Studying Movement of Avian Scavengers to Understand Carrion Ecology

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Introduction

Studying carrion ecology and their importance in the ecosystem is difficult in the field, because carrions presence is usually unpredictable in time and space. Moreover, carrion is a pulsed resource that can be quite ephemeral in the ecosystems as they are usually rapidly eliminated by scavengers. Therefore, studying scavengers' movement ecology can help to a better understanding of the scavenging-related patterns and processes. The role of vultures in the ecosystems are of prime importance because they are the most specialized terrestrial vertebrate scavengers (Ruxton and Houston 2004) and they are highly skilled movers able to transport scavenging services over large areas (DeVault et al. 2016). In this chapter we will focus on the methods to study vulture movement ecology, and review recent results about their

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foraging ecology and movements. Tracking vultures can help identifying mortality of them as well as of both wild and domesticated ungulates. Thus, tracking scavengers can be highly important in the context of global environmental change for detecting alterations in the ecosystems derived from changes in the carrion availability.

Trapping Vultures

Trapping vultures is generally not an easy task and must be performed professionally in order to minimize the possibility of injury or stress to birds. When planning trapping efforts, the time of day, season (breeding status of the birds), weather, number of birds to be captured, staff required, and the possibility of predation should be taken into account (Bird and Bildstein 2007).

It is possible to mark chicks at nest but climbing skills and gear are required. Furthermore, a detailed nest monitoring, from hatching date, is crucial because early arrival to the nest will prevent deployment of tagging equipment as it may affect body growth, whereas delayed arrival to the nest may entail premature fledging (and death).

After fledging, the most common methods are based on attracting vultures to a food source as bait to catch them on the ground (Fig. 1). There are several alternatives, most described in details by Bloom et al. (2007), and summarized in Table 1. According to the review detailed in Table 1, the most common method of capture was walk-in traps (10 studies), followed by leg-hold traps, projected-nets and nestling (4 studies each) and rehabilitated birds (2).

Tagging and Tracking Vultures

The possibilities to tag vultures are diverse and so are the costs and the potential output for management and research (Fig. 2). Darvic rings (numbered plastic rings) are good for mass tagging and allow long distance observation, typically up to 400 m on large vultures (even 700 m for color-ring codes). However because they might be broken or lost (Mihoub et al. 2013), they must be complemented by metal rings that would allow a re-identification of bird if recaptured. In addition, leg rings are not suitable for Cathartidae due to their habit to defecate on their legs, presumably for thermoregulation (Houston 1994). Wing tags (also called "patagial tags") enhance resighting of birds at long distance and in flight (Wallace et al. 1980; Reading et al. 2014). However, it must be reminded that the impact of wing tags on bird flight (by increasing drag) has never been properly investigated in large soaring raptors (Trefry et al. 2013). Radio Frequency Identification Tags (RFID) allow detection (presence-absence) by passive tags at focal sites (Bonter and Bridge 2011). RFID can be either passive and provide presence data at short distances (up

Fig. 1 Four different systems of traps for capturing vultures: (**a**) Walk-in trap in an aviary (active because an observer is hidden nearby to trigger the sliding door, France; Photo credit O.Duriez); (**b**) Cage trap (passive because vultures fall into the cage through openings in the roof, Israel, Photo credit I. Shaked); (**c**) leg-hold trap (here more specifically Phai traps as noose surrounding a bait; the rope linking the nooses is hidden under the snow or ground; France, Photo credit O. Duriez); (**d**) Californian condor chick equipped at the nest with GPS tag embedded in patagial tag (photo courtesy of Joseph Brandt, USFWS California Condor Recovery Program)

to 0.5 m), or active (powered by batteries) and detected at longer distance (up to 100 m). If base stations are deployed in advance around carrions, data collected can provide information of arrival time, duration of stay and departure time.

Several techniques can be used to track vultures and we review here only the methods useful to study vulture foraging ecology. For foraging studies, we advise to use interval <10 min between consecutive positions because vultures can cover several km in a few minutes (see below) and sometimes can spend <15 min to land, feed and take off (Harel et al. 2016a; Monsarrat et al. 2013). VHF radio-tracking should not be advised nowadays for foraging studies because of its low precision and relative inefficiency (as flying vultures move much faster than land-based observers) despite intense fieldwork requirement (observers need to follow each bird and manually find its position by triangulation). Satellite telemetry using Argos transmitters provide geographic positions anywhere in the world but are not recommended for detailed foraging studies, due to low precision (typically >1 km) and time interval between positions often >1 h. GPS tracking is the most widely used system nowadays which allows precise tracking (typically <100 m error) at short time interval. Solar powered devices are preferred for multi-annual studies

Table 1 Summary of methods used to trap vultures, with main advantages and disadvantages

Trapping methods	Use	Advantage	Disadvantage	Source
Walk-in cage trap (active)	Mass capturing	Easy to handle, safe for the vultures	Time consuming as triggered by observers	Bloom et al. (2007), Barber and Bildstein (2011), Avery et al. (2011), Dodge et al. (2014), Harel et al. (2016a), Monsarrat et al. (2013), Garcia-Ripolles et al. (2011), Phipps et al. (2013a), Bamford et al. (2007), Kane et al. (2016), Vasilakis et al. (2016)
"Fall-in" cage trap (passive)	Mass capturing	Easy to handle, safe for the vultures, passive trapping (vultures enter in "their free time")	May be hard to attract vultures, not efficient where food is available in large quantities	Iezekiel et al. (2003), Harel et al. (2016a)
Cannon/ rocket-projected/ pneumatic-nets	Mass capturing	Highly efficient, selective (triggered by observer)	Projectiles can rarely hurt or kill birds, stressful, big team to handle, handling explosives may be complicated	Bamford et al. (2009), Lambertucci et al. (2014), Gil et al. (2014), Carrete et al. (2013), Lopez-Lopez et al. (2014)
Leg-hold traps ("padded jaws")/nooses carpets/Phai traps	For single birds/small numbers	Simple, small team required	Non species selective, need constant presence	Bloom et al. (2007), Dodge et al. (2014), Urios et al. (2010), Spiegel et al. (2013a)
Pit trap	For single birds (bearded vultures, condors)	Can be performed by only one person	Time consuming	Reid et al. (2015)

Credit: the chapter authors

(the longest tracking duration in France and in Israel was 5 years; Duriez and Hatzofe, unpublished). GPS transmitters usually store data on-board but several companies have developed systems to remotely download data using a radio-link, GSM or satellite transmission.

Tracking devices should be placed near the center of gravity on the bird's back. The common attachment method includes a Teflon ribbon harness which is robust and non-abrasive for skin. Some elasticity can be added by inserting a silicon tube inside the ribbon. Back-pack and body harness are efficient methods of attachment, but there is a risk of entanglement of the bird if one string is broken (Bögel et al.

Fig. 2 Eurasian griffon vultures *Gyps fulvus* carrying a GPS tag, (top) attached by a back-pack harness in silicon threaded Teflon ribbon (photo by I. Shaked); and (bottom) attached by a leg-loop harness (photo by O. Duriez). The position of both tags is located close to the bird's center of gravity. For long-distance visual identification, these birds are also marked with wing tags (top) and with a darvic coded ring (bottom)

2000). Leg-loop harness (Rappole and Tipton 1991) is fast and easy to fit, secure for the birds (as it prevents entanglement when broken), but power charging can sometimes be made more difficult because solar panels can be covered by wings when vultures are perched (Duriez unpublished). In condors telemetry devices have been mounted on wing-tag (Wallace et al. 1980), but this method is questionable because it adds weight on a sensitive place of the wing and can potentially change lift or drag forces.

Additional sensors coupled with the GPS transmitter can enhance the information collected on the behavior of individuals. Accelerometers are useful to estimate body posture and movements, and ultimately feeding behavior and thus determining the location of carrions found and eaten by vultures (Spiegel et al. 2013b; Nathan et al. 2012). Magnetometer data can provide additional data on body position and help in discriminating between different behaviors (Williams et al. 2017). In the near future, we believe that cameras can be deployed also on vultures' back to collect data on social behavior around carrions, as done on seabirds (Tremblay et al. 2014), however this technique is currently limited by the technical difficulty to download large amount of image data remotely without recapturing the bird. Nowadays the use of cameras is limited to the ground, with camera traps that can record attendance of scavengers (obligate and facultative) around carrions and help population monitoring by reading rings (Mateo-Tomas et al. 2017; Wilson 2015; Moreno-Opo et al. 2015; Ogada et al. 2012).

How Carrion Affect Foraging Movement of Vultures?

A main research question concerning the study of vulture movements in space and time is "how vultures make use of unpredictable food like carrions, and how does this affect their foraging strategies depending on the environmental context?"

We reviewed 39 studies published between 2007 and 2018 about vulture foraging movements using telemetry (Table 2), excluding studies about migration, dispersal or demography. 34 studies (87%) used GPS tracking devices and the 5 others used combinations of Argos or VHF telemetry units. 31 studies (79%) concerned Old-World vultures (family Accipitridae) and 8 concerned New-World vultures (family Cathartidae). Studies on Old-World vultures concerned 9 species out of 16 described (56%) and studies on Cathartidae concerned 4 species out of 7 described (57%). The 10 species where no data on foraging movements has been published (thus absent from Table 2) are *Gypohierax angolensis, Gyps indicus, G. ruppellii, G. tenuirostris, Necrosyrtes monachus, Sarcogyps calvus, Trigonoceps occipitalis*, and *Cathartes burrovianus, C. melambrotus, Sarcoramphus papa.* From a biogeographical perspective, while all species from Palearctic and Nearctic have been studied (at least once), only half of the species from Afrotropical and Neotropical regions have been studied and only one species from the Indo-Malayan region (Fig. 3). A similar pattern can be found regarding the main habitat, where all species from temperate-mountainous habitat have been studied, half of species from arid-Savanna habitats have been studied and only one species from tropical forest (Fig. 3). There are studies from all IUCN Red-list groups, however only a third of the species listed as Critically Endangered have been studied, as well as 42% of Least-Concerned species (Fig. 3). Finally, most studies concerned species displaying social behaviors for nesting or feeding, and few studies concerned territorial species (the notable exceptions being the bearded, lappet-faced and Egyptian vultures).

Therefore, our review points a lack of studies of vultures from the tropics, where vulture communities are (or were) the most abundant and diverse. This sample is

Table 2 Summary of methods used to track vultures and main results of home range size, daily distance travelled and daily maximum displacement (radius of feeding events from colony or roost), in 39 studies dealing with vulture foraging ecology

Species	Country	Tracking	Fix interval	home range[a]	Bird status[b]	Season	Home range (km²)[d]	daily distance travelled (km)[d]	Radius of displacement[c,d] (km)	Source
Cathartes aura	USA	GPS	1 h	95% FK	Imm and ad	Summer	Med 551 [R 26–2860]			Avery et al. (2011)
					Imm and ad	Winter	Med 68 [R 36–25056]			
			Variable	95% MBK	Ad	Breed	53 ± 34			Holland et al. (2017)
					Ad	Non breed	65 ± 63			
	USA	GPS	1 h	–	Br ad	Summer		25 ± 25		Dodge et al. (2014)
	Argentina			–				59 ± 60		
	USA				Non-br ad	Winter		36 ± 36		
	S America							43 ± 34		
Coragyps atratus	USA	GPS		95% FK	Imm and ad	Summer	Med 143 [R 2–3106]			Avery et al. (2011)
					Imm and ad	Winter	Med 11 [R 1–3985]			
			Variable	95% MBK	Ad	Breed	46 ± 40			Holland et al. (2017)
					Ad	Non breed	23 ± 23			

(continued)

Table 2 (continued)

Species	Country	Tracking	Fix interval	home range[a]	Bird status[b]	Season	Home range (km²)[d]	daily distance travelled (km)[d]	Radius of displacement[c,d] (km)	Source
Gymnogyps californicus	USA	GPS	1 h	99% FK	Ad	Annual	562 [CI 427–741]			Rivers et al. (2014)
					Imm		413 [CI 300–568]			
Vultur gryphus	Chile, Argentina	GPS	1 h	MCP	Ad	Annual	16,284 ± 14,370			Lambertucci et al. (2014), Alarcon et al. (2017)
Gypaetus barbatus	Spain	Argos	1 h	95% FK	Imm	Annual	11,765 ± 7999			Gil et al. (2014)
				90% FK	br Ad	Annual	57 ± 36	24 ± 22	8 ± 13 (M)	Margalida et al. (2017)
					Non-Br ad		12,063 ± 5513	39 ± 38	23 ± 27 (M)	
	S Africa	GPS	1 h/15 min	MCP	Imm	Annual	38,500	66		Urios et al. (2010)
			3 h	95% FK	Imm	Annual	11,466 ± 4540			Krüger and Amar (2017)
			3 h	90% FK	Imm	Annual	21,880 ± 8187			Krüger et al. (2014), Reid et al. (2015)
					Br ad	Annual	95 ± 19		5.5 (M)	
Neophron percnopterus	Spain	VHF	Irregular	MCP	Imm and non-br ad	Summer	2370 ± 1493			Carrete et al. (2013)
	West Africa	Argos	1 h	MCP	Imm and non-br ad	Winter	78,016 ± 72,909			

Species	Location	Method	Interval	Estimator	Status	Season				Reference
	Spain	GPS	2 h	95% FK	Br ad	Summer	253 [202–1670]			Lopez-Lopez et al. (2014)
	Sahel	GPS	1 h	95% FK	Imm	Winter	211,777 ± 189,896			Oppel et al. (2015)
Gyps africanus	Namibia	GPS	10 min	–	Ad	Annual		120 ± 10	55 ± 3 (M)	Spiegel et al. (2013a)
	S Africa	GPS	1 h	95% FK	Imm	Annual	334,923 ± 286,062	34 ± 11		Phipps et al. (2013a)
Gyps bengalensis	Pakistan	GPS	1 h	MCP	Non-br ad	Annual	24,155 ± 29,625	33 ± 14		Gilbert et al. (2007)
Gyps fulvus	Spain	GPS	1 h	95% FK	Non-br ad	Annual	4078 ± 8630	Med 18 ± 18		Garcia-Ripolles et al. (2011)
			10 min	95% FK	Br ad	Annual	23,924 ± 25,216			Arrondo et al. (2018)
					Non-br ad	Annual	33,864 ± 36,714			
	France	GPS	10 min	95% MBK	Br ad	Spring	1272 ± 752	92 ± 6		Monsarrat et al. (2013), Fluhr et al. (2017)
			1 h	95% MBK	Br ad	Winter	473 ± 237	29 ± 6		
			3 s	–	Br ad	Summer		141 ± 92	24 ± 12 (M)	Harel et al. (2016a)
	Greece	VHF	Irregular	95% FK	Br ad	Winter-spring	692 ± 299		29 ± 10 (M)	Xirouchakis and Andreou (2009)
	Israel	GPS	10 min	–	Br ad and imm	Annual		90 ± 30	30 ± 13 (M)	Harel et al. (2016a, b)
			1 s	–		Annual		160 ± 110	32 ± 15 (M)	

(continued)

Table 2 (continued)

Species	Country	Tracking	Fix interval	home range[a]	Bird status[b]	Season	Home range (km²)[d]	daily distance travelled (km)[d]	Radius of displacement[c,d] (km)	Source
Gyps himalayensis	Asia		30 min	95% FK	Imm	Summer	61,130 ± 20,062			Sherub et al. (2017)
	Buthan					Winter	13,973 ± 6507			Bamford et al. (2007)
Gyps coprotheres	Namibia	GPS	1 h	MCP	Ad	Annual	38,327			
				MCP	Imm	Annual	482,276			
	S Africa	GPS	4 h	99% FK	Ad	Annual	80,752 ± 40,095	48 ± 26		Phipps et al. (2013b)
					imm	Annual	401,107 ± 244,042	37 ± 7		
	S Africa	GPS	15 min/4 h	95% FK	Ad	Dry	31,040 ± 45,598			Kane et al. (2016)
				95% FK	Ad	Wet	75,162 ± 130,832			
Aegypius monachus	Spain	Pellets		95% FK (colony)	Ad	Annual	1523		26 ± 36 (F)	Moreno-Opo et al. (2011)
			1 h	95% FK	Imm	Annual	3307 ± 2948			Castaño et al. (2015)
			3 h	95% FK	Imm and non-br ad	Annual	49,508 ± 34,236			Arrondo et al. (2018)
	Turkey	GPS	1 h	90% FK	Imm	Pre-migratory	356 ± 54	5 ± 4		Yamaç and Bilgin (2012)
	Caucasus-Middle east	GPS, Argos	1 h	95% FK	Imm	Summer	3847 ± 3120			Gavashelishvili et al. (2012)

			95% FK	Imm	Winter		
Greece	GPS	45 min to 2 h	95% FK	Imm and ad	Annual	1763 ± 839	3870 ± 2541	Vasilakis et al. (2016)
Mongolia	Argos	Irregular	MCP	Ad	Summer		[R 540–2653]	Batbayar et al. (2008)
Torgos tracheliotus Namibia	GPS	10 min	–	Ad	Annual	122 ± 11	48 ± 9 (M)	Spiegel et al. (2013a)

Credit: the chapter authors

[a]*MCP* minimum convex polygon, *FK* fixed Kernel, *MBK* movement based Kernel

[b]*ad* adult, *imm* immature birds, *br* breeding, *non-br* non breeding

[c]Radius of displacement can refer to (M) maximal distance of displacement from central place, or (F) radius of feeding place from central place

[d]Unless specified, results are presented as Mean ± SD, otherwise, Med is for median; in brackets: R is for range, and CI is for 95% confidence intervals
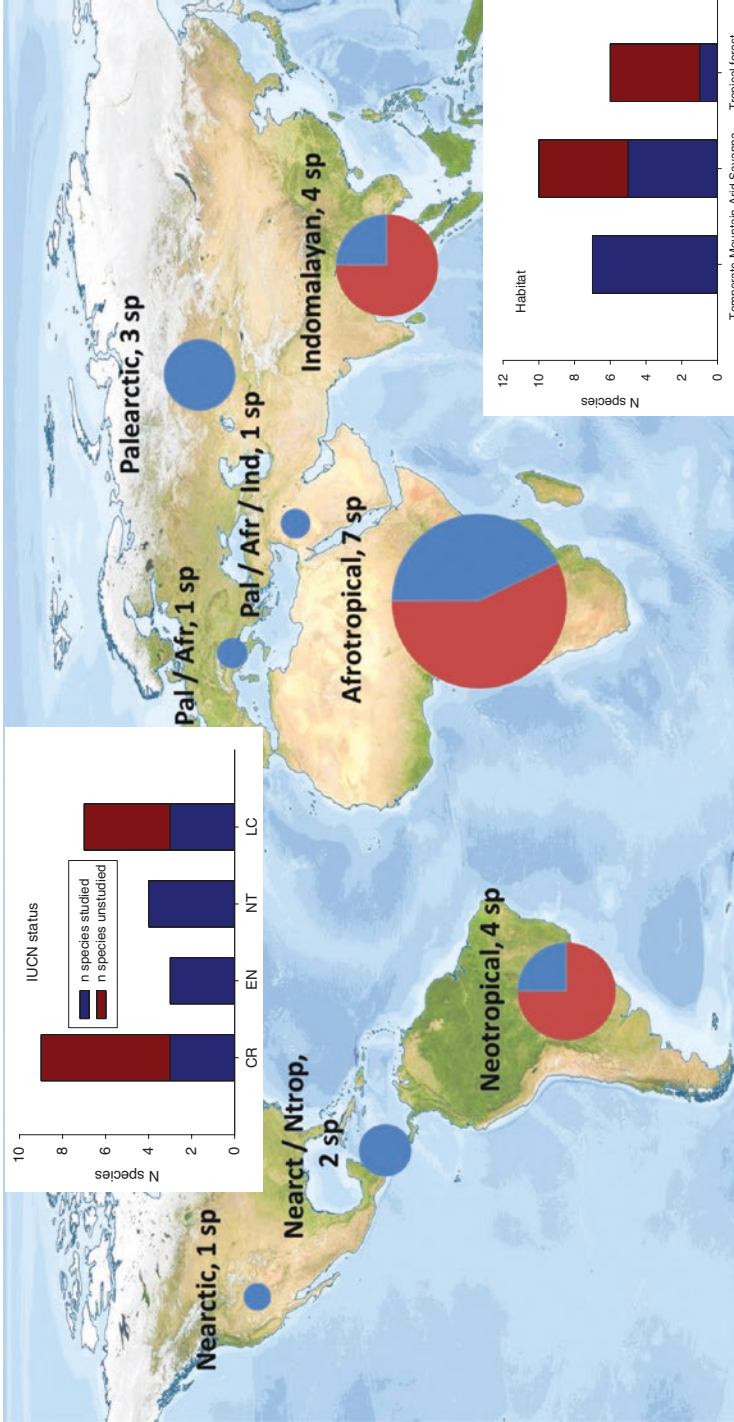
Fig. 3 Number of species in which detailed foraging studies have been performed (in blue) and species unstudied (in red), according to IUCN red list status (*CR* critically endangered, *EN* endangered, *NT* near threatened, *LC* least concerned), biogeographical region (distinguishing when species are found in different regions) and main habitat used (from studies detailed in Table 2). Credit: the chapter authors

therefore biased taxonomically, geographically and behaviorally and our knowledge of vulture movements mostly represents the behavior of social species in temperate mountains or arid areas (savannas or deserts).

With the aim to compare foraging movement behaviors from various species and derive general patterns, we reported in Table 2 the most widely computed parameters: the radius of displacement from central place, the daily distance travelled and home range size.

The radius of displacement from central place (roost or nest) has been reported in 9 studies only, however it is probably the most repeatable metric because it is less dependent of technology and sampling rate. Yet, caution is needed in interpretation because some studies measured the daily maximal distance from central place while other measured the mean radius of feeding event from the central place (e.g. even possible to compute from pellet analyses in which ear-tags of livestock can be found; (Moreno-Opo et al. 2011). As expected, the foraging radius is shorter in territorial species than in social species, among which it varies between c. 30 km in European vultures and c. 50 km in African species (Table 2).

The daily distance travelled per day has been computed in 13 studies. It varies between 5 km day^{-1} in *A. monachus* juvenile birds in Caucasus before migration (Yamaç and Bilgin 2012) and 160 km day^{-1} in *G. fulvus* in Israel (Harel et al. 2016a). However the value reported is highly dependent on the interval between fixes, as illustrated in Israel in *G. fulvus* at the same time of year, with values of 90 km day^{-1} when recording at interval of 10 min and 160 km day^{-1} when recording at interval of 1 s (Harel et al. 2016a). Such difference is due to the high flight speed of vultures (mean "cross-country" speed ranging 20–40 km h^{-1}, combining vertical soaring phases and horizontal gliding phases, but instantaneous ground speed >50 km h^{-1}; (Pennycuick 1972)): at interval of 1 h between fixes, two fixes could be spaced of a few km while the bird could have travelled in reality several tens of km in one direction and be back on its sinuous path. At interval shorter than 5 s, the soaring circles become visible and further increase the distance covered (Harel et al. 2016a; Treep et al. 2016). When considering only studies with interval between fixes 1–10 min, the mean daily distances varied between 90 km (*G. fulvus* in France and Israel) and 120 km (*G. africanus* and *T. tracheliotus* in Namibia) (Harel et al. 2016a; Spiegel et al. 2013a). When considering only studies with interval between fixes around 1 h, the mean daily distances varied between 5 and 66 km, with an average at 34.9 ± 21.6 km. This range of values between 30 and 60 km day^{-1} are remarkably similar for *C. aura* in the Americas, *G. africanus* in Africa and *G. fulvus* in Europe.

The home range is defined as the area in which an animal lives and moves on a periodic basis. The simplest method uses Minimum Convex Polygon (MCP) to delineate all recorded positions of an animal, although it is well known to greatly overestimate home range size. More recent methods use kernel density methods to estimate Utilization Distributions (UD) as the probability that an animal has to be in each cell of its home range (Worton 1989). When positions are supposed to be independent (i.e. collected at large interval of time) it is possible to use fixed-kernel method, while movement-based kernels are advised when data are collected at short time intervals (Benhamou and Cornélis 2010). Home range methods have been the

most popular methods to describe vultures' space use since it was used in 46 sub-populations or seasons and in 31 studies. However inter specific and intra-specific comparisons are made difficult because of the heterogeneity of methods, and within a method, the researcher's decision to use a probability threshold of 99%, 95% or 90% to define his home range (Table 2). When considering only studies using the most popular 95% kernel estimators, individual home range sizes of vultures varied tremendously between 11 km^2 and 334,923 km^2, with a mean of 42,680 ± 105,244 km^2. The smallest home ranges (<100 km^2) belonged to the two New-World species *C. aura* and *C. atratus*, while the largest home ranges, >10,000 km^2, all belonged to species in Africa: *G. africanus*, *N. percnopterus* and *G. barbatus*. The season often played a role in home range size, but there was no clear general trend. In temperate and sedentary species, like *G. fulvus, G. coprotheres* or *C. atratus*, home ranges tended to be larger in summer than in winter, when flight is more constrained by adverse aerological conditions (Kane et al. 2016; Avery et al. 2011; Monsarrat et al. 2013). In migratory species like *N. percnopterus*, home ranges were smaller in breeding season in temperate summer than in tropical winter, where movements are not constrained by returning to a nest (Carrete et al. 2013; Lopez-Lopez et al. 2014). However the opposite pattern was found in the long-distance migrant *C. aura* (Dodge et al. 2014). The status or age of the birds also played a role, with breeding adults tending to have smaller home ranges than non-breeding adults or immature birds.

Foraging activity of avian scavengers may serve as an estimator for carrion distribution (Fig. 4). When searching for food, avian scavengers may follow specific
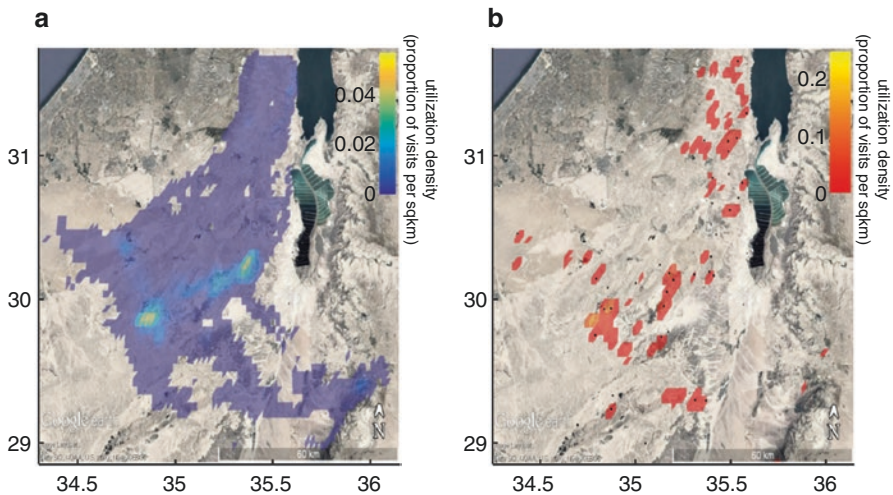

Fig. 4 Space-use patterns of griffon vultures *Gyps fulvus* in Israel as an estimator for carrion distribution patterns. (**a**) The spatial utilization distribution of foraging flights of GPS-tracked vultures may serve as a proxy for the area scanned by scavengers, while (**b**) feeding events (classified by accelerometry and movement data) represent the actual use of carrions available in the region. Colors in both panels represent the proportion of visits in a 2 × 2 km cell grid over the study period. Black dots in panel (**b**) represent active feeding stations. Credit: the chapter authors

land cover features, which are correlated with the presence of carrions (Houston 1974; Monsarrat et al. 2013) and may be limited by other factors, such as the roost site locations. However, within a suitable habitat, vultures may search in a random manner for food resources, or using their personal knowledge of the most likely places to find carrion (Kendall et al. 2014; Fluhr et al. 2017). To locate carrions, most vultures also use information retrieved from conspecifics (Houston 1974) or from other species (Kane et al. 2014; Spiegel et al. 2013a). Some gregarious species may use communal roosts as information centers to follow specifically the individuals that have been successful in foraging the previous day, probably using the state of the crop (extended) as proxy (Buckley 1996; Harel et al. 2017). Therefore, in order to establish the link between scavenger movements and the actual carrion distribution, the composition of foraging groups should be taken into account. Nevertheless, competition, diet preferences, human disturbance, topography and land cover may affect scavengers access to carrions and is expected to cause mismatches between the observed feeding behavior and the actual carrion distribution. Few modeling studies have compared the importance of self and social-information for vultures' foraging efficiency and population persistence (Jackson et al. 2008; Deygout et al. 2009, 2010; Cortes-Avizanda et al. 2014). They suggested that acute reduction in population densities of avian scavengers may impair their foraging efficiency. Such models could be developed to predict the actual effect that avian scavengers can have on carrion distribution, but should incorporate individual characteristics, such as fasting period (Spiegel et al. 2013b), dominance hierarchies within species (Bosè et al. 2012) and between species (Houston 1975; Moreno-Opo et al. 2016; Sebastián-González et al. 2016), and different scenarios of population or community densities (Dupont et al. 2011).

Conclusions and Future Perspectives

In conclusion it is still premature to derive general conclusions about vulture foraging movements in space, partly due to the different methods used for tracking and estimating movement metrics, but also due to large differences in ecology and habitat of vulture species around the world. The only general conclusion possible to say so far is that vultures are able to cover large distances of tens of km per day, in search of carrions, over very large areas, and thus can extend scavenging services well beyond reach of their colonies. But we still lack data on many species, particularly from the tropics. However, the methods to catch vultures are plentiful and the development of GPS technology and remote download of data offers avenues for promising future research about the spatial use of carrions by specialized scavengers.

More practically, to improve intra-specific and inter-specific comparisons, we encourage researchers to standardize their methods. The most important would be to homogenize the statistical methods to describe space use, and systematically report for each individual or each group the daily maximal displacement (which is

the less biased metric), daily travelled distance and 95% kernel UD. To study fine details about foraging behavior, vulture biologists must aim at collecting tracking data at intervals <5 min (Fluhr et al. 2017). Regarding the choice of loggers, the GPS system with automatic download with GSM network is by far the most accurate and cheaper. The most recent GPS devices, powered by solar panels over several years, allow recording GPS positions at intervals <5 min, and including burst of high resolutions recording 1 position per second, where it becomes easy to distinguish fine behavioral details (Harel et al. 2016a, b; Sherub et al. 2016). Two additional features can be very useful to study vulture feeding behavior if integrated into the device. The accelerometer can record body posture and movements associated with feeding events, and eventually can be used as a proxy of energy expenditure (Nathan et al. 2012; Spiegel et al. 2013b; Duriez et al. 2014). The possibility to define a "GPS fence" around areas of interest (like feeding stations, or wind farms) can allow to use special settings to be applied (like high resolution GPs recording), to better understand vulture behavior in these areas.

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