



Vultures as an overlooked model in cognitive ecology

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Abstract

Despite important recent advances in cognitive ecology, our current understanding of avian cognition still largely rests on research conducted on a few model taxa. Vultures are an ecologically distinctive group of species by being the only obligate carrion consumers across terrestrial vertebrates. Their unique scavenging lifestyle suggests they have been subject to particular selective pressures to locate scarce, unpredictable, ephemeral, and nutritionally challenging food. However, substantial variation exists among species in diet, foraging techniques and social structure of populations. Here, we provide an overview of the current knowledge on vulture cognition through a comprehensive literature review and a compilation of our own observations. We find evidence for a variety of innovative foraging behaviors, scrounging tactics, collective problem-solving abilities and tool-use, skills that are considered indicative of enhanced cognition and that bear clear connections with the eco-social lifestyles of species. However, we also find that the cognitive basis of these skills remain insufficiently studied, and identify new research areas that require further attention in the future. Despite these knowledge gaps and the challenges of working with such large animals, we conclude that vultures may provide fresh insight into our knowledge of the ecology and evolution of cognition.

Keywords Foraging cognition · Social cognition · Socio-ecology · Vultures

Introduction

Cognition is considered fundamental in the process of flexible decision-making and the emergence of intelligent behaviors (Shettleworth 2009), contributing to improve fitness by reducing environmental and social uncertainties (Morand-Ferron et al. 2019). However, only a few animals are thought to excel in their abilities to modify decision-making processes by advanced cognitive processes, that is,

combining previous knowledge with an understanding of the problem. In mammals, these include primates and cetacean; in birds, corvids and parrots (Lefebvre et al. 2004). These animals have evolved unusual abilities for innovativeness, social learning and tactical deception, as well as a high level of encephalization—that is, a brain is that is much larger than would be expected given their body size (reviewed in Lefebvre and Sol 2008). Not surprisingly, most past research on the cognitive basis of flexible decision-making and intelligence has focused on these few model taxa. To understand the evolution of cognition, however, we need additional cases where it has evolved independently.

Here, we critically examine whether vultures can be considered a good study system for advanced cognition and brain evolution. Our suggestion that vultures can provide key information on cognition is based on five arguments. First, vultures tend to have relatively high levels of encephalization (Fig. 1). Although the role of encephalization on cognition remains controversial (e.g., Healy and Rowe 2007), empirical work has revealed that encephalization reflects a disproportionate increase of the associative areas of the brain involved in domain-general cognition (Sayol et al. 2016) and

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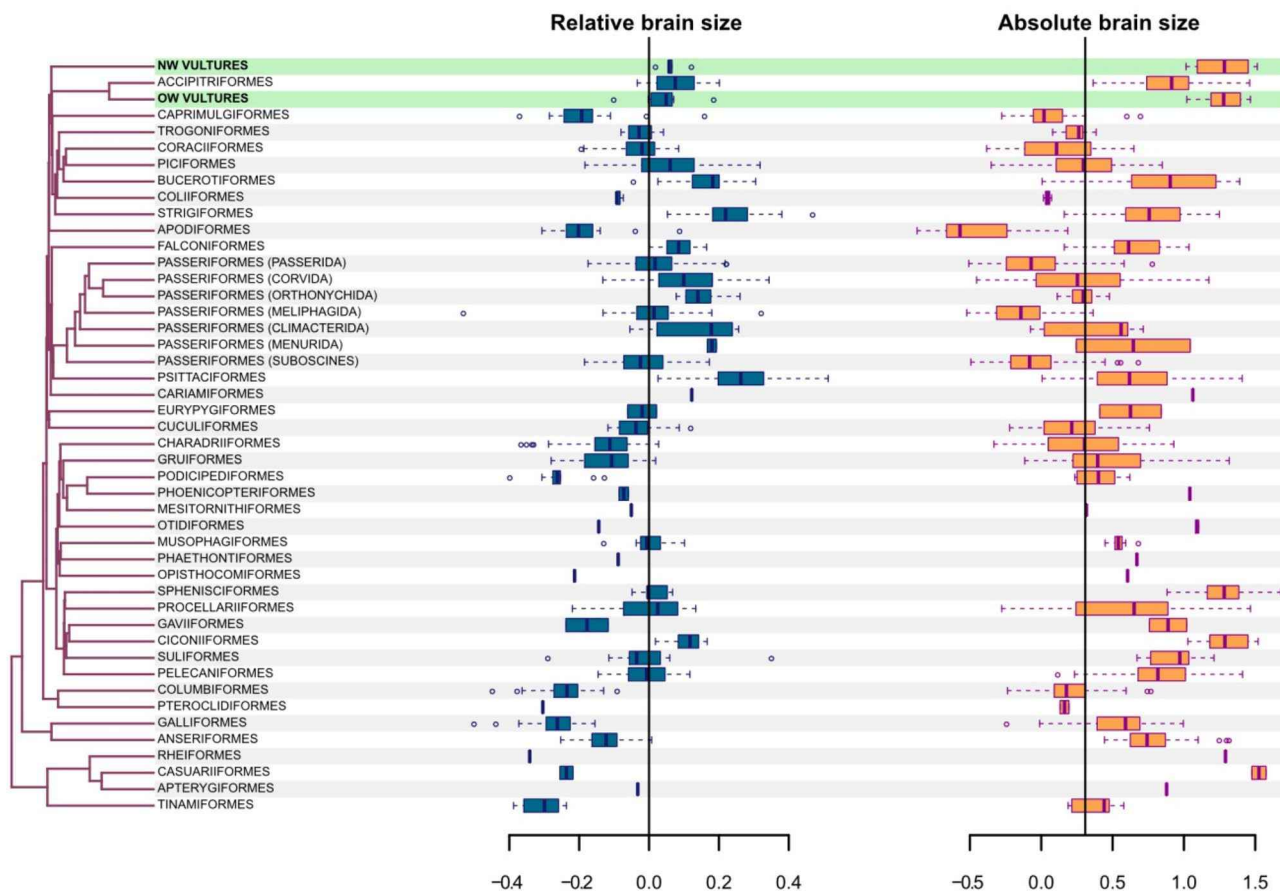


Fig. 1 Encephalization in vultures. As encephalization describes the extent to which the size of the brain departs from that expected by body size, we estimate it using the residuals of a log–log regres-

sion of brain mass against body mass. Brain residuals of 9 Old world vultures and 5 New World vultures are compared with those of 2047 other extant bird species

that is associated with higher performance in problem-solving, learning and tool use (e.g., Benson-Amram et al. 2016; Overington et al. 2009; Street et al. 2017). Second, vultures exhibit signatures of complex cognition in the foraging and social domains. These include many cases of feeding innovations and cooperative behaviors (see details below). Third, vultures show a slow pace of life characterized by long periods of chick development, an extended juvenile period, delayed sexual maturity, low fertility and long life spans. Such a life history is expected to enhance cognition by facilitating the growth and development of enlarged brains and by increasing the net benefits of learning (reviewed in Sol et al. 2016). A long-life span also means that environmental conditions encountered early in life can largely differ from those found in the future, which may further select for enhanced flexibility in decision-making. Four, vultures show an unusual ecology. Vultures are the only obligate carrion consumers among terrestrial vertebrates (Houston 2001; Mundy et al. 1992; van Overveld et al. 2020a). Yet unlike previous model taxa used in cognitive research, which are all highly social, vultures have largely diverged in their social lifestyle.

Thus, this group offers a unique perspective to study the relative roles of social and ecological pressures in selecting for enhanced cognition. Finally, vultures comprise 2 distinct lineages, the New World vultures (Cathartidae, 7 species) and Old World vultures (Accipitridae, 16 species; Ferguson-Lees and Christie 2010) (Fig. 2) that have independently converged to similar foraging habits. The existence of convergent solutions to similar problems is a major signature of selection, and hence finding similar patterns in New and Old World vultures may provide important insight into the selective processes that have shaped cognition.

Our paper is structured as follows. First, we present social and ecological hypotheses that have been put forward to explain brain expansion and the evolution of sophisticated behaviors. Second, we show that vulture species are distributed along a socio-ecological gradient reflecting different degrees of specialization, which may have played a role in shaping cognition and brain size evolution. Third, we use this framework to examine vulture cognition through a comprehensive review of published and unpublished snapshot observations of complex

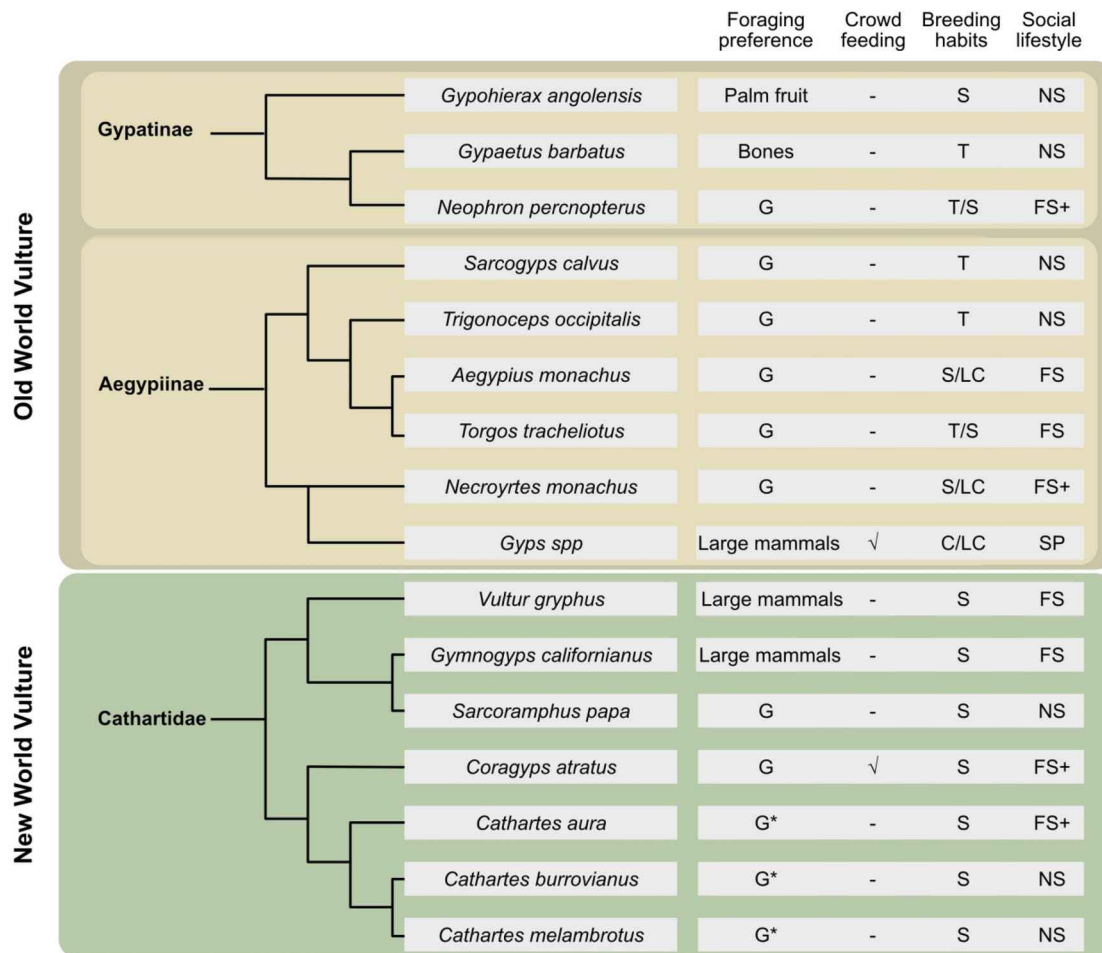


Fig. 2 Socio-ecology of vultures, described in terms of foraging habits (generalist (G) or as stated otherwise), social structure (species displaying crowd-foraging lack clear dominance structures), breeding habits (S solitary, T territorial, LC loose-colonial, C cohesive colonial) and degree of sociality (NS non-social, FS facultative social, SP semi-permanently social). FS+: small-bodied facultative social species that are highly gregarious at food bonanzas and nocturnal roost-

ing sites (up to 100–500 individuals depending on local abundance). FS: facultative social species that are gregarious at nocturnal roosts (ranging between ~50–100 individuals), but with small intraspecific group sizes at carcasses (range ~1–20 individuals). *Species from the genus *Cathartes* evolved well-developed olfactory sense in addition to visual cues, which allow them to locate carrion

and unusual behaviors. Specifically, we assess whether species with different social lifestyles differ in foraging cognition (innovative foraging techniques, scrounging tactics, collective problem-solving, and tool-use habits), and whether different social lifestyles are associated with different forms of social cognition (conflict management, social bonding and cooperation). We discuss the available evidence supporting that vultures may be a good model for cognitive studies, especially regarding their cognitive adaptations associated with the challenges imposed by their unique scavenging lifestyle and varying social strategies. Finally, we suggest new research lines that require further attention to fulfil current gaps of knowledge in vulture cognition.

Theoretical framework

Current debate regarding the drivers of brain expansion and cognition in animals have primarily focused on the relative roles of social and ecological factors (Navarrete et al. 2016; Street et al. 2017). According to the “Social intelligence hypothesis”, social challenges posed by group-livings, like the need to understand and anticipate the behavior of conspecifics, are the key drivers of enhanced cognition and enlarged brains (Byrne and Whiten 1988; Dunbar 1998). By contrast, the “Ecological intelligence hypothesis” states that ecological challenges like the need to exploit a wide variety of food or to access food that is difficult to obtain are the most important selective factors shaping cognitive skills and larger brains (Milton 1988). Finally, the “cognitive buffer

hypothesis” seeks to integrate social and ecological perspectives, suggesting that enhanced cognition and enlarged brains are part of a slow-lived strategy aimed at buffering animals against socio-ecological challenges through learned responses (Allman 1999; Deaner et al. 2003; Sol 2009a).

While evidence is accumulating that large brains and behavioral flexibility help animals to solve problems in the foraging domain (Lefebvre et al. 2004) or, more generally, to successfully cope with ecological challenges (Fristoe et al. 2017; Sayol et al. 2018; Sol 2009b; Sol et al. 2005, 2007, 2008; van Woerden et al. 2012), the importance of social factors should not be under-appreciated (Dunbar and Shultz 2007). Most animals that use advanced cognitive skills to solve problems are highly social. Moreover, the influence of ecological and social factors cannot be treated as if they were disconnected. Cognitive abilities associated with foraging (e.g., cognitive mapping skills, associative learning, innovative ability and flexible learning (Henke-von der Malsburg et al. 2020)) are likely to also play a role in social foraging tactics (Street et al. 2017). Indeed, many animals rely on social cues from conspecific, close relatives or even distantly related species for finding food (Giraldeau and Caraco 2000), to learn new foraging techniques (Klump et al. 2021) or to steal food from each other (Iyengar 2008; Morand-Ferron et al. 2007). Yet, to date, insufficient attention has been paid to examine the combined effects of social and/or ecological intelligence in food acquisition. This is surprising given the existence of ample evidence that the use of collective behaviors or the exploitation of knowledge and cognitive abilities of others can largely reduce resource uncertainty and improve foraging efficiency. Thus, a better understanding of cognition in species with different social systems may provide a more precise understanding about the role of social and ecological factors in shaping cognition and brain size evolution.

A socio-ecological framework to study cognition in vultures

Most vultures are habitat generalists that live in a variety of natural environments, including rain forests, savannas, deserts and mountain areas. Within these habitats, different species often co-occur in the so-called vulture-guilds, in which species coexistence is facilitated by a number of morphological differences (body size, wing morphology and beak shape) and social adaptations (Fig. 2). These socio-ecological differences are primarily associated with the differential consumption of carcasses varying in size and predictability (reviewed in van Overveld et al. 2020a) which, in turn, confront them to contrasting cognitive demands.

Vultures from the *Gyps* guild differs from all other vultures in their social lifestyle and foraging habits. They are

highly social year-round, breed in cohesive or loose colonies and form large communal roosts. Foraging occurs in loose or highly dispersed groups, and they extensively rely on conspecifics to locate large carcasses of ungulates and livestock (Cortés-Avizanda et al. 2014; Dermody et al. 2011; Harel et al. 2017; Jackson et al. 2008), which are exploited through crowd-foraging (Houston 2001; Mundy et al. 1992). All other vultures mainly search for carrion alone (or in couples) and display solitary to territorial breeding habits (reviewed in van Overveld et al. 2020a). The majority of these species are highly polyphagous, and can be typified as foraging generalists (Fig. 2). There are, however, considerable differences among species in the degree of sociality, with some being highly gregarious at carcasses and roosts while others have more solitary lifestyles, especially once recruited into the breeding population (Fig. 2). Hereafter, we will consider *Gyps* as a separate group of social specialists (referred to as ‘social *Gyps*’) and the other vultures will be split in ‘facultative social’ or ‘non-social’. Although these categories are labeled according to sociality, they also involve ecological differences in niche breadth and foraging techniques.

Cognition of vultures in foraging contexts

Resource innovations

Resource innovations involve the adoption of novel food items (Overington et al. 2009). Studies on food remains in nests and anecdotal reports show that generalist foragers (both facultative social and non-social) consume almost any kind of carrion available. In addition to a wide diversity of birds and mammals, this includes reptiles, amphibians, fish and a variety of invertebrates such as mussels, shrimps, and insects (Ferguson-Lees and Christie, 2010). The dietary spectrum is particularly broad, and well documented, for small-bodied species (Egyptian vulture *Neophron percnopterus* (Fig. 3a), Black vulture *Coragyps atratus* (Fig. 3b), and Turkey vulture *Cathartes aura*), which also regularly feed on fruits, dung and various types of human debris and vegetable matter (Ferguson-Lees and Christie, 2010). The presence of taxa from aquatic and terrestrial systems points towards broad ecological knowledge and enhanced food searching skills in solitary foraging species. This strongly contrasts with the diets from Griffon vulture *Gyps fulvus* (Fig. 3d) that is typically composed of large wild and domestic ungulates (Ferguson-Lees and Christie 2010). While consumer innovations/broad dietary range may not require sophisticated cognition (Overington et al. 2009), an opportunist–generalist lifestyle frequently exposes individuals to new foraging challenges that may select for enhanced cognition (Sol et al. 2016).

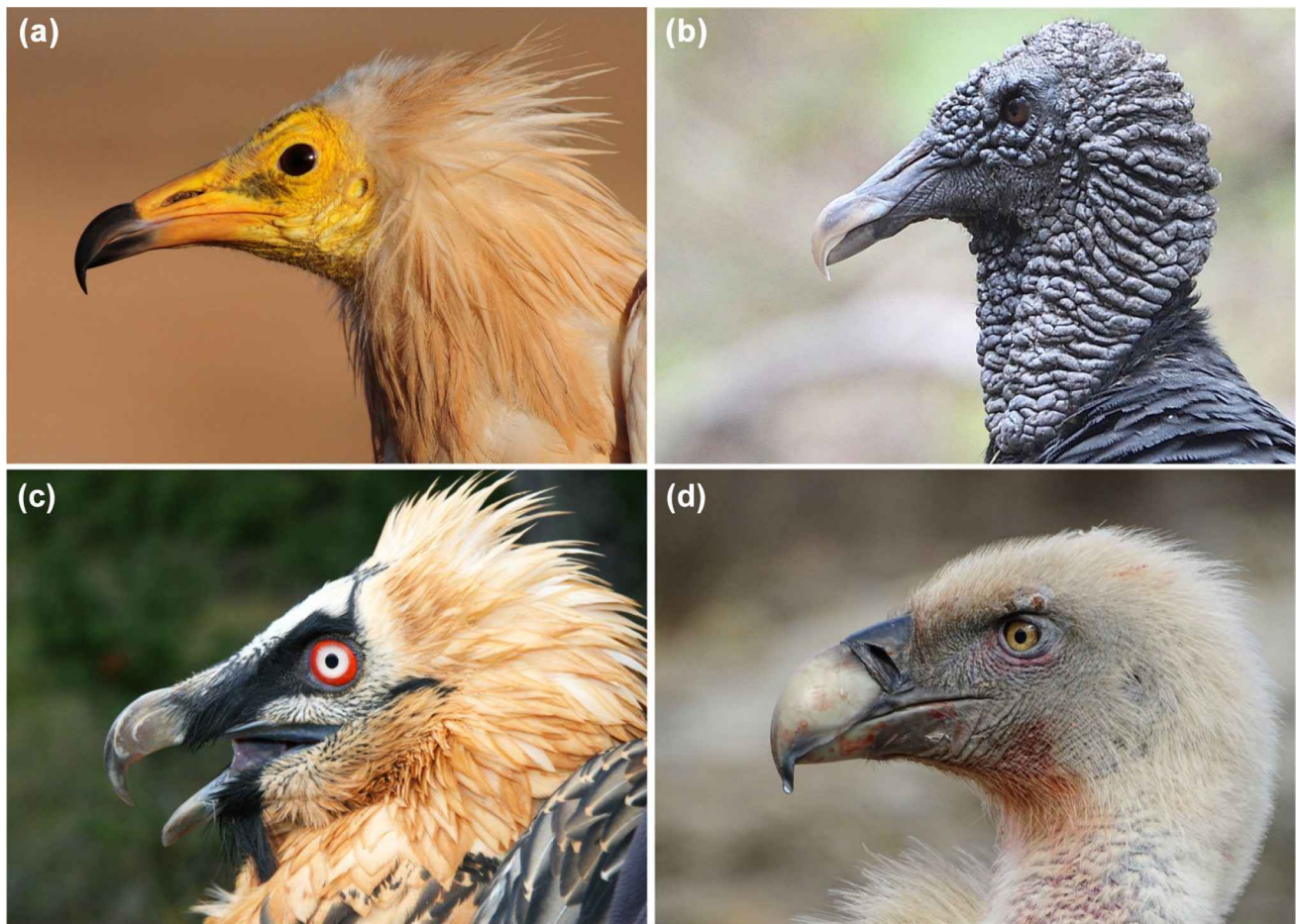


Fig. 3 Heads shots of most well-studied vultures: **a** Canary Egyptian vulture *Neophron percnopterus majorensis* (credits: T. van Overveld), **b** Black vulture *Coragyps atratus* (credits: P. Tella), **c** Bearded

vulture *Gypaetus barbatus* (credits: A. Margalida), **d** Griffon vulture *Gyps fulvus* (credits: T. van Overveld)

Innovative foraging techniques

Technical innovations describe novel behaviors involving the adoption of new searching or handling techniques, and are generally considered to be cognitively more demanding than resource innovations (Overington et al. 2009). Indeed, technical innovativeness designates the possibility of devising new learnt behaviors to respond to ecological challenges, and hence is considered a major component of intelligence.

Anecdotal observations suggest that the Black vulture possess exceptional skills for innovation. This species, but also the Turkey vulture, regularly engages in fishing activities, usually by catching dead or injured fish using their beak. In several occasions, individuals have even been observed performing actual dives, in which the body and head are completely submerged by water (Jackson et al. 1978). There are also several reports of Black vultures cleaning other mammals to feed on ticks, organic debris, or even flesh from open wound (Coulson et al. 2018; Melo et al. 2018; Sazima

2007b, 2010). They also can feed on the placenta of sea lions by cutting the pup's umbilical cord (Pavés et al. 2008). Although mutualistic in nature, these interactions seem to have a clear self-serving function. More intriguingly, Black vultures also frequently engage in interspecific allopreening with Crested Caracaras *Polyborus plancus* (Lopes Palmeira 2008; NG and Jaspersen 1984; Souto et al. 2009). Black vultures have learned to open bags at garbage dumps and nowadays also dismantle bags left unattended by bathers at coastlines and in refuse containers (Sazima 2007a). They are the only vulture known to have successfully colonized highly urbanized environments where it may scrounge for food within city streets, harass residents and also enter houses to steal food (Buckley 2020). The great diversity and type of foraging techniques expressed by this species exceeds that of all other vultures and is quite unique even among birds in general.

Scrounging tactics

Scrounging tactics—the exploitation of food made available by others (Vickery et al. 1991)—are a key aspect of vultures foraging strategies. Studies have shown scrounging tactics to have an important cognitive basis, especially with regard to behavioral reading skills (e.g., Gallego-Abenza et al. 2020), rather than being the result of aggression per se. Indeed, analyses in birds have shown that kleptoparasitic tactics are more frequent in lineages that have larger brains relative to body size (Morand-Ferron et al. 2007). Vulture scrounging tactics come about in many forms and can vary considerable in their complexity.

Facultative social Turkey and Egyptian vultures display unique innovative scrounging tactics particularly suggestive of enhanced cognition. For example, an adult Turkey vulture was once observed beating up a heron nestling with its wings until it regurgitated food, which was then used to feed its own young (Temple 1967). Similar behaviors have been observed in adult Egyptian vultures, which frequently steal regurgitated food at nest of Griffon vultures (Pascual and Santiago 1991) (Fig. S1) and sometimes also harass nestlings to prompt food regurgitation (Fernández and Fernández-Arroyo 1994, authors unpublished). Both Egyptian and Turkey vultures feed nestlings through food regurgitation, although this technique is used very rarely by the former species (Renaudin et al. 1984, authors unpublished). They also vomit when stressed and/or as an antipredator strategy. An intriguing question is whether these vultures understand that discomfort causes vomiting or whether these scrounging tactics are the result of simpler associative learning mechanisms. Interestingly, recently fledged young of Egyptian vulture already actively rob food at nearby nests of conspecifics, and intriguingly, sometimes even join nestlings from other nests and try to retrieve food from (foster) adults by begging/harassment (Donazar and Ceballos 1990a). These observations suggest that young birds possess an innate motivation to scrounge for food.

In non-social species, there are various observations of individuals stealing food from other vulture species, raptors and marabous (Ferguson-Lees and Christie 2010). In contrast, intra-specific food piracy seems absent or uncommon. An exception is found in the Bearded vulture *Gypaetus barbatus* (Fig. 3c), which in the Pyrenees frequently steal bones from conspecifics (Fig. S2). Although this species has a solitary lifestyle in most part of its range, their densities are unusual high in the Pyrenees. Many individuals can thus be attracted to supplementary feeding stations (up to 30), where high-levels of competition for bones may favor the development of kleptoparasitic habits (Margalida and Bertran 2003). This population therefore offers interesting opportunities to investigate the expression of social-cognitive skills in solitary living vultures with specialized diets.

In highly non-social species, particularly in the Red-headed vulture *Sarcogyps calvus* and King vulture *Sarcoramphus papa*, there are claims suggesting that individuals can specifically keep track of the movements of solitary hunting carnivores (*Panthera* and *Puma* spec.) to feed on their fresh kills (Chhangani 2010; Schlee 2007). This would imply cognitive skills to interpret presence-absence cues of highly mobile individuals in dense vegetation, although compelling scientific prove for such abilities is lacking. In closed rain forest, king vultures have been also claimed to engage in transect soaring at high altitude to keep track of the activities of *Cathartes* vultures, which locate carrion by smell (Houston 1988). However, in other areas with more open vegetation king vultures are often the first to arrive at carcasses (Lemon 1991). This points towards skills to detect food both independently and through inter-specific social information use.

Lastly, in social specialist, there are very few cases of intra- and interspecific food piracy. Even though species such as the Griffon vulture are well studied in colonies, adults have never been observed to steal food from conspecifics nor are there observations of food piracy on eagles. Nevertheless, social *Gyps* typically rely on conspecifics to detect food. Although the tracking of soaring conspecifics may not be cognitively demanding, the highly complex fission–fusion dynamics used while soaring may require cognitive skills like individual recognition, social learning and memorization. Interestingly, Griffon vultures have been reported to sometimes feed at night (Mateo-Tomás and Olea 2018), as shown also by an individual sneaking into an open cage trap to feed on leftovers (Supplementary Material video 1). These night feeding activities could be interpreted as individual food stealing tactics from particular “bold”, or weak individuals.

Collective problem-solving

The ability to coordinate activities during foraging is commonly viewed as an advanced form of intelligence, requiring enhanced communication skills as well as abilities to interpret and anticipate the actions of others. Cooperative foraging is rare in birds (Bednarz 1988), although well developed in socially hunting carnivores forming packs of related individuals (Brosnan et al. 2010).

There is one observation suggesting that Griffon vultures can collectively reach individually unattainable food resources. While trapping Griffon vultures with a cage-trap [a metal construction, covered by a net, that vulture only can enter through a door (Fig. S3)], they managed to consume several hundreds of kilograms of meat despite the cage-trap being closed. This was only possible if vultures gathered in large numbers on the top net of the cage, so that eventually, their collective weight allowed them reaching the

food. However, the degree of coordination of the action performed does not necessarily need to be particularly sophisticated, and it remains unclear whether Griffon vultures had a clear understanding of the role of conspecifics to accomplish this foraging task.

There is another report of collective foraging, in this case hunting, in the facultative social Lappet-faced vulture *Torgos tracheliotos*. On various occasions, groups of 15–22 individuals were seen attacking together crèches of flamingos. Apparently, they did so by circling around the crèche, and taking their turn to catch hatchlings (McCulloch 2006). At a later stage, small groups of Lappet-faced vultures were observed to pursue full-grown immatures in flight, to kill them and feed on this prey together. These seemingly well-coordinated attacks suggest capacities to interact cooperatively that resemble those of socially hunting carnivores.

Tool-use habits

The use of tools to access unattainable food is relatively rare in birds, and considered an important aspect of innovative foraging and intelligence, being associated with encephalization in various bird species (Lefebvre et al. 2002). In vultures, the closely related Egyptian and Bearded vultures are both well known for their tool-use habits, involving true tool use, i.e., stone-throwing to open up eggs, in the former (Fig. S4) (van Lawick-Goodall and van Lawick-Goodall 1966), and proto tool-use, i.e., bone-dropping to fragment them for consumption, in the latter species (Boudoint 1976).

Evidence for a link of these tool-use skills to domain-general technical intelligence is, however, somewhat mixed. Provisioning of Ostrich eggs to naïve captive Egyptian vultures showed stone-throwing to be innate (Thouless et al. 2008). However, the behavior is only elicited when the experimenter shows them that eggs contain food (Thouless et al. 2008). In wild Canarian Egyptian vultures, the response to Ostrich eggs is highly individual-specific (Carrete et al. 2017). However, variation among individuals may be driven by motivation, since eggs were provisioned at a supplementary feeding site. There is only one published record of stone-throwing in a natural context in Europe, in which a pair of Egyptian vultures was seen cracking together an egg of a Griffon vulture (Barcell et al. 2015, discussed further below). We know of one observation of an Egyptian vulture throwing a stone at an old carcass, suggesting they may use stones for other purposes than egg-breaking, although in this case it is unclear why (Fig. S5). There are some claims of Egyptian and Bearded vultures dropping turtles from the air (or even lizards) and/or for the use of stones to break open their shells in case of Egyptian vultures. However, we could not find detailed descriptions of turtle dropping in the literature. This behavior seems unlikely in Egyptian vultures given they do not carry prey in talons as

opposed to Bearded vulture. Claims also exist of Egyptian vultures using sticks to collect nesting material (Stoyanova et al. 2010). Although this behavior has neither been verified, the observation of twigs with wool sticks is relatively common (Fig. S6).

Social drivers of vulture cognition

Agonistic interactions

Being obligated carrion consumers, vultures experience some of the highest levels of food competition in nature. Large carcasses (or so-called pulsed food resources) may be of particular importance in this respect. These carcasses can attract a large number of vultures of the same and/or different species, as well as a wide variety of facultative scavenging birds and mammals. In these temporal and high challenging ‘social hotspots’, we can speculate that the need to avoid injuries, predation and kleptoparasitism may have been an important force shaping cognition.

Most information about intraspecific competitive interactions and social intelligence is currently restricted to the facultative social Canarian Egyptian vulture. Although this species breeds solitary and searches for food alone, individuals often interact with conspecifics at carcasses, feeding stations and communal roost, especially outside the breeding season (van Overveld et al. 2020b). Extensive observations of feeding interactions have revealed a rather complex structure in their social system. Females, the slightly larger sex, are dominant over males with territorial birds having higher ranks compared to unpaired birds and with dominance also increasing with age in both sexes (van Overveld et al. 2020b). Despite high-levels of fission–fusion social dynamics at feeding sites, and hence unstable group sizes and composition, levels of aggressiveness during food displacements are typically low. This suggests that the species has mechanisms to assess the social rank of other individuals. Indeed, individuals sometimes settle conflicts through ritualized dominance displays, i.e., so called ‘duels’, whereby birds parade face-to-face until one retreats (Supplementary Material video 2). The possibility that Egyptian vultures also recognize other individuals cannot be discarded. Although this possibility remains to be investigated, individuals have distinctive yellow wrinkled faces that should facilitate recognition. Interestingly, escalated fights, although rare, often attract the attention of conspecifics (Supplementary Material video 3), suggesting that individuals actively keep track of social disputes and/or shifts in social rank. While these observations seem to indicate that cognition plays a key role in regulating social interactions, it remains to be established whether they also possess more advanced forms of social reasoning, such as abilities to make logic inferences about their own rank and those of others (Massen et al.

2014; Paz-y-Miño et al. 2004), and whether they are able to use social information in a strategic manner, for instance, to improve status (Hobson 2020).

The social structure and organization of social *Gyps* are fundamentally different than those of Egyptian vultures. Most species of this genus breed in colonies and display year-round, semi-permanent groups, with individuals heavily relying on each other for locating carcasses. Although carcasses are often large, and hence individually indefensible, indiscriminate fighting over food is common in the large groups assembled during crowd-foraging. Furthermore, the observation that marked Griffon vultures with full crops often visit feeding stations on consecutive days, without participating in foraging activities (Acha et al. 1998), suggests that individuals gather at food resources also for social purposes, possibly to collect public information about conspecifics.

Like the social *Gyps*, the Black vulture has evolved crowd-foraging habits (Buckley 2020). This facultative social species is renowned for its high-levels of aggressiveness. Despite being relatively small in size, the cooperation between individuals allows to displace from carcasses more powerful species such as Andean condors *Vultur gryphus* (Carrete et al. 2010). Their foraging groups are thought to be composed of sub-coalitions of several breeding pairs and their offspring (Parker et al. 1995). Group members maintain social ties through extensive allopreening (Rabenold 1987) and, presumably, they might also provide each other social support during feeding and at roosts (Buckley 2020). Their crowd-foraging habits further stresses that this type of feeding strategy may not necessarily be indicative of poorly developed cognitive skills generally.

Social bonds and cooperative partnerships

The ability to form non-reproductive social bonds for tactical reasons, for example to gain access to food or to improve status, is widely recognized as a key facet of social complexity in birds and mammals (Boucherie et al. 2019; Bugnyar 2013; Dunbar 2009; Emery et al. 2007). Indeed, there is evidence that complex social bonding during the pre-reproductive social life is critical to develop the socio-cognitive skills needed to form long-term partnerships and to optimize parenting (Kaplan 2020).

In vultures, there is little evidence that individuals form strategic alliances outside the breeding pair. Nevertheless, several facultative social species display intriguing allopreening activities not linked to pair-bond maintenance, similar to many parrots and corvids (Picard et al. 2020). In Canarian Egyptian vultures, for instance, allopreening can take place between paired and unpaired birds, between unrelated adults and immatures, and between individuals

from the same sex, especially females (van Overveld et al. 2020b). Allopreening activities can be brief contacts (Fig. S7) or elaborated socializing activities (Fig. S8, S9), involving preening of the neck and head feathers (Supplementary Material video 4). Interestingly, in contrast with mutual allopreening among mated pairs, this behavior is usually non-reciprocal in the short-term. Allopreening is also well known for Black vultures, particularly between family members (see earlier), but also between unrelated young birds and adults of neighboring nests, often in the presence of their mates (Rabenold 1987). Noteworthy, compulsive allopreening was observed once in Griffon vulture between a parent and its offspring just after our access to the nest to ring the nestling, which was interpreted as a way to reduce its stress after being handled by researchers. Although vulture allopreening activities seem an important, possibly multi-functional affiliative display, too little information is currently available to fully understand its function(s).

Once mated, pairs of solitary breeding species (both facultative and non-social) form very tight partnerships. A number of striking examples in Egyptian vultures illustrate the well-developed cooperative skills among pair-members. In one occasion, a pair was seen cooperating to steal regurgitated food at a Griffon vulture nest; while one of the individuals distracted the fully grown nestling, the other snatched away part of the food (Camiña 2017). In another occasion, a pair was seen feeding together on an abandoned egg of a Griffon vulture. In this case, the male searched for a suitable stone and cracked the egg, after which the female pecked it open with her beak (Barcell et al. 2015). In a last example, a female Canarian Egyptian vulture was once observed walking around restlessly with a piece of meat in her beak for more than 10 min at a feeding station. After noticing her partner, she handed over the food item to the male, which then flew away immediately, probably to feed their fully grown nestlings (Supplementary Material video 5, Fig. S10). Cooperation has also been observed in other species. In the White-headed vulture *Trigonoceps occipitalis*, pair-members have been observed killing a live mongoose together, a technique that requires close cooperation (Murn 2014). In Red-headed vulture and the King vulture, pair-members are often observed arriving at carcasses simultaneously (Bhusal and Paudel 2016; Haenn et al. 2014).

Overall, the above examples suggest that in vultures, pair members seem well able to cooperate (e.g., read, predict and/or anticipate to the behavior of others) when foraging together in a manner that extends beyond what is commonly seen in most other birds. How these social competencies develop is unclear. Socio-cognitive skills could in principle be developed during post-fledging care (Uomini et al. 2020), yet the post-fledging dependency period is relatively short in most vultures and/or involves little parental care (Donázar and Ceballos 1990b). Canarian Egyptian vultures do not

provide post-fledging care at all. Because soon after fledging most young can be seen at a supplementary feeding station in the center of the island, it may be that they develop social skills by interacting with other non-related young and adults.

Conflicts and social bonds in reproductive trios

An interesting aspect of the reproductive behavior of vultures is the relative high frequency of polygynous trios in a same nest. While unusual in other birds, reproductive trios are common in some vultures. In Bearded vultures, the frequency of trios is *ca.* 30–35% in the Pyrenees (Margalida et al. 2020), usually involving the presence of an additional male in the territory or, incidentally, an extra female (Fasce and Fasce 2011; Gil et al. 2017). Canarian Egyptian vultures may regularly form both polyandrous and polygynous trios (*ca.* 5–10% of breeding pairs, authors unpublished). Polygynous and polyandrous trios have also been described in other species, such as Cinereous vultures *Aegypius monachus* and California condor *Gymnogyps californianus* (Ferguson-Lees and Christie 2010).

Trio formations are of particular interest given the complexity of social interactions and unusual behaviors they can generate. Polyandrous trios, for instance, typically do not involve alliances among males, but instead are characterized by high-levels of sexual conflict. Extensive observations in Bearded vultures' trios have revealed that aggression between males decreases with time, occurring less often in well-established trios than in those formed more recently, despite the fact that the frequency of heterosexual copulations—the cause of conflicts—was similar (Bertran et al. 2009). The frequency of homosexual interactions tended to increase in established trios, suggesting that this behavior may help regulate aggression within these groups (Bertran et al. 2009). Reverse mountings between the female and the alpha male suggest an active participation by the female in conflict management (Bertran and Margalida 2006). While tension mitigation through sexual activity is well known for some non-human primate species, particularly bonobo's (de Waal 1987), it is highly unusual in birds.

In Egyptian vultures, there is no evidence for conflict resolution through sexual activities. However, in one trio, an alpha male of Canarian Egyptian vulture engaged in non-stop mate-guarding of the female, for instance, by standing next to her most of the time while she was feeding (Fig. S11). At some point, this male even interrupted another pair copulating, triggered by a loud copulation call at an unguarded moment. This impulsive response illustrates his focus on copulation activities. The beta male, in one occasion tried to impress the female (guarded by the alpha-male) with a beak full of wool for more than 20 minutes (Fig. S12). This beta male also tried to copulate, unsuccessfully, with the female while holding a piece of meat in his beak. Such

object use has also been observed in an already paired male which tried to attract the attention from an unpaired female by picking up a stone (*ca.* 8 cm) which was displayed to her for a few seconds. It is unclear whether this male tried to depict certain skills (i.e., strength, feeding capacity) or picked up this stone out of excitement. We are unaware of other cases of object use in social contexts in this or other vulture species.

As opposed to polyandry, levels of conflicts in polygynous trios of Canarian Egyptian vulture are much lower, despite the fact that territorial females can be very aggressive towards each other (Fig. S13). Occasionally, polygynous trio remain together for long periods (6–10 years), but only during the breeding season. Observations revealed that both females contribute to reproductive tasks, i.e., incubation, chick feeding and nest attendance. However, in one trio, only the alpha females associated with the male during the chick stage (enter/leave the nesting site together), while the beta females operated seemingly independently. This role division, however, reversed over time. In another trio, all members were regularly seen feeding together on a carcass at the feeding station, suggesting the development of a closer social relation among females (Fig. S14). Nevertheless, affiliative contacts (i.e., preening) between alpha and beta females have never been observed in any polygynous trio. More studies are needed to unravel whether the tolerance of a subordinate female in the territory is part of a tactical investment to improve reproductive success (Noë 2006).

Cognition of vultures in other contexts

A last intriguing behavior of Bearded and Egyptian vultures, further adding to their unique behavioral repertoire, is their habit to deliberately stain feathers with red soil through mud bathing (Negro et al. 1999; van Overveld et al. 2017) (Fig. S15, S16). This highly unusual type of 'cosmetics' is not known in other birds (Delhey et al. 2007). Although suggested to provide sanitary benefits (Arlettaz et al. 2002) or to act as a signal of dominance (Negro et al. 1999), none of these functions has so far been clearly proven (Margalida et al. 2019; van Overveld et al. 2017). The behavior nevertheless seems to be tailored to some specific needs. For example, before taking mud baths, Egyptian vultures seem to judge the muddiness of the water by scratching the sediment with their feet (Fig. S17). Experiments are needed to examine whether they do so to assess certain properties of the mud, such as its stickiness or possibly also its coloration. Observations of collective mud bathing events in summer on hot days (i.e., when many individuals take mud baths in a few hours, often simultaneously), suggest it may serve as a simple cooling function and/or to protect against UV-radiation. However, extensive mud bathing also takes place during rainy periods in autumn. Observation of extremely

red unpaired birds, or those recently paired, may suggested feather painting is linked to internal state (i.e., pairing motivation, excitement). Future studies are needed to prove whether this is the case and whether such social signal has a particular functional benefit.

Conclusions and future directions

Our literature review supports the notion that vultures may potentially be a good study system in cognitive ecology, exhibiting a remarkable repertoire of innovative and sophisticated behaviors adapted to their unique scavenging lifestyle. Their outstanding perceptual abilities and navigation skills allow vultures to exploit an extraordinary diversity of carrion types. Their remarkable ability for innovative behaviors also allows individuals to exploit new food opportunities. However, ecological factors are not enough to understand vulture's cognition. Our literature review suggests that cognition may also have been shaped by social factors. Because they exhibit substantial variation in social life styles, vultures offer unique opportunities to extend our knowledge about how ecological and social factors interact to shape cognition.

Vultures can also be relevant to examine the interplay between competition and cooperation. Facultative social species live in highly despotic societies structured by individualized (hierarchical) relationships, but do not seem to have evolved sophisticated social bonding strategies to acquire food and/or to improve rank acquisition. However, anecdotal observations suggest that some species have excellent cooperative skills once mated. While in social Gyps, crowd-foraging habits may appear rather primitive, there are some indications of abilities to solve relative complex foraging problems together, which capacities should be address in future experimental studies. Vultures may thus serve as important models to broaden knowledge about how differences in the type and strength of food competition promote and/or constrain avian cognitive expression, which knowledge still largely rest on research performed in corvids.

Studying pair-living in vultures may be another interesting avenue to gain insight into their socio-cognitive capacities. In general, for solitary breeding and foraging vultures, within-pair cooperation may be a critical adaptation to their scavenging lifestyle, providing key fitness benefits, and thus be subject to strong selection. Comparison of levels of cooperation (i.e., joint foraging, information sharing) between solitary/territorial species and social Gyps may help to gain important insights about such social selective pressures, given that colonial species can rely on conspecifics for food acquisition. Understanding pair formation and the development of cooperative skills over time may shed light on how individuals make the transition from a hierarchical group-living to cooperative

pair-living. Such information is of particularly importance to the role of social learning mechanisms underlying cooperative interactions.

One last avenue of research that we envision that vultures could play a relevant role is the influence of emotional responses on problem-solving. As a result of their extreme slow life histories and particular foraging habits, vultures often face a conflict between the need to approach and to explore new resource opportunities and the need to avoid unnecessary risks (Sol et al. 2011). This makes the group ideal to examine how cognition is influenced by motivation and emotional responses.

Unfortunately, our literature review reveals that we still know little about the cognitive processes through which vultures make decisions, reflecting an insufficient appreciation of their interest in cognitive studies. This is exemplified with the scarcity of problem-solving experiments, arguably the most common approach to study cognition in animals (Ellison et al. 2014). The origin of the egg-breaking behavior by Egyptian vultures is particularly intriguing. Like in other birds, tool use in Egyptian vultures can be an exaptation that has been subsequently reinforced by genetic assimilation (Sol 2015). However, why is this behavior only observed in Egyptian vultures? Can Egyptian vultures flexibly use stones in other contexts than egg-breaking? Can other species that regularly feed on eggs, such as Black and Turkey vultures, learn to use tools to break eggs? Is social learning key to achieve good proficiency in tool use?

Devising experiments in large animals, like vultures, is not easy. However, feeding stations provide excellent opportunities to conduct field experiments using free-ranging, banded individuals. Conducting the experiments in their “real world”, rather than in common garden arenas, is challenging but avoids biases associated with the artificial and stressful conditions of captivity. Feeding stations also allow to alter the spatiotemporal availability of food resources, providing opportunities to study how cognition enables individuals to cope with resource unpredictability. Finally, the accumulation of long-term data on fitness components (lifetime reproductive success, fecundity, lifespan), resource use and specialization, social structure and large-scale movements of vultures (reviewed in van Overveld et al. 2020b) allow to assess the fitness benefits and costs of flexible decision-making and intelligence in nature, providing important insight into their function and evolution.

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Author contributions TO devised the project, developed the main conceptual ideas and conducted the literature search. DS performed data analysis of brain size. TO wrote the manuscript, assisted by DS and GB, AM, MdlR, JAD. All authors reviewed and approved the final manuscript.

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