Margalida et al. 2011, Margalida and Colomer 2012, Moreno-Opo et al. 2015b). Although surplus food, or other types of waste and carrion produced or provided by humans usually attract large numbers of vultures (and other facultative scavengers; Oro et al. 2013, Plaza and Lambertucci 2017), it is unclear whether this should be interpreted as surplus food being important to vultures. Rather, vultures just could be taking advantage of the easy availability and/or gathering at these sites for social purposes.

Assessments of the effectiveness of feeding stations should not be based on interspecific competitive skills alone, but also include detailed information about a species socio-ecology (carcass size preferences, breeding habits, hierarchical structures, social organization). In particular, more information is needed about the natural (solitary) food-searching habits of territorial/solitary breeding species (e.g., Walters et al. 2010, Bakker et al. 2017). Their reliance on small/medium carrion items, and the presence of strong hierarchical social structures, may in part explain why surplus food may only have a limited demographic impact, especially taking into consideration historic population sizes (Oro et al. 2008, Margalida 2010, Lieury et al. 2015, Oppel et al. 2016). By contrast, feeding stations seem to have a more clear positive influence on population demography in colonial species (Piper et al. 1999, Kane et al. 2015, Schabo et al. 2017) and serve as an important support tool during reintroduction projects (Terrasse et al. 2004). However, *Gyps* spp. are particularly prone to overcrowding effects, requiring a network of small and large feeding stations to minimize the formation of artificial large groupings (Duriez et al. 2012). Moreover, the supply of carcasses from intensive farming may expose them to livestock pathogens and the pharmaceuticals used to combat them (Blanco et al. 2016, 2017, Casas-Díaz et al. 2016), as well as synthetic hormones and other drugs applied to livestock that can interfere with the endocrine system of vultures. These pathogens and chemicals represent novel threats altering normal physiology and behavior of wildlife (Zala and Penn 2004), with potential but unknown impacts on sexual physiology, behavior, and social dynamics of vultures.

The Importance of Natural Carrion

Research to date often still focuses on the use of large carcasses ("pulsed" food sources), while few studies have examined baseline carrion biomass availability and predictability of small- and medium-sized vertebrate and invertebrate carcasses (DeVault et al. 2003). Consequently, the role of natural carrion diversity in shaping species' foraging patterns and/or reproductive success remains poorly evaluated (but see Carrete and Donázar 2005, Margalida et al. 2012, Donázar et al. 2020). The use of vegetation greenness (i.e. normalized difference vegetation index) as a proxy for carrion availability may provide valuable insights into the species specificity of natural carrion use patterns by solitary and social foraging vultures species (Santangeli et al. 2018, Donázar et al. 2020). In particular, increased attention should be given to the potential impact of high livestock numbers and associated overgrazing effects on primary consumer abundance (rabbits and rodents), which may represent an underestimated negative influence on carcass availability to solitary foraging vulture species (Donázar et al. 2020).

Overall, an important, but challenging, goal is to better quantify baseline carrion availability (Barton et al. 2019, Moleón et al. 2020), including both livestock and wildlife carrion. Currently, no up-to-date general overview exists of species-specific (or population-specific) foraging and behavioral adaptations and dietary breadth in relation to local and broad-scale changes in carrion resource landscapes (but see Lambertucci et al. 2009, Donázar et al. 2010). However, given the existence of large differences in carrion preferences among vulture species, to sustain healthy scavenger populations and communities, the main focus of conservation efforts should still be on the protection of foraging and breeding habitat, and restoration of carrion resource diversity, rather than the provisioning of additional food supply (Cortés-Avizanda et al. 2016, Sebastián-González et al. 2019).

Mating Behaviors and Settlement Decisions

On one hand, little attention has been given to mate choice criteria and the behavioral processes leading to pair formation in vultures, despite its importance in captive breeding and reintroduction programs. In general, given seemingly complex pairing processes and high mate selectivity, especially in territorial vultures, any changes to the size and composition of the mating pool should be avoided, given its potential disrupting impact on pairing, settlement, and reproductive behaviors. On the other hand, however, the gregarious habits of vultures, combined with their capacities to travel and disperse over large distances (Alarcón and Lambertucci 2018), may act as important mechanisms to locate mates, buffering against mate-finding Allee effects. Lack of knowledge about mate-finding strategies and reproductive decision-making, especially at the individual level, and the potential role of social groupings and roosts in shaping pairing dynamics, currently hampers a clear understanding of local settlement processes and dispersal tendencies. Despite the increasing use of global positioning system transponders, the social factors (roosting, mate-finding) shaping vulture movements are rarely taken into consideration (but see Spiegel et al. 2015, Byrne et al. 2018, Holland et al. 2019, van Overveld et al. 2020).

Furthermore, information is virtually absent about vulture reproductive strategies, especially their willingness to delay reproduction to be able to compete for preferred territories (Sanz-Aguilar et al. 2017) and how such decisions relate to the quality and distribution of existent territories and affect population expansion processes (Jenny et al. 2017). In addition, while clutch and chick removal from nests for translocation purposes is sometimes used as an alternative, cheaper option to breeding programs (Ferrer et al. 2018), the long-term impact of such removal activities on local population dynamics and viability are poorly known and typically difficult to predict (Margalida et al. 2015, Margalida et al. 2017b, Colomer et al. 2020). Overall, more detailed knowledge about vulture mating behavior and strategic reproductive decision-making is crucial for a better understanding of the mechanisms and time necessary for population recovery; importantly, such knowledge may improve the cost-efficiency of reintroduction programs.

Gathering Behavior and Social Structures

We recommend researchers and conservationists to carry out more studies investigating the nature and patterning of social interaction at social gatherings. Overall, current observations suggest that social gatherings in vultures, whether associated with food resources or not, may play an important, but scarcely investigated, social role with potentially key implications for the social structuring and dynamics of vulture populations. The social functions of nocturnal roosts and diurnal gatherings should be studied as an integral part of vulture social systems, focusing on their role in the maintenance of population-level social cohesion, the development of social hierarchy structures and other social relationships, and mating dynamics. In turn, such information would greatly help to better understand how reductions in vulture numbers may affect the social functioning of roosts/social gatherings, and thereby influence local population dynamics.

Despite the widespread use of feeding stations, studies describing social interactions at these sites are remarkably scarce. Although we have addressed a wide range of negative effects associated with supplementary feeding practices, in some specific situations feeding sites may potentially also fulfill an important social role, especially when taking into consideration the absence of naturally occurring food bonanzas nowadays. Overall, more carefully planned supplementary feeding experiments are needed, combined with extensive behavioral observations, to assess their influence (positive or negative) on the social structuring of populations, but also to examine potential positive effects on mate-finding and recolonization processes (Walters et al. 2010).

Concluding Remarks

With this review, we hope to stimulate more field-based research into the causes and consequences of vulture sociality, which is still a relatively neglected area of research; we know little about general aspects of the social biology of most vulture species. Apart from a more complete understanding of vulture social ecology and breeding system evolution, such information may help to better inform the specific conservation needs of different vulture species, including those critically endangered. Improved knowledge about the social life of vultures may be a critical step in order to harmonize anthropogenic activities with conservation programs.

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LITERATURE CITED

Acha, A., G. Blanco, P. Ruiz, O. F. Martinez, and G. Doval (1998). A great banquet at a Spanish vulture restaurant. Does Europe end at the Pyrenees? Vulture News 39:34–39.
Alarcón, P. A. E., and S. A. Lambertucci (2018). A three-decade review of telemetry studies on vultures and condors. Movement Ecology 6:13.
Anderson, M. D. (1999). Africa's hooded vulture: A dichotomy of lifestyle. Vulture News 41:3–5.
Angulo, E., G. M. Luque, S. D. Gregory, J. W. Wenzel, C. Bessa-Gomes, L. Berec, and F. Courchamp (2018). Allee effects in social species. Journal of Animal Ecology 87:47–58.
Antor, R. J., A. Margalida, H. Frey, R. Heredia, L. Lorente, and J. A. Sesé (2007). First breeding age in captive and wild Bearded Vultures *Gypaetus barbatus*. Acta Ornithologica 42:114–118.

Baker, A. J., and D. F. Whitacre (1996). Observations of King Vultures (*Sarcoramphus papa*) drinking and bathing. Journal of Raptor Research 30:246–247.
Bakker, V. J., D. R. Smith, H. Copeland, J. Brandt, R. Wolstenholme, J. Burnett, S. Kirkland, and M. E. Finkelstein (2017). Effects of lead exposure, flock behavior, and management actions on the survival of California Condors (*Gymnogyps californianus*). EcoHealth 14:92–105.
Ballejo, F., S. A. Lambertucci, A. Trejo, and L. De Santis (2018). Trophic niche overlap among scavengers in Patagonia supports the condor–vulture competition hypothesis. Bird Conservation International 28:390–402.
Bamford, A. J., A. Monadjem, and I. C. W. Hardy (2010). Associations of avian facial flushing and skin colouration with agonistic interaction outcomes. Ethology 116:1163–1170.
Barton, P. S., M. J. Evans, C. N. Foster, J. L. Pechal, J. K. Bump, M.-M. Quaggiotto, and M. E. Benbow (2019). Towards quantifying carrion biomass in ecosystems. Trends in Ecology & Evolution 34:950–961.
Bassi, E., P. Trotti, M. Brambilla, F. Diana, F. Sartirana, L. Galli, and L. Pedrotti (2017). Parental investment in two large raptors breeding in a high prey density area. Journal of Ornithology 158:549–559.
Becker, N., M. Inbar, O. Bahat, Y. Choresh, G. Ben-Noon, and O. Yaffe (2005). Estimating the economic value of viewing Griffon Vultures *Gyps fulvus*: A travel cost model study at Gamla Nature Reserve, Israel. Oryx 39:429–434.
Berger-Tal, O., T. Polak, A. Oron, Y. Lubin, B. P. Kotler, and D. Saltz (2011). Integrating animal behavior and conservation biology: A conceptual framework. Behavioral Ecology 22:236–239.
Bertran, J., and A. Margalida (1999). Copulatory behavior of the Bearded Vulture. The Condor 101:164–168.
Bertran, J., and A. Margalida (2003). Male–male mountings in polyandrous Bearded Vultures *Gypaetus barbatus*: An unusual behaviour in raptors. Journal of Avian Biology 34:334–338.
Bertran, J., and A. Margalida (2006). Reverse mounting and copulation behavior in polyandrous Bearded Vulture (*Gypaetus barbatus*) trios. The Wilson Journal of Ornithology 118:254–256.
Bertran, J., A. Margalida, and B. E. Arroyo (2009). Agonistic behaviour and sexual conflict in atypical reproductive groups: The case of Bearded Vulture *Gypaetus barbatus* polyandrous trios. Ethology 115:429–438.
Bhusal, K. P., and K. Paudel (2016). Distribution and breeding ecology of Red-headed Vulture *Sarcogyps calvus* in Nepal. Bird Conservation Nepal 25:1–4.
Bijleveld, A. I., M. Egas, J. A. Van Gils, and T. Piersma (2010). Beyond the information centre hypothesis: Communal roosting for information on food, predators, travel companions and mates? Oikos 119:277–285.
Blanco, G., F. Martínez, and J. M. Traverso (1997). Pair bond and age distribution of breeding Griffon Vultures *Gyps fulvus* in relation to reproductive status and geographic area in Spain. Ibis 139:80–183.
Blanco, G., and F. Martínez (1996). Sex difference in breeding age of Griffon Vultures (*Gyps fulvus*). The Auk 113:247–248.
Blanco, G. (2018). Supplementary feeding as a source of multiresistant *Salmonella* in endangered Egyptian vultures. Transboundary and Emerging Diseases 65:806–816.
Blanco, G., D. Hornero-Méndez, S. Lambertucci, L. M. Bautista, G. Wiemeyer, J. A. Sanchez-Zapata, J. Garrido-Fernández, F. Hiraldo, and J. A. Donázar (2013). Need and seek for dietary micronutrients: Endogenous regulation, external signalling and food sources of carotenoids in New World vultures. PLoS One 8:e65562.
Blanco, G., A. Junza, and D. Barrón (2017). Food safety in scavenger conservation: Diet-associated exposure to livestock pharmaceuticals and opportunist mycoses in threatened cinereous and Egyptian vultures. Ecotoxicology and Environmental Safety 135:292–301.
Blanco, G., A. Junza, D. Segarra, J. Barbosa, and D. Barrón (2016). Wildlife contamination with fluoroquinolones from livestock: Widespread prevalence of enrofloxacin and marbofloxacin in vultures. Chemosphere 144:1536–1543.
Blanco, G., and J. L. Tella (1999). Temporal, spatial and social segregation of Red-billed Choughs between two types of communal roost: A role for mating and territory acquisition. Animal Behaviour 57:1219–1227.
Blumstein, D. T., and E. Fernández-Juricic (2010). A Primer of Conservation Behavior. Sinauer Associates, Boston, MA, USA.
Bosè, M., O. Duriez, and F. Sarrazin (2012). Intra-specific competition in foraging Griffon Vultures *Gyps fulvus*: 1. Dynamics of group feeding. Bird Study 59:182–192.
Bosè, M., and F. Sarrazin (2007). Competitive behaviour and feeding rate in a reintroduced population of Griffon Vultures *Gyps fulvus*. Ibis 49:490–501.
Boucherie, P. H., M. C. Loretto, J. J. M. Massen, and T. Bugnyar (2019). What constitutes “social complexity” and “social intelligence” in birds? Lessons from ravens. Behavioral Ecology and Sociobiology 73:12.
Brakes, P., S. R. X. Dall, L. M. Aplin, S. Bearhop, E. L. Carroll, P. Ciucci, V. Fishlock, J. K. B. Ford, E. C. Garland, S. A. Keith, et al. (2019). Animal cultures matter for conservation. Science 363:1032–1034.
Buckley, N. J. (1996). Food finding and the influence of information, local enhancement, and communal roosting on foraging success of North American vultures. The Auk 113:473–488.
Buckley, N. J. (1997). Experimental tests of the information-center hypothesis with Black Vultures (*Coragyps atratus*) and Turkey Vultures (*Cathartes aura*). Behavioral Ecology and Sociobiology 41:267–279.
Buckley, N. J. (1998). Interspecific competition between vultures for preferred roost positions. The Wilson Bulletin 110:122–125
Buckley, N. J. (2020). Black Vulture (*Coragyps atratus*), version 1.0. In Birds of the World (A. F. Poole and F. B. Gill, Editors). Cornell Lab of Ornithology, Ithaca, NY, USA. https://doi.org/10.2173/bow.blkvul.01
Buechley, E. R., and Ç. H. Şekercioğlu (2016). The avian scavenger crisis: Looming extinctions, trophic cascades, and loss of critical ecosystem functions. Biological Conservation 198:220–228.
Butler, J. R. A., and J. T. du Toit (2002). Diet of free-ranging domestic dogs (*Canis familiaris*) in rural Zimbabwe: Implications for wild scavengers on the periphery of wildlife reserves. Animal Conservation 5:29–37.
Byrne, M. E., A. E. Holland, K. L. Turner, A. L. Bryan, and J. C. Beasley (2019). Using multiple data sources to investigate foraging niche partitioning in sympatric obligate avian scavengers. Ecosphere 10:e02548.
Carneiro, C., M. Henriques, C. Barbosa, Q. Tchantchalam, A. Regalla, A. R. Patrício, and P. Catry (2017). Ecology and behaviour of Palm-nut Vultures (*Gypohierax angolensis*) in the Bijagós Archipelago, Guinea-Bissau. Ostrich 88:113–121

Caro, T. M. (2007). Behavior and conservation: A bridge too far? Trends in Ecology & Evolution 22:494–400.
Carrete, M., and J. A. Donázar (2005). Application of central-place foraging theory shows the importance of Mediterranean dehesas for the conservation of the Cinereous Vulture. Biological Conservation 126:582–590.
Carrete, M., J. A. Donázar, and A. Margalida (2006b). Density-dependent productivity depression in Pyrenean Bearded Vultures: Implications for conservation. Ecological Applications 5:1674–1682.
Carrete, M., J. A. Donázar, A. Margalida, and J. Bertran (2006a). Linking ecology, behaviour and conservation: Does habitat saturation change the mating system of Bearded Vultures? Biology Letters 2:624–627.
Carrete, M., S. A. Lambertucci, K. Speziale, O. Ceballos, A. Travaini, M. Delibes, F. Hiraldo, and J. A. Donázar (2010). Winners and losers in human-made habitats: Interspecific competition outcomes in two Neotropical vultures. Animal Conservation 13:390–398.
Casas-Díaz, E., C. Cristofol, R. Cuenca, S. Agustín, M. Carneiro, I. Marco, S. Lavín, and A. Margalida (2016). Determination of antibiotic residues in plasma of two populations of Eurasian Griffon Vulture (*Gyps fulvus*) in Spain. Science of the Total Environment 557:620–626.
Ceballos, O., and J. A. Donázar (1990). Roost-tree characteristics, food habits and seasonal abundance of roosting Egyptian Vultures in northern Spain. Journal of Raptor Research 24:19–25.
Chamberlain, C. P., J. R. Waldbauer, K. Fox-Dobbs, S. D. Newsome, P. L. Koch, D. R. Smith, M. E. Church, S. D. Chamberlain, K. J. Sorenson, and R. Risebrough (2005). Pleistocene to recent dietary shifts in California Condors. Proceedings of the National Academy of Sciences USA 102:16707–16711.
Coleman, J. S., and J. D. Fraser (1987). Food habits of Black and Turkey vultures in Pennsylvania and Maryland. The Journal of Wildlife Management 51:733–739.
Collins, P. W., N. F. R. Snyder, and S. D. Emslie (2000). Faunal remains in California Condor nest caves. The Condor 102:222–227.
Colomer, M. A., P. Oliva-Vidal, J. Jiménez, J. M. Martinez, and A. Margalida (2020). Prioritizing removal actions for the reintroduction of endangered species: Insights from bearded vulture simulation modeling. Animal Conservation. https://doi.org/10.1111/acv.12549
Cortés-Avizanda, A., P. Almaraz, M. Carrete, J. A. Sánchez-Zapata, A. Delgado, F. Hiraldo, and J. A. Donázar (2011). Spatial heterogeneity in resource distribution promotes facultative sociality in two trans-Saharan migratory birds. PLoS One 6:e21016.
Cortés-Avizanda, A., M. Carrete, and J. A. Donázar (2010). Managing supplementary feeding for avian scavengers: Guidelines for optimal design using ecological criteria. Biological Conservation 143:1707–1715.
Cortés-Avizanda, A., R. Jovani, M. Carrete, and J. A. Donázar (2012). Resource unpredictability promotes species diversity and coexistence in an avian scavenger guild: A field experiment. Ecology 93:2570–2579.
Cortés-Avizanda, A., R. Jovani, J. A. Donázar, and V. Grimm (2014). Bird sky networks: How do avian scavengers use social information to find carrion? Ecology 95:1799–1808.
Cortés-Avizanda, A., G. Blanco, T. L. DeVault, A. Markandya, M. Z. Virani, J. Brandt, and J. A. Donázar (2016). Supplementary feeding and endangered avian scavengers: Benefits, caveats, and controversies. Frontiers in Ecology and the Environment 14:191–199.
Cugnasse, J. M. (2000). Fonction sociale de l'accouplement chez le vautour percnoptère *Neophron percnopterus*. Alauda 68:326–327.
de Araujo, G. M., C. A. Peres, F. B. Baccaro, and R. S. Guerta (2018). Urban waste disposal explains the distribution of Black Vultures (*Coragyps atratus*) in an Amazonian metropolis: Management implications for birdstrikes and urban planning. PeerJ 6:e5491.
Del Hoyo, J., A. Elliot, and J. Sargatal (1994). Handbook of the Birds of the World, Volume 2: New World Vultures to Guineafowl. Lynx Edicions, Barcelona, Spain.
Dermody, B. J., C. J. Tanner, and A. L. Jackson (2011). The evolutionary pathway to obligate scavenging in *Gyps* vultures. PLoS One 6:e24635.
DeVault, T. L., J. C. Beasley, Z. H. Olson, M. Moleón, M. Carrete, A. Margalida, and J. A. Sánchez-Zapata (2016). Ecosystem services provided by avian scavengers. In Why Birds Matter. Avian Ecological Function and Ecosystem Services (Ç. H. Şekercioğlu, D. G. Wenny, and C. J. Whelan, Editors). University of Chicago Press, Chicago, IL, USA.
DeVault, T. L., O. E. Rhodes Jr., and J. A. Shivik (2003). Scavenging by vertebrates: Behavioral, ecological, and evolutionary perspectives on an important energy transfer pathway in terrestrial ecosystems. Oikos 102:225–234.
Deygout, C., A. Gault, O. Duriez, F. Sarrazin, and C. Bessa-Gomes (2010). Impact of food predictability on social facilitation by foraging scavengers. Behavioral Ecology 21:1131–1139.
Dhakal, H., K. M. Baral, K. P. Bhusal, and H. P. Sharma (2014). First record of nests and breeding success of Red-headed Vulture *Sarcogyps calvus* and implementation of Vulture Conservation Programs in Nepal. Ela Journal 3:9–15.
Dobado, P., and R. Arenas (2012). The Black Vulture: Status, Conservation and Studies. Consejeria de Medio Ambiente de la Junta de Andalucía, Córdoba, Spain.
Donázar, J. A. (1993). Los Buitres Ibéricos: Biología y Conservación. J.M. Reyero, Madrid, Spain.
Donázar, J. A., J. M. Barbosa, M. García-Alfonso, T. van Overveld, L. Gangoso, and M. de la Riva (2020). Too much is bad: Increasing numbers of livestock and conspecifics reduce body mass in an avian scavenger. Ecological Applications. https://doi.org/10.1002/eap.2125
Donázar, J. A., O. Ceballos, and J. L. Tella (1994). Copulation behaviour in the Egyptian Vulture *Neophron percnopterus*. Bird Study 41:37–41.
Donázar, J. A., O. Ceballos, and J. L. Tella (1996). Communal roosts of Egyptian Vultures (*Neophron percnopterus*): Dynamics and implications for the species conservation. In Biology and Conservation of Mediterranean Raptors (J. Muntaner and J. Mayol, Editors). SEO/BirdLife, Madrid, Spain.
Donázar, J. A., A. Cortés-Avizanda, and M. Carrete (2010). Dietary shifts in two vultures after the demise of supplementary feeding stations: Consequences of the EU sanitary legislation. European Journal of Wildlife Research 56:613–621.
Donázar, J. A., A. Cortés-Avizanda, O. Ceballos, E. Arrondo, J. M. Grande, and D. Serrano (2020). Epizootics and sanitary regulations drive long-term changes in fledgling body condition of a threatened vulture. Ecological Indicators 113:106188.
Donázar, J. A., and J. E. Feijóo (2002). Social structure of Andean Condor roosts: Influence of sex, age, and season. The Condor 104:832–837.

Donázar, J. A., A. Margalida, M. Carrete, and J. A. Sánchez-Zapata (2009a). Too sanitary for vultures. Science 326:664–664.
Donázar, J. A., A. Margalida, and D. Campíon (2009b). Vultures, Feeding Stations and Sanitary Legislation: A Conflict and Its Consequences from the Perspective of Conservation Biology. Sociedad de Ciencias Aranzadi, San Sebastián, Spain.
Donázar, J. A., A. Travaini, O. Ceballos, A. Rodríguez, M. Delibes, and F. Hiraldo (1999). Effects of sex-associated competitive asymmetries on foraging group structure and despotic distribution in Andean Condors. Behavioral Ecology and Sociobiology 45:55–65.
Duriez, O., S. Herman, and F. Sarrazin (2012). Intra-specific competition in foraging Griffon Vultures *Gyps fulvus*: 2. The influence of supplementary feeding management. Bird Study 59:193–206.
Etxebarria, J. M., P. López-López, and I. Z. Arroyo (2019). Parental investment asymmetries of a globally endangered scavenger: Unravelling the role of gender, weather conditions and stage of the nesting cycle. Bird Study 66:329–341.
Evans, B. A., and T. A. Sordahl (2009). Factors influencing perch selection by communally roosting Turkey Vultures. Journal of Field Ornithology 80:364–372.
Evans, J. C., S. C. Votier, and S. R. X. Dall (2016). Information use in colonial living. Biological Reviews 91:658–672.
Fargallo, J. A., G. Blanco, and F. Soto-Largo (1998). Forest management effects on nesting habitat selected by Eurasian Black Vultures *Aegypius monachus* in central Spain. Journal of Raptor Research 32:202–207.
Farine, D. R., P. O. Montiglio, and O. Spiegel (2015). From individuals to groups and back: The evolutionary implications of group phenotypic composition. Trends in Ecology & Evolution 30:609–621.
Fasce, P., and L. Fasce (2011). First polygynous trio of Bearded Vulture (*Gypaetus barbatus*). Journal of Raptor Research 46:216–219.
Ferguson-Lees, J., and D. A. Christie (2010). Raptors of the World. Bloomsbury Publishing, London, UK.
Ferrer, M., V. Morandini, G. Baguena, and I. Newton (2018). Reintroducing endangered raptors: A case study of supplementary feeding and removal of nestlings from wild populations. Journal of Applied Ecology 55:1360–1367.
Gangoso, L., R. Agudo, J. D. Anadón, M. de la Riva, A. S. Suleyman, R. Porter, and J. A. Donázar (2013). Reinventing mutualism between humans and wild fauna: insights from vultures as ecosystem services providers. Conservation Letters 6:172–179.
García-Heras, M. S., A. Cortés-Avizanda, and J. A. Donázar (2013). Who are we feeding? Asymmetric individual use of surplus food resources in an insular population of the endangered Egyptian Vulture *Neophron percnopterus*. PLoS One 8:e80523.
Gil, J. A., G. Chéliz, I. Zuberogoitia, and P. López-López (2017). First cases of polygyny for the Bearded Vulture *Gypaetus barbatus* in the central Pyrenees. Bird Study 64:65–568.
Gilbert, M., R. T. Watson, S. Ahmed, M. Asim, and J. A. Johnson (2007). Vulture restaurants and their role in reducing diclofenac exposure in Asian vultures. Bird Conservation International 17:63–77.
Giraldeau, L. A., and T. Caraco (2000). Social Foraging Theory. Princeton University Press, Princeton, NJ, USA.
Gomez, L. G., D. C. Houston, P. Cotton, and A. Tye (1994). The role of Greater Yellow-headed Vultures *Cathartes melambrotus* as scavengers in neotropical forest. Ibis 136:193–196.
Green, R. E., I. Newton, S. Shultz, A. A. Cunningham, M. Gilbert, D. J. Pain, and V. Prakash (2004). Diclofenac poisoning as a cause of vulture population declines across the Indian subcontinent. Journal of Applied Ecology 41:793–800.
Grigg, N. P., J. M. Krilow, C. Gutierrez-Ibanez, D. R. Wylie, G. R. Graves, and A. N. Iwaniuk (2017). Anatomical evidence for scent guided foraging in the turkey vulture. Scientific Reports 7:17408
Haddaway, N. R., P. Woodcock, B. Macura, and A. Collins (2015). Making literature reviews more reliable through application of lessons from systematic reviews. Conservation Biology 29:1596–1605.
Haenn, N., B. Schmook, Y. M. Reyes, and S. Calmé (2014). A cultural consensus regarding the King Vulture? Preliminary findings and their application to Mexican conservation. Ethnobiology and Conservation 3:1.
Harel, R., O. Spiegel, W. M. Getz, and R. Nathan (2017). Social foraging and individual consistency in following behaviour: testing the information centre hypothesis in free-ranging vultures. Proceedings of the Royal Society B 284. https://doi.org/10.1098/rspb.2016.2654
Henriques, M., J. P. Granadeiro, H. Monteiro, A. Nuno, M. Lecoq, P. Cardoso, A. Regalla, and P. Catry (2018). Not in wilderness: African vulture strongholds remain in areas with high human density. PLoS One 13:e0190594.
Heredia, R., and J. A. Donázar (1990). High frequency of polyandrous trios in an endangered population of Lammergeiers *Gypaetus barbatus* in Northern Spain. Biological Conservation 53:163–171.
Hernández, M., and A. Margalida (2009). Poison-related mortality effects in the endangered Egyptian Vulture (*Neophron percnopterus*) population in Spain. European Journal of Wildlife Research 55:415–423.
Hertel, F. (1994). Diversity in body size and feeding morphology within past and present vulture assemblages. Ecology 75:1074–1084.
Hille, S. M., F. Korner-Nievergelt, M. Bleeker, and N. J. Collar (2016). Foraging behaviour at carcasses in an Asian vulture assemblage: Towards a good restaurant guide. Bird Conservation International 26:263–272.
Hiraldo, F. (1976). Diet of the Black vulture (*Aegypius monachus*) in the Iberian Peninsula, Doñana. Acta Vertebrata 3:19–31.
Hiraldo, F., M. Delibes, and J. A. Donázar (1991). Comparison of diets of Turkey Vultures in three regions of northern Mexico. Journal of Field Ornithology 62:319–324.
Holland, A. E., M. E. Byrne, J. Hepinstall-Cymerman, A. L. Bryan, T. L. DeVault, O. E. Rhodes Jr, and J. C. Beasley (2019). Evidence of niche differentiation for two sympatric vulture species in the Southeastern United States. Movement Ecology 7:31.
Houston, D. C. (1986). Scavenging efficiency of Turkey Vultures in tropical forest. The Condor 88:318–323.
Houston, C. S. (1988). Competition for food between Neotropical vultures in forest. Ibis 130:402–417.
Houston, D. C. (2001). Vultures and Condors. Colin Baxter, Granton on Spey, UK.
Houston, D. C., A. Mee, M. McGrady, and I. G. Warketin (2007). Why do condors and vultures eat junk? The implications for conservation. Journal of Raptor Research 41:235–238.
Jackson, A. L., G. D. Ruxton, and D. C. Houston (2008). The effect of social facilitation on foraging success in vultures: a modelling study. Biology Letters 4:311–313.

Jenny, D., M. Kéry, P. Trotti, and E. Bassi (2017). Philopatry in a reintroduced population of Bearded Vultures *Gypaetus barbatus* in the Alps. Journal of Ornithology 159:507–515.

Kane, A., A. L. Jackson, D. L. Ogada, A. Monadjem, and L. McNally (2014). Vultures acquire information on carcass location from scavenging eagles. Proceedings of the Royal Society B 281:1793.

Kane, A., A. L. Jackson, A. Monadjem, M. A. Colomer, and A. Margalida (2015). Carrion ecology modelling for vulture conservation: Are vulture restaurants needed to sustain the densest breeding population of the African White-backed vulture? Animal Conservation 18:279–286.

Kelly, N. E., D. W. Sparks, T. L. DeVault, and O. E. Rhodes Jr. (2007). Diet of Black and Turkey Vultures in a forested landscape. The Wilson Journal of Ornithology 119:267–270.

Karimov, T., and G. Guliyev (2017). Diet composition of four vulture species in Azerbaijan. Ardea 105:163–168.

Kendall, C. (2013). Alternative strategies in avian scavengers: How subordinate species foil the despotic distribution. Behavioral Ecology and Sociobiology 67:383–393.

Kendall, C., M. Z. Virani, P. Kirui, S. Thomsett, and M. Githiru (2012). Mechanisms of coexistence in vultures: Understanding the patterns of vulture abundance at carcasses in Masai Mara National Reserve, Kenya. The Condor 114:523–531.

Kenny, E., T. R. Birkhead, and J. P. Green (2017). Allopreening in birds is associated with parental cooperation over offspring care and stable pair bonds across years. Behavioral Ecology 28:1142–1148.

Kirk, D. A., and D. C. Houston (1995). Social dominance in migrant and resident Turkey Vultures at carcasses: Evidence for a despotic distribution? Behavioral Ecology and Sociobiology 35:323–332.

König, C. (1983). Interspecific and intraspecific competition for food among Old World vultures in vulture biology and management. In Vulture Biology and Management (S. R. Wilbur and J. A. Jackson, Editors). University of California Press, Berkeley, CA, USA. pp. 153–171.

Krüger, S. C. (2007). Polyandrous trios in the southern African Bearded Vulture *Gypaetus barbatus meridionalis*? Vulture News 57:60–61.

Kruuk, H. (1967). Competition for food between vultures in East Africa. Ardea 55:171–193.

Lambertucci, S. A. (2010). Size and spatio-temporal variations of the Andean Condor *Vultur gryphus* population in north-west Patagonia, Argentina: Communal roosts and conservation. Oryx 44:441–447.

Lambertucci, S. A. (2013). Variability in size of groups in communal roosts: Influence of age-class, abundance of individuals and roosting site. Emu 113:122–127.

Lambertucci, S. A., N. L. Jácome, and A. Trejo (2008). Use of communal roosts by Andean Condors in northwest Patagonia, Argentina. Journal of Field Ornithology 79:138–146.

Lambertucci, S. A., and O. A. Mastrantuoni (2008). Breeding behavior of a pair of free-living Andean Condors. Journal of Field Ornithology 79:147–151.

Lambertucci, S. A., J. Navarro, J. A. Sánchez-Zapata, K. A. Hobson, P. A. E. Alarcón, G. Wiemeyer, G. Blanco, F. Hiraldo, and J. A. Donázar (2018). Tracking data and retrospective analyses of diet reveal the consequences of loss of marine subsidies for an obligate scavenger, the Andean Condor. Proceedings of the Royal Society B 285:1879.

Lambertucci, S. A., and A. Ruggiero (2013). Cliffs used as communal roosts by Andean Condors protect the birds from weather and predators. PLoS One 8:e67304.

Lambertucci, S. A., A. Trejo, S. Di Martino, J. A. Sánchez-Zapata, J. A. Donázar, and F. Hiraldo (2009). Spatial and temporal patterns in the diet of the Andean Condor: Ecological replacement of native fauna by exotic species. Animal Conservation 12:338–345.

Lemon, W. C. (1991). Foraging behavior of a guild of Neotropical vultures. The Wilson Bulletin 103:698–702.

Liberatori, F., and V. Penteriani (2001). A long-term analysis of the declining population of the Egyptian Vulture in the Italian peninsula: Distribution, habitat preference, productivity and conservation implication. Biological Conservation 101:381–389.

Lieury, N., M. Gallardo, C. Ponchon, A. Besnard, and A. Millon (2015). Relative contribution of local demography and immigration in the recovery of a geographically-isolated population of the endangered Egyptian Vulture. Biological Conservation 191:349–356.

Manandhar, S., T. K. Shrestha, B. Maharjan, and A. Parajuli (2019). Population status and nesting behavior of Red-Headed Vultures (*Sarcogyps Calvus*) at Dhorfirdi, Tanahun District, Nepal. International Journal of Zoological Research 5:22–32.

Manchiryala, R., and R. M. Medicheti (2014). Breeding biology of critically endangered Long-billed Vulture (*Gyps indicus*) at a unique site in Telangana State, India. Ambient Science 3:49–51.

Maphalala, M. I., and A. Monadjem (2017). White-backed Vulture *Gyps africanus* parental care and chick growth rates assessed by camera traps and morphometric measurements. Ostrich 88:123–129.

Margalida, A. (2010). Supplementary feeding during the chick-rearing period is ineffective in increasing the breeding success in the Bearded Vulture (*Gypaetus barbatus*). European Journal of Wildlife Research 56:673–678.

Margalida, A., J. R. Benítez, J. A. Sánchez-Zapata, E. Ávila, R. Arenas, and J. A. Donázar (2012). Long-term relationship between diet breadth and breeding success in a declining population of Egyptian Vultures *Neophron percnopterus*. Ibis 154:184–188.

Margalida, A., and J. Bertran (2000). Breeding behaviour of the Bearded Vulture *Gypaetus barbatus*: Minimal sexual differences in parental activities. Ibis 142:225–234.

Margalida, A., and J. Bertran (2005). Territorial defence and agonistic behaviour of breeding bearded vultures *Gypaetus barbatus* toward conspecifics and heterospecifics. Ethology Ecology & Evolution 17:51–63.

Margalida, A., J. Bertran, and R. Heredia (2009). Diet and food preferences of the endangered Bearded Vulture *Gypaetus barbatus*: A basis for their conservation. Ibis 151:235–243.

Margalida, A., G. Bogliani, C. Bowden, J. A. Donázar, F. Genero, M. Gilbert, W. Karesh, R. Kock, J. Lubroth, X. Manteca, et al. (2014). One health approach to the use of veterinary pharmaceuticals. Science 346:1296–1298.

Margalida, A., and J. Boudet (2003). Dynamics and temporal variation in age structure at a communal roost of Egyptian Vultures (*Neophron percnopterus*) in northeastern Spain. Journal of Raptor Research 37:252–256.

Margalida, A., and M. A. Colomer (2012). Modelling the effects of sanitary policies on European vulture conservation. Scientific Reports 2:753.

Margalida, A., M. A. Colomer, D. Oro, R. Arlettaz, and J. A. Donázar (2015). Assessing the impact of removal scenarios on population viability of a threatened, long-lived avian scavenger. Scientific Reports 5:16962.

Margalida, A., M. A. Colomer, and D. Sanuy (2011). Can wild ungulate carcasses provide enough biomass to maintain avian scavenger populations? An empirical assessment using a bio-inspired computational model. PLoS One 6:e20248.

Margalida, A., J. A. Donázar, M. Carrete, and J. A. Sánchez-Zapata (2010). Sanitary versus environmental policies: Fitting together two pieces of the puzzle of European vulture conservation. Journal of Applied Ecology 47:931–935.

Margalida, A., D. García, and J. Bertran (1997). A possible case of a polyandrous quartet in the Bearded Vulture (*Gypaetus barbatus*). Ardeola 44:109–111.

Margalida, A., J. M. Martínez, A. Gómez de Segura, M. A. Colomer, R. Arlettaz, and D. Serrano (2017b). Supplementary feeding and young extraction from the wild are not a sensible alternative to captive breeding for reintroducing bearded vultures *Gypaetus barbatus*. Journal of Applied Ecology 54:334–340.

Margalida, A., and M. Moleón (2016). Toward carrion-free ecosystems? Frontiers in Ecology and the Environment 14:183–184.

Margalida, A., J. M. Pérez-García, and R. Moreno-Opo (2017a). European policies on livestock carcasses management did not modify the foraging behavior of a threatened vulture. Ecological Indicators 80:66–73.

Margalida, A., M. Pérez-García, I. Afonso, and R. Moreno-Opo (2016). Spatial and temporal movements in Pyrenean Bearded Vultures (*Gypaetus barbatus*): Integrating movement ecology into conservation practice. Scientific Reports 6:35746.

Marinero, N. V., V. B. Cailly-Arnulphi, S. A. Lambertucci, and C. E. Borghi (2018). Pigmentation and not only sex and age of individuals affects despotism in the Andean Condor. PLoS One 13:e0205197.

Markandya, A., T. Taylor, and A. Longo (2008). Counting the cost of vulture declines – economic appraisal of the benefits of the *Gyps* Vulture in India. Ecological Economics 67:194–204.

Martínez, F., and G. Blanco (2002). Use of alternative nests for clutch replacement in the Egyptian Vulture *Neophron percnopterus*. Ardeola 49:297–299.

Mateo-Tomás, P., and P. P. Olea (2011). The importance of social information in breeding site selection increases with population size in the Eurasian Griffon Vulture *Gyps fulvus*. Ibis 153:832–845.

McGahan, J. (2011). The Andean Condor: A Field Study. Self-published.

McVey, K. J., P. D. B. Skrade, and T. A. Sordahl (2008). Use of a communal roost by Turkey Vultures in northeastern Iowa. Journal of Field Ornithology 79:170–175.

Mee, A., G. Austin, M. Barth, C. Beestman, T. Smith, and M. Wallace (2004). Courtship behaviour in reintroduced California Condors: Evidence for extra-pair copulations and female mate guarding. In Raptors Worldwide: Proceedings of the VI World Conference on Birds of Prey and Owls, Budapest, Hungary, 18–23 May 2003 (R. D. Chancellor and B.-U. Meyburg, Editors). World Working Group on Birds of Prey and Owls, MME/BirdLife Hungary, Budapest, Hungary. pp. 75–81.

Meretsky, V. J., N. F. R. Snyder, S. R. Beissinger, D. A. Clen-Denen, and J. W. Wiley (2000). Demography of the California Condor: Implications for reestablishment. Conservation Biology 14:957–967.

Moleón, M., J. A. Sánchez-Zapata, N. Selva, J. A. Donázar, and N. Owen-Smith (2014a). Inter-specific interactions linking predation and scavenging in terrestrial vertebrate assemblages. Biological Reviews 1045:1042–1054.

Moleón, M., J. A. Sánchez-Zapata, A. Margalida, M. Carrete, N. Owen-Smith, and J. A. Donázar (2014b). Humans and scavengers: The evolution of interactions and ecosystem services. BioScience 64:394–403.

Moleón, M., N. Selva, and J. A. Sánchez-Zapata (2020). The components and spatiotemporal dimension of carrion biomass quantification. Trends in Ecology & Evolution 35:91–92.

Morales-Reyes, Z., J. M. Pérez-García, M. Moleón, F. Botella, M. Carrete, C. Lazcano, R. Moreno-Opo, A. Margalida, J. A. Donázar, and J. A. Sánchez-Zapata (2015). Supplanting ecosystem services provided by scavengers raises greenhouse gas emissions. Scientific Reports 5:7811.

Moreno-Opo, R., A. Trujillano, A. Arredondo, L. M. González, and A. Margalida (2015a). Manipulating size, amount and appearance of food inputs to optimize supplementary feeding programs for European vultures. Biological Conservation 181:27–35.

Moreno-Opo, R., A. Trujillano, and A. Margalida (2015b). Optimization of supplementary feeding programs for European vultures depends on environmental and management factors. Ecosphere 6:1–15.

Moreno-Opo, R., A. Trujillano, and A. Margalida (2016). Behavioral coexistence and feeding efficiency drive niche partitioning in European avian scavengers. Behavioral Ecology 27:1041–1052.

Moreno-Opo, R., A. Trujillano, and A. Margalida (2020). Larger size and older age confer competitive advantage: Dominance hierarchy within European vulture guild. Scientific Reports 10:2430.

Mullié, W. C., F. X. Couzi, M. S. Diop, B. Piot, T. Peters, P. A. Reynaud, and J. M. Thiollay (2017). The decline of an urban Hooded Vulture *Necrosyrtes monachus* population in Dakar, Senegal, over 50 years. Ostrich 88:131–138.

Mundy, P., D. Butchart, J. Ledger, and S. Piper (1992). The Vultures of Africa. Acorn Books, R. Friedman Books & Vulture Study Group, Randburg, South Africa.

Murn, C., and G. J. Holloway (2014). Breeding biology of the White-headed Vulture *Trigonoceps occipitalis* in Kruger National Park, South Africa. Ostrich 85:125–130.

Negro, J. J., J. M. Grande, J. L. Tella, J. Garrido, D. Hornero, J. A. Donázar, J. A. Sanchez-Zapata, J. R. Benítez, and M. Barcell (2002). An unusual source of essential carotenoids. Nature 416:807–808.

Negro, J. J., A. Margalida, F. Hiraldo, and R. Heredia (1999). The function of the cosmetic coloration of Bearded Vultures: When art imitates life. Animal Behaviour 58:F14–F17.

Negro, J. J., J. H. Sarasola, F. Fariñas, and I. Zorilla (2006). Function and occurrence of facial flushing in birds. Comparative Biochemistry and Physiology Part A 143:78–84.

Newton, I. (1979). Population Ecology of Raptors. Academic Press, San Diego, CA, USA.

Newton, I. (1998). Population Limitation in Birds. Academic Press, San Diego, CA, USA.

Novaes, W. G., and R. Cintra (2013). Factors influencing the selection of communal roost sites by the Black Vulture *Coragyps atratus* (Aves: Cathartidae) in an urban area in Central Amazon. Zoologia 30:607–614.

Ogada, D., A. Botha, and P. Shaw (2016b). Ivory poachers and poison: Drivers of Africa's declining vulture populations. Oryx 50:593–596.

Ogada, D., F. Keesing, and M. Z. Virani (2012). Dropping dead: Causes and consequences of vulture population declines worldwide. Annals of the New York Academy of Sciences 1249:57–71.

Ogada, D., P. Shaw, R. L. Beyers, R. Buij, C. Murn, J. M. Thiollay, C. M. Beale, R. M. Holdo, D. Pomeroy, N. Baker, et al. (2016a). Another continental vulture crisis: Africa's vultures collapsing toward extinction. Conservation Letters 9:89–97.

Olea, P. P., and P. Mateo-Tomás (2009). The role of traditional farming practices in ecosystem conservation: The case of transhumance and vultures. Biological Conservation 142:1844–1853.

Oppel, S., V. Dobrev, V. Arkumarev, V. Saravia, A. Bounasc, E. Kret, T. Skartsi, M. Velevski, S. Stoychev, and S. Nikolov (2016). Assessing the effectiveness of intensive conservation actions: Does guarding and feeding increase productivity and survival of Egyptian Vultures in the Balkans? Biological Conservation 198:157–164.

Oro, D., M. Genovart, G. Tavecchia, M. S. Fowler, and A. Martínez-Abrahín (2013). Ecological and evolutionary implications of food subsidies from humans. Ecology Letters 16: 1501–1514.

Oro, D., A. Margalida, M. Carrete, R. Heredia, and J. A. Donázar (2008). Testing the goodness of supplementary feeding to enhance population viability in an endangered vulture. PLoS One 3:e4084.

Parker, P. G., T. A. Waite, and M. D. Decker (1995). Kinship and association in communally roosting Black Vultures. Animal Behaviour 49:395–401.

Parmenter, R. R., and J. A. MacMahon (2009). Carrion decomposition and nutrient cycling in a semiarid shrub–steppe ecosystem. Ecological Monographs 79:637–661.

Parra, J., and J. L. Tellería (2004). The increase in the Spanish population of Griffon Vulture *Gyps fulvus* during 1989–1999: Effects of food and nest site availability. Bird Conservation International 14:33–41.

Pavez, E. F., M. Duclos, J. R. Rau, S. Sade, and F. M. Jaksic (2019). Evidence of high consumption of waste by the Andean Condor (*Vultur gryphus*) in an anthropized environment of chile. Ornitología Neotropica 30:185–191.

Piper, S. E. (2005). Supplementary feeding programmes: How necessary are they for the maintenance of numerous and healthy vulture populations. In Proceedings of the International Conference on Conservation and Management of Vulture Populations: 14–16 November 2005, Thessaloniki, Greece (D. C. Houston and S. E. Piper, Editors). Natural History Museum of Crete, Thessaloniki, Greece. pp. 41–50.

Piper, S. E., A. F. Boshoff, and H. A. Scott (1999). Modelling survival rates in the Cape Griffon *Gyps coprotheres*, with emphasis on the effects of supplementary feeding. Bird Study 46:S230–S238.

Pitarch, A., C. Gil, and G. Blanco (2017). Oral mycoses in avian scavengers exposed to antibiotics from livestock farming. Science of the Total Environment 605:139–146.

Plaza, P. I., and S. A. Lambertucci (2017). How are garbage dumps impacting vertebrate demography, health, and conservation? Global Ecology and Conservation 12:9–20.

Plaza, P. I., and S. A. Lambertucci (2018). More massive but potentially less healthy: Black Vultures feeding in rubbish dumps differed in clinical and biochemical parameters with wild feeding birds. PeerJ 6:e4645.

Plaza, P. I., G. Blanco, M. J. Madariaga, E. Boeri, M. L. Teijeiro, G. Bianco, and S. A. Lambertucci (2019). Scavenger birds exploiting rubbish dumps: Pathogens at the gates. Transboundary and Emerging Diseases 66:873–881.

Pfeiffer, M. B., J. A. Venter, and C. T. Downs (2016). Cliff characteristics, neighbour requirements and breeding success of the colonial Cape Vulture *Gyps coprotheres*. Ibis 159:26–37.

Porter, R. F., and D. Quiroz (2010). Social behaviour of the Egyptian Vulture. British Birds 103:60–64.

Porter, R. F., and A. S. Suleiman (2012). The Egyptian Vulture *Neophron percnopterus* on Socotra, Yemen: Population, ecology, conservation and ethno-ornithology. Sandgrouse 34:44–62.

Prior, K., and P. J. Weatherhead (1991). Competition at the carcass: Opportunities for social foraging by turkey vultures in southern Ontario. Canadian Journal of Zoology 69:1550–1556.

Prior, K., and P. J. Weatherhead (2004). Turkey Vultures foraging at experimental food patches: A test of information transfer at communal roosts. Behavioral Ecology and Sociobiology 28:385–390.

Rabenold, P. P. (1986). Family associations in communally roosting Black Vultures. The Auk 103:32–41.

Rabenold, P. P. (1987a). Recruitment to food in Black Vultures: Evidence for following from communal roosts. Animal Behaviour 35:1775–1785.

Rabenold, P. P. (1987b). Roost attendance and aggression in Black Vultures. The Auk 104:647–653.

Ramo, C., and B. Busto (1988). Observations at a King Vulture (*Sarcoramphus papa*) nest in Venezuela. The Auk 105:195–196.

Réale, D., S. M. Reader, D. Sol, P. T. McDougall, and N. J. Dingemanse (2007). Integrating animal temperament within ecology and evolution. Biological Reviews 82:291–318.

Robertson, A. (1986). Copulations throughout breeding in a colonial Accipitrid vulture. The Condor 88:535–539.

Robertson, A. (1986b). Notes on the breeding cycle of Cape Vultures (*Gyps coprotheres*). Raptor Research 20:51–60.

Rollack, C. E., K. Wiebe, M. Stoffel, and C. S. Houston (2013). Turkey Vulture breeding behavior studied with trail cameras. Journal of Raptor Research 47:153–160.

Roller MaMing, R., L. Li Lee, X. Yang, and P. Buzzard (2016). Vultures and sky burials on the Qinghai-Tibet Plateau. Vulture News 71:22–35.

Ruxton, G. D., and D. C. Houston (2004). Obligate vertebrate scavengers must be large soaring fliers. Journal of Theoretical Biology 228:431–436.

Santangeli, A., O. Spiegel, P. Bridgeford, and M. Girardello (2018). Synergistic effect of land-use and vegetation greenness on vulture nestling body condition in arid ecosystems. Scientific Reports 8:13027.

Sanz-Aguilar, A., A. Cortés-Avizanda, D. Serrano, G. Blanco, O. Ceballos, J. M. Grande, J. L. Tella, and J. A. Donázar (2017). Sex- and age-dependent patterns of survival and breeding success in a long-lived endangered avian scavenger. Scientific Reports 7:40204.

Sapolsky, R. M. (2005). The influence of social hierarchy on primate health. Science 308:648–652.

Sauer, E. G. F. (1973). Notes on the behavior of Lappet-faced Vultures and Cape Vultures in the Namib Dessert of South West Africa. Madoqua 2:62–68.

Schabo, D., S. Heuner, M. V. Neethling, S. Rösner, R. Uys, and N. Farwig (2017). Long-term data indicates that supplementary food enhances the number of breeding pairs in a Cape Vulture *Gyps coprotheres* colony. Bird Conservation International 27:140–152.

Schaub, M., R. Zink, H. Beissmann, F. Sarrazin, and R. Arlettaz (2009). When to end releases in reintroduction programmes: Demographic rates and population viability analysis of Bearded Vultures in the Alps. Journal of Applied Ecology 46:92–100.

Schlee, M. A. (1995). Nest records for the King Vulture (*Sarcoramphus papa*) in Venezuela. Journal of Raptor Research 29:269–272.

Sebastián-González, E., J. Magalhães Barbosa, J.M. Pérez-García, Z. Morales-Reyes, F. Botella, P. P. Olea, P. Mateo-Tomás, M. Moleón, F. Hiraldo, E. Arrondo, and J. A. Donázar (2019). Scavenging in the Anthropocene: human impact drives vertebrate scavenger species richness at a global scale. Global Change Biology 25:3005–3017.

Shobrak, M. (1996). Ecology of Lappet-faced Vulture *Torgos tracheliotos* in Saudi Arabia. Ph.D. dissertation, Glasgow, UK.

Sih, A., S. F. Hanser, and K. A. McHugh (2009). Social network theory: New insights and issues for behavioral ecologists. Behavioral Ecology and Sociobiology 63:975–998.

Snyder, N. F. R., and H. A. Snyder (2000). The California Condor: A Saga of Natural History and Conservation. Academic Press, San Diego, CA, USA.

Spiegel, O., W. M. Getz, and R. Nathan (2013). Factors influencing foraging search efficiency: Why do scarce Lappet-faced Vultures outperform ubiquitous White-backed Vultures? The American Naturalist 181:102–115.

Spiegel, O., R. Harel, A. Centeno-Cuadros, O. Hatzofe, W. M. Getz, and R. Nathan (2015). Moving beyond curve fitting: Using complementary data to assess alternative explanations for long movements of three vulture species. The American Naturalist 185:E44–E54.

Spiegel, O., S. T. Leu, C. M. Bull, and A. Sih (2017). What's your move? Movement as a link between personality and spatial dynamics in animal populations. Ecology Letters 20:3–18.

Stier, A. C., J. F. Samhouri, M. Novak, K. N. Marshall, E. J. Ward, R. D. Holt, and P. S. Levin (2016). Ecosystem context and historical contingency in apex predator recoveries. Science Advances 2:e1501769.

Ssemmanda, R. (2005). An apparent increase in Hooded Vulture *Necrosyrtes monachus* numbers in Kampala, Uganda. Vulture News 53:10–14.

Tauler-Ametller, H., A. Hernández-Matías, J. L. Pretus, and J. Real (2017). Landfills determine the distribution of an expanding breeding population of the endangered Egyptian Vulture *Neophron percnopterus*. Ibis 159:757–768.

Tella, J. L. (1993). Polyandrous trios in a population of Egyptian Vultures. Journal of Raptor Research 27:119–120.

Terrasse, M., F. Sarrazin, J. P. Choisy, C. Clémente, S. Henriquet, P. Lécuyer, J. L. Pinna, and C. Tessier (2004). A success story: The reintroduction of Eurasian Griffon *Gyps fulvus* and Black Vultures *Aegypius monachus* in France. In Raptors Worldwide: Proceedings of the VI World Conference on Birds of Prey and Owls, Budapest, Hungary, 18–23 May 2003 (R. D. Chancellor and B.-U. Meyburg, Editors). World Working Group on Birds of Prey and Owls, MME/BirdLife Hungary, Budapest, Hungary.

Thakur, M. L. (2015). Breeding ecology and distribution of White-rumped Vultures (*Gyps bengalensis*) in Himachal Pradesh, India. Journal of Raptor Research 49:183–191.

Thompson, L. J., D. R. Barber, M. J. Bechard, A. J. Botha, K. Wolter, W. Neser, E. R. Buechley, R. Reading, R. A. Garbett, P. Hancock, et al. (2020). Variation in monthly sizes of home-ranges of Hooded Vultures *Necrosyrtes monachus* in western, eastern and southern Africa. Ibis. https://doi.org/10.1111/ibi.12836

Utt, A. C., N. C. Harvey, W. K. Hayes, and R. L. Carter (2008). The effects of rearing method on social behaviors of mentored, captive-reared juvenile California Condors. Zoo Biology 27:1–18.

van Overveld, T., M. García-Alfonso, N. J. Dingemanse, W. Bouten, L. Gangoso, M. de la Riva, D. Serrano, and J. A. Donázar (2018). Food predictability and social status drive individual resource specializations in a territorial vulture. Scientific Reports 8:15155.

van Overveld, T., L. Gangoso, M. García-Alfonso, W. Bouten, M. de la Riva, and J. A. Donázar (2020). Seasonal grouping dynamics in a territorial vulture: Ecological drivers and social consequences. Behavioral Ecolology and Sociobiology 74:28.

Venkitachalam, R., S. Senthil Nathan, and S. Bharathidasan (2013). Some aspects of breeding biology of the White-backed Vulture *Gyps bengalensis* nilagiri North forest division in western Ghats, Tamil Nadu. International Journal of Science and Nature 4:411–414.

Vickery, W. L., L. A. Giraldeau, J. J. Templeton, D. L. Kramer, and C. A. Chapman (1991). Producers, scroungers, and group foraging. The American Naturalist 137:847–863.

Wallace, M. P., and S. A. Temple (1987a). Competitive interactions within and between species in a guild of avian scavengers. The Auk 104:290–295.

Wallace, M., and S. A. Temple (1987b). Releasing captive-reared Andean Condors to the wild. Journal of Wildlife Managment 51:541–550.

Walters, J. R., S. R. Derrickson, D. M. Fry, S. M. Haig, J. M. Marzluff, and J. M. Wunderle Jr. (2010). Status of the California Condor (*Gymnogyps californianus*) and efforts to achieve its recovery. The Auk 127:969–1001.

Ward, P., and A. Zahavi (1973). The importance of certain assemblages of birds as "information-centres" for food-finding. Ibis 115:517–534.

Wilbur, S., and J. A. Jackson (1983). Vulture Biology and Management. University of California Press, Berkeley, CA, USA.

Xirouchakis, S. (2005). The diet of Eurasian Griffons (G*yps fulvus*) on Crete. Journal of Raptor Research 39:179–183.

Xirouchakis, S. (2007). Seasonal and daily activity pattern in Griffon Vulture (*Gyps fulvus*) colonies on the island of Crete (Greece). Ornis Fennica 84:39–46.

Xirouchakis, S., and M. Mylonas (2004). Griffon vulture (*Gyps fulvus*) distribution and density in Crete. Israel Journal of Zoology 50:341–354.

Xirouchakis, S. M., and M. Mylonas (2007). Breeding behaviour and parental care in the Griffon vulture *Gyps fulvus* on the island of Crete (Greece). Ethology Ecology & Evolution 19:1–26.

Zala, S. M., and D. J. Penn (2004). Abnormal behaviours induced by chemical pollution: A review of the evidence and new challenges. Animal Behaviour 68:649–664.