

# Factors Influencing Foraging Search Efficiency: Why Do Scarce Lappet-Faced Vultures Outperform Ubiquitous White-Backed Vultures?

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**ABSTRACT:** The search phase is a critical component of foraging behavior, affecting interspecific competition and community dynamics. Nevertheless, factors determining interspecific variation in search efficiency are still poorly understood. We studied differences in search efficiency between the lappet-faced vulture (*Torgos tracheliotus*, LFV) and the white-backed vulture (*Gyps africanus*, WBV) foraging on spatiotemporally unpredictable carcasses in Etosha National Park, Namibia. We used experimental food supply and high-resolution GPS tracking of free-ranging vultures to quantify search efficiency and elucidate the factors underlying the observed interspecific differences using a biased correlated random walk simulation model bootstrapped with the GPS tracking data. We found that LFV's search efficiency was higher than WBV's in both first-to-find, first-to-land, and per-individual-finding rate measures. Modifying species-specific traits in the simulation model allows us to assess the relative role of each factor in LFV's higher efficiency. Interspecific differences in morphology (through the effect on perceptual range and motion ability) and searchers' spatial dispersion (due to different roost arrangements) are in correspondence with the empirically observed advantage of LFV over WBV searchers, whereas differences in other aspects of the movement patterns appear to play a minor role. Our results provide mechanistic explanations for interspecific variation in search efficiency for species using similar resources and foraging modes.

**Keywords:** avian visual acuity, individual-based simulation model, interspecific competition, movement ecology, optimal foraging, vulture conservation.

## Introduction

The search phase is an important component of animal foraging efficiency. It affects energy expenditure and time

allocation during foraging and has confounding effects on the animal's competitive ability and fitness (Bell 1991; Stephens et al. 2007; Preston et al. 2010). Search efficiency is usually quantified as the rate of finding items in a given environment, either per unit time, per unit distance traveled during a foraging bout, or per unit energy invested in searching (Bartumeus et al. 2002; Sims et al. 2006). Although the importance of search costs has long been recognized in fundamental models of optimal foraging (e.g., Charnov 1976; Grünbaum 1998), we still poorly understand which factors determine interspecific variation in search efficiency. Among species exploiting similar food or other resources, these differences likely play a significant role in determining the stability and resilience of consumer community and associated food webs (Stephens et al. 2007). Nevertheless, resource detection is only the first rate-limiting step in the subsequent cascade of competitive interactions (Pearce-Duvel et al. 2011). If information regarding a detected item is shared, an efficiently searching species could provide a cue to other species exploiting the same resource (Buckley 1996). Alternatively, if information is not shared ("finders-keepers"), differences in search efficiency may affect species coexistence through competitive exclusion (Tilman 1982). Quantifying differences in search efficiency among species is important for conservation (Carrete et al. 2010) and for examining basic principles of search theory in real-life complex systems (Bell 1991; Benhamou 2007).

In a given environment, an animal's search performance is constrained by its motion and navigation (sensory and cognitive) capabilities (Bell 1991; Nathan et al. 2008), as well as its behavior, which influences the characteristics of its movement pattern (Bartumeus et al. 2002). For instance, a species with comparatively inferior search abilities (e.g.,

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with lower sensory or motion capacities hence lower detection ability) may, at least theoretically, compensate by using a more efficient search path or by adjusting the timing or the duration of search. Theoretical work on optimal search strategies as functions of resource distributions (e.g., clumped or scattered distribution) and foraging strategy (e.g., central place foraging), suggest some search patterns are more efficient than others, thereby providing testable predictions (Bovet and Benhamou 1991; Viswanathan et al. 1999; Sims et al. 2008). Empirical (field) tests of these predictions have focused on the statistical properties of movement paths, whereas the elucidation of the underlying factors has been hampered by the practical difficulty of tracking the movement of free-ranging animals while simultaneously collecting relevant covariate data such as the density of the exploited resources or the occurrence of predators (Edwards et al. 2007; Sims et al. 2008). Most previous empirical studies that explicitly examine the factors underlying variation in search efficiency among closely related species have compared distinct movement modes (e.g., sit-and-wait vs. active foraging; Huey et al. 1984; McLaughlin 1989). More general insights into the factors determining search efficiency can be obtained by comparing closely related species that use the same movement modes, cues, and resources (Pearce-Duvet et al. 2011).

To find carcasses that are typically unpredictable in space and time (lacking landscape cues and available for a relatively short time), Old World vultures rely exclusively on vision (Mundy et al. 1992). They search over huge areas through energetically efficient soaring flight (Ruxton and Houston 2004) and by forming diffusive foraging groups. The combination of large body size, extended search distances, and well-defined resources make vultures particularly suitable for studying the search phase of foraging. They are sufficiently large to enable researchers to track their movements at high temporal resolution for extended periods, through the deployment of GPS tracking devices. Feeding occurs over a sufficiently long period of time to permit the stationary carcass-handling phase to be easily distinguishable from the mobile search phase. Furthermore, although herd-following behavior by *Gyps* vultures (Pennycuick 1972) may limit the search to areas of high ungulate activity, searches for isolated carcasses can still be considered independent events due to the unpredictable nature of carcass locations within these areas.

A long-standing body of literature on intraspecific differences in foraging among several vulture species in Africa (Kruuk 1967; Pennycuick 1972; Houston 1974, 1975) provides important guidelines for studying interspecific variation in vultures' search efficiency. Consider, for example, the two most common vulture species in Etosha National Park, Namibia: the lappet-faced vulture (*Torgos tracheliotus* [LFV]) and the white-backed vulture (*Gyps africanus*

[WBV]). According to Kruuk (1967), WBVs travel long distances in search of food, relying heavily on observing other vulture species (and other scavengers) to help detect the carcasses of, mostly, large ungulates. By contrast, LFVs usually search for carcasses by regularly patrolling the same restricted range, often detecting carcasses before the more numerous WBVs do, and feeding on a range of carcass sizes from small mammals to large ungulates. These patterns were supported in subsequent studies (e.g., Pennycuick 1972; Houston 1975) but until now were not quantitatively tested at the individual level. Further, reasons for these differences in foraging behavior and carcass size preference remained uninvestigated.

Here we combine manipulated food supply field experiments and GPS tracking of free-ranging LFVs and WBVs in Etosha National Park with an empirically calibrated biased correlated random walk simulation to elucidate the factors influencing search efficiency in these two species that use similar resources and foraging modes.

## Material and Methods

### *Study Site and Species*

Field work was conducted in the extensive plains surrounding the Okaukuejo area of Etosha National Park, Namibia (19°02'16"S, 16°03'30"E; averaging approximately 1,000 m above sea level). The vegetation varies from arid to semiarid savanna and supports a variety of free-ranging large ungulate herbivores, including plains zebra (*Equus quagga*), springbok (*Antidorcas marsupialis*), gemsbok (*Oryx gazella*), and blue wildebeest (*Connochaetes taurinus*; Turner and Getz 2010). The park is surrounded by large seminatural game farms where carcasses are also available, and vultures readily fly in and out of the park and many hundreds of kilometers beyond. In addition to the two focal species, WBV (*Gyps africanus*) and LFV (*Torgos tracheliotus*), the scavenger guild in the area includes bateleur (*Terathopius ecaudatus*), yellow-billed kite (*Milvus aegyptius*), and tawny eagle (*Aquila rapax*), as well as spotted hyena (*Crocuta crocuta*), black-backed jackal (*Canis mesomelas*), and opportunistic lion (*Panthera leo*). Other vulture species in the region are very rare, and the two focal species dominate our study site (hereafter referred to as the "vulture community").

Both focal species are large soaring obligate scavengers that search visually for food items. Both species have a wide distribution in open habitats throughout southern and east Africa, with the smaller gregarious WBV being much more common than LFVs (usually fewer than 4 LFVs vs. 20–50 WBVs per 100 km<sup>2</sup>; Mundy et al. 1992) throughout the region and at Etosha. Both species roost in trees, with LFVs usually roosting and foraging solitary

or in pairs (Pennycuik 1976). WBVs are more social: breeding colonies consist of many individuals, with more than one pair occasionally sharing the same tree (Kemp and Kemp 1975; Mundy et al. 1992). Tens to hundreds WBVs around a given carcass is common scene in Etosha (O. Spiegel, personal observations) and elsewhere in the region (Houston 1974, 1975; Pennycuik 1976). LFVs are heavier than WBVs (mean, range: 6.78, 6.10–7.95 vs. 5.46, 4.15–7.20 kg; data for 9 LFVs and 34 WBVs) and have longer (wing span: 2.80 vs. 2.18 m) and proportionally wider wings, leading to lower wing loading (6.4 vs. 7.8 kg m<sup>-2</sup>; Pennycuik 1971; Mundy et al. 1992). The latter enables LFVs to use weaker thermals than WBV and hence more efficiently search fixed and relatively small foraging territories. The nonterritorial *Gyps* vultures, with their higher wing loading, are better suited to the fast cross-country travel needed to forage widely (Pennycuik 1972). LFVs and WBVs are known to compete for large ungulate carcasses, their main food source, and have been frequently observed fighting and displacing each other from carcasses (Kruuk 1967; Houston 1975; Mundy et al. 1992; Kendall et al. 2012). Mechanisms for reducing direct conflict include partitioning of edible parts of large carcasses, and consumption of different carcass types. Thus LFVs, with their larger skulls and beaks and mandible, are able to consume the harder parts of the carcass, including tendons and skin (Houston 1975; Mundy et al. 1992). Also, LFVs are known to locate and consume small food items that WBVs appear to ignore while searching for large ungulates (Kruuk 1967; Houston 1975; Pennycuik 1976).

#### *Empirical Data: Field Methods and Analysis Techniques*

*Carcass Observations and Experimental Supply.* To examine differences between the two species in efficiency of searching for carcasses, we explored the deviation from a null model that assumes equal search efficiency: detection rates are assumed to be proportional to the relative abundance of both species, based on head count surveys at naturally occurring carcasses in the study area. In contrast to this null hypothesis, we a priori expected higher carcass search efficiency in LFV compared to WBV, based on previously described patterns (Kruuk 1967; see “Introduction”). Since identifying the first vulture to detect a naturally occurring carcass is logistically difficult, we experimentally supplied zebra carcasses around 10 a.m. (3 h 14 min ± 23 min after sunrise; mean ± SE) at arbitrarily selected locations in the study region, during two field seasons (March–April 2008 and January–February 2009). Importantly, this practice enabled continuous monitoring (from a few hundred meters) of scavenger arrival and activity, starting before the arrival of any scavenger. In six cases the carcass was first located by other species such as kites, jackals, and

bateleur eagles before the arrival of the first vulture. Such cases were included in our analysis, since we still recorded the first of our two vulture species to arrive.

Since species may differ in their tendency to land near a carcass, regardless of detection, we used two distinct measures of carcass search efficiency: (a) the first to find, identified by the first species of vulture seen soaring above the carcass, and (b) the first to land, identified by the first species of vulture to land near the carcass. Previous studies used only the latter to estimate search success (Kruuk 1967; Prior and Weatherhead 1991; Carrete et al. 2010), yet the former better indicates the first individual to find the carcass. We applied a binomial test to contrast observed and expected probabilities of LFV “winner” events in which an individual LFV was the first to arrive or to land at the carcass. Conservatively, to minimize the likelihood of a false positive error in the binomial test, the expected probability was based on the upper 95% confidence interval (CI) of the LFV ratio (rather than on the mean or the median) and cases in which individuals of the two species arrived together were scored as “failed trials” events.

*GPS Tracking.* We used GPS telemetry to sample the movement of free-ranging individuals at high spatiotemporal resolution. This allows us to examine differences in carcasses detection among individuals of the two species, as well as differences in movement patterns and behavior. Birds were trapped using a Victor 3 soft-catch leg-hold trap deployed around the supplied carcasses. Once caught, they were banded and tagged with patagial tags according to the South African Bird Ringing Unit protocol, weighed, and measured. Close-up photographs were taken to determine eye corneal diameter, which was used to calculate visual acuity and carcass detection range (see app. A). Adults in good physical condition were fitted with a GPS tag (160 g, E-Obs, Munich) attached using a backpack configuration. GPS tags provide the speed and position in three spatial dimensions (longitude, latitude, and elevation) for each data point. Due to the diurnal activity regime typical of vultures, transmitters were set to operate on a 12-h duty cycle starting 7:00 a.m. each day. GPS locations were recorded every 10 min, and data were stored on board until downloaded via UHF communication to a handheld receiver.

Downloaded GPS data were filtered to include only reliable locations; 1.4% of the locations gathered were excluded because fixes were based on fewer than four satellites. Tracks were analyzed to determine roost locations, daily roost departure, and arrival times (to the nearest 10 min), as well as the main (most frequently visited) roost over the whole track of each individual. The beeline distances from the morning roost to the evening roost and to the most remote location of the day are respectively

termed the “daily overall displacement” (DOD) and the “daily maximum displacement” (DMD). The deviation angle of the DOD line from the azimuth to the main roost we termed “DDA.” The daily distance traveled (DDT) is the sum of distances between all consecutive locations in day, and the partial DDT until the DMD point we denote as DDT’. The DOD/DDT ratio is not an informative straightness index because vultures frequently return to the same roost (i.e., DOD = 0). We thus calculated the straightness of a daily path (SDP) as DMD/DDT; this parameter satisfies  $0 \leq \text{SDP} \leq 1$  approaching 1 for perfectly straight flight.

Our high sampling rate enables identifying the ground stops of individuals after they depart from their morning roost and before landing at their evening roost, provided the stops exceeded 20 min at the same location (i.e., points within a circle of radius <100 m). Based on our experience with ground-truthed and acceleration-based classification of feeding events of griffon vultures (*Gyps fulvus*) in Israel (Nathan et al. 2012), we assumed that this 20-min threshold reliably discriminates a high proportion of stops at carcass locations. We thus calculated the mean frequency of these >20-min stops for each individual during a 30-day period. To compare the movement descriptors between species, we applied a correction for the substantial differences in tracking duration among individuals using a one-sided *t*-test and ratio estimator technique with Fisher’s method for variance estimation and Welch’s calculation for degrees of freedom (see app. B).

### Modeling

*General Model Structure.* We developed a biased correlated random walk (BCRW) simulation model for exploring the processes responsible for observed differences in search efficiency between the two species. Specifically, we focused on distinguishing the effects of species-specific detection ranges, movement properties and spatial distribution of roost locations on carcass detection success (hereafter termed “search efficiency” since both species are compared over the same period and travel similar distances). The BCRW model simulates the movement of individuals in a homogenous habitat where each day 300 carcasses are randomly placed across the landscape. An individual’s movement is biased toward its main roost site, randomly located within the central region of the simulated domain (for more detailed model description and for alternative representation of carcass availability, see app. C, available online). Our BCRW simulation was implemented in Matlab (MathWorks, Natick, MA), and a single model run encompasses 25 diurnal paths (12 h each) constructed using 10-min time interval segments between location points on each path.

*Simulating Movement of Individuals.* We pooled our empirical data (950 LFV and 2200 WBV daily tracks) and binned them (using an interval of 10 km) based on the distance of their first point from the main roost. To simulate the daily movement of an individual, two variables—DOD and DDA (see “GPS Tracking” above)—were randomly selected from the corresponding bin of the species’ pool (e.g., if a simulated WBV starts the day ~86 km from its main roost, DOD and DDA values for this day were drawn from the values of 123 data days in the 80–90-km distance bin). For both species, the DDA is smaller when the bird is farther from its main roost, especially for days with high DOD implying a “centripetal” tendency to head back toward the main roost. This tendency was, as expected (Kruuk 1967; Pennycuik 1972), stronger for LFV than for WBV, leading to shorter displacement distances from the main roost for the former species. Once the end location of the day was determined, the movement path was simulated using the species-specific statistical properties of correlated random walks (see app. C). Carcasses were detected if they occurred within the species-specific detection distance (see app. A). Vultures usually eat every 2 to 4 days (Mundy et al 1992) and rarely more than once a day. Thus, simulated birds were limited to one carcass a day. After carcass detection, the bird stopped searching and flew to its predetermined end point.

*Simulating Individual Movements in a Community Context.* We used our empirical ratio of 1 LFV to 9 WBV (see “Results”), which closely corresponds to observed ratios across Africa and at our study site (Kruuk 1967; Kemp and Kemp 1975; Mundy et al. 1992). Each simulation included 24 LFVs and 216 WBVs roosting at a species-specific main roost, with *k* individuals per roost starting at each main roost (i.e., the colony). Individual vultures in our simulations did not interact with each other, neither at the roost nor during foraging. Thus, simulated birds were not affected by the presence of, or the carcass detection by, conspecifics. Also, birds from the same colony left independently in random directions (see app. C for empirical justification). All birds in each simulation foraged on the same set of randomly located carcasses (with a new set generated each day). Thus, simulated carcasses could be found by one or more individuals from one or two species, allowing us to determine the species of the first finder of each carcass and to calculate the value of the first-to-find measure (the population-level measure of search efficiency). Because all experimentally deployed carcasses were eventually found by both species, we report here simulation results for the proportion of carcasses found first by an LFV out of the fraction of carcasses found by both species; however, results are qualitatively similar when all carcasses are considered. The per-individual car-

carcass detection rate was also calculated from the simulation outcomes.

*The Effect of Detection Range and Movement Pattern on Search Efficiency.* The differences between the two focal species in both measures of search efficiency might be attributed to one or more differences in their morphology and behavior. To evaluate the explanatory power of potential factors and, consequently, to implement differences in these specific factors in the simulations, we considered the differences revealed in this study (e.g., detection range). Clearly, properties that are similar for both species, such as the DDT and DMD (table 1), are unlikely to contribute to the observed differences in search efficiency. Some of the properties that were only marginally significantly different between species in our data set (presumably due to our limited sample size) were suggested by Kruuk (1967) and Pennycuik (1972) to explain LFV higher efficiency. Therefore, we conservatively considered also the potential contribution of these properties (e.g., affinity to the main roost, roost departure time, SDP, and DOD).

Remarkably, the two strongest differences between the species—flight (ground) speed and elevation (above ground)—have rather complicated effects on carcass detection ability that cannot be fully quantified. The effect of the angular rate of change (of the projected image on the retina, which potentially leads to a smeared picture at high velocities) is quantifiable, however, using Land's (1999) method. LFVs' lower elevation and slower speed (table 1) have counterbalancing effects on the angular velocity, resulting in values of  $1.272^\circ \text{ s}^{-1}$  that are similar to the  $1.198^\circ \text{ s}^{-1}$  calculated for the WBVs. Thus, differences in flight speed and elevation are unlikely to explain LFVs' higher search efficiency and were not included in the model (but see "Discussion" for further details).

In contrast, LFVs' higher efficiency might be attributed to its enhanced detection range in a more straightforward

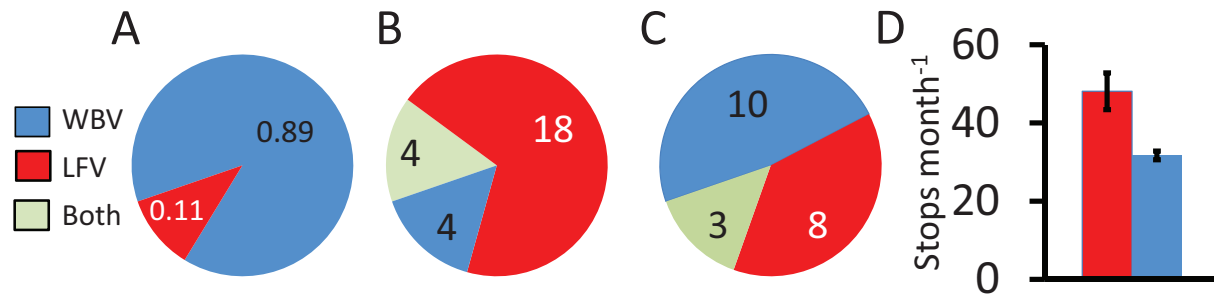
manner. The earlier roost departure time of LFVs (table 1) is expected to affect the timing but not the number of carcass detection events. The higher roost affinity of LFVs (i.e., more confined home range) was long considered to reflect a better search of a more restricted area (Kruuk 1967; Houston 1975). The straightness of the movement path is expected to affect the number of detected carcasses (Bovet and Benhamou 1991) but not necessarily the timing of carcass detection events. Yet, it is difficult to predict a priori the effect of path shape on overall search efficiency, since it depends on resource distribution in relation to the main roost (where search typically commences) and on resource renewal rate, two properties that are not known in sufficient detail for our study site.

To evaluate the potential role of these specific properties in determining search efficiency, we used our BCRW simulation approach to create variant species (labeled SPECIES<sub>var#</sub>), each with a single modified feature, and compared the search performance of the variant versus the wildtype (var0) in our BCRW simulations. Each variant had the same features of the species it denotes, except for a specific feature taken from the other species, as label by the "var#" subscript. This procedure was repeated for both species and for all relevant properties: detection range (var1), affinity to the main roost (var2), roost departure time (var3), and daily straightness (var4). For instance, to explore the importance of detection range, a variant of LFV with the estimated WBV detection range and a variant of WBV with the estimated LFV detection range were compared to the wildtypes of the other species (i.e., LFV<sub>var1</sub> vs. WBV<sub>var0</sub> and LFV<sub>var0</sub> vs. WBV<sub>var1</sub>, using LFV<sub>var0</sub> vs. WBV<sub>var0</sub> as a reference). Nine different communities (240 individuals each) were simulated, one for the two wildtypes, four with a variant LFV, and another four with variant WBV. We repeated the simulations 10 times for each community, totaling 90 community simulations. Results were compared using one-way ANOVA and a post hoc comparison

**Table 1:** Comparisons of movement properties between species based on GPS tracking data (mean  $\pm$  SE)

Property	Lappet-faced vultures	White-backed vultures	Statistical results
DDT: daily distance traveled (km)	122.8 $\pm$ 10.7	120.7 $\pm$ 10.4	$t_{6,3} = .13, P = .447$
SDP: straightness of the daily path	.608 $\pm$ .016	.632 $\pm$ .016	$t_{6,7} = 1.04, P = .168$
DMD: daily maximum displacement (km)	48.4 $\pm$ 9.3	55.2 $\pm$ 2.8	$t_{2,4} = .7, P = .272$
DOD: daily overall displacement (km)	33.4 $\pm$ 8.2	44.2 $\pm$ 2.6	$t_{2,4} = 1.24, P = .158$
<b>Mean flight elevation (m above ground)</b>	431.2 $\pm$ 8.8	506.2 $\pm$ 8.1	$t_{5,8} = 7.78, P < .0002$
Distance from main roost (km)	33.5 $\pm$ 12.4	65.7 $\pm$ 10.6	$t_{5,4} = -1.96, P = .052$
<b>Flight speed (km h<sup>-1</sup>)</b>	44.4 $\pm$ .6	50.3 $\pm$ .7	$t_{8,5} = -6.5, P < .0001$
Roost departure time (h after sunrise)	03:30:42 $\pm$ 00:09:23	03:56:34 $\pm$ 00:11:17	$t_{8,2} = 1.76, P = .057$
Daily flight duration (h between two successive roosts)	06:09:56 $\pm$ 00:16:20	05:16:17 $\pm$ 00:26:37	$t_{10,4} = 1.72, P = .058$
<b>Day stops frequency (stops month<sup>-1</sup>)</b>	48.1 $\pm$ 4.7	31.7 $\pm$ 1.2	$t_{2,3} = -3.32, P = .034$

Note: Properties highlighted in bold are significantly different between species.



**Figure 1:** Comparison of different measures of search efficiency between white-backed vultures (WBVs) and lappet-faced vultures (LFVs). *A*, Relative abundance of the two species in the study site, estimated by head counts at sites with naturally occurring carcasses ( $n = 31$ ) and used as the expected proportion (the null hypothesis of equal carcass detection success). LFVs account for ~11% of individuals in the community (95% confidence interval: 9%–14%). *B*, First to find, estimated at the species level by considering the first bird observed soaring above the carcass. *C*, First to land, also estimated at the species level by identifying the first bird to land near the experimentally supplied baits ( $n = 26$ ). An LFV was the first to land next to a carcass in a significantly higher-than-expected proportion of cases, and the LFV advantage is even more pronounced when the former measure is considered. The significant difference between the two phases (69% of the first to find and only 44% of the first to land) suggests that despite a higher finding rate, LFVs in many cases avoid landing near the carcass until WBVs arrive at the scene. *D*, Carcass detection rate, estimated at the individual level as the number of stops on the ground per month, based on tracks from GPS-tagged vultures. Each stop presumably represents a visit to a carcass, suggesting an individual LFV reaches 1.5 times more carcasses per unit time.

procedure with Bonferroni adjustments to compensate for multiple comparisons (see app. C for further details and validation data).

*The Effect of Roost Spatial Arrangement on Search Efficiency.* To examine the role of interspecific differences in the spatial arrangement of roosts in determining carcass search efficiency, we repeated the community simulations (wildtypes only) for different numbers of (main) roosts, while keeping the overall 1 : 9 LFV : WBV abundance ratio. We used the original 24 : 216 ratio of LFV : WBV individuals as a basis for designing BCRW simulation experiments encompassing all possible birds-per-roost values for the two species (i.e., 1, 2, 3, 4, 6, 8, 12, and 24 LFVs per roost; 1, 2, 3, 4, 6, 8, 9, 12, 18, 24, 27, 36, 54, 72, 108, and 216 WBVs per roost), with 128 community simulations in total. For example, one simulated community reflected a combination of 12 different randomly located LFV roosts (2 birds each) and 6 WBV roosts (36 birds each), suggesting LFVs have twice as many roosting colonies as WBV (LFV : WBV roost ratio = 2). Consequently, the simulated LFV : WBV roost ratio ranged from 1/216 (all LFVs in the one roost and each WBV in a separate roost) up to 24/1 (each LFV in a separate roost and all WBVs in one roost). Assuming that the realistic range of LFV : WBV roosts ratio in our study system varies only between 1.5–3 (corresponding to an average of roughly 1.5–2 LFVs and 20–50 WBVs per roost; O. Spiegel, personal observation), we used 2 LFVs and 36 WBVs per roost for all simulations of variants mentioned above. A possible bias in the results of the number of carcasses

found by both species, due to the effect of differences in roost numbers on number of carcasses found by both species, was prevented by restoring the same carcass set daily.

## Results

### Empirical Patterns

*Carcass Observations and Experimental Supply.* The relative proportion of the two species in their joint community was estimated at 31 naturally occurring carcasses. A mean of 45 WBV and 7.5 LFV were counted around these carcasses, with LFV being  $10.9\% \pm 2.5\%$  of the community (mean  $\pm$  SE; 95% CI limits 9%–14%). Overall, we experimentally deployed 27 zebra carcass baits. Data on the first bird soaring above the carcass were available for 26 cases, including four where both species were seen soaring together and 18 cases in which LFV was seen first (fig. 1). Thus, considering the first-to-find measure, the search efficiency of LFV is much higher than that of WBV, being significantly higher than the null model expectation ( $X \sim B(26, 0.14)$ ,  $P(X \geq 18) < .001$ ). Data on landing were available for 21 cases, including three cases where both species landed together and eight cases in which LFV landed first. Thus, considering the first-to-land measure, the search efficiency of LFV is significantly higher than the expectation ( $X \sim B(21, 0.14)$ ,  $P(X \geq 8) < .006$ ). Yet there is a significant difference between the two measures ( $X \sim B(18, 0.69)$ ,  $P(X \leq 8) = .025$ ), implying that despite their

higher carcass detection success, LFVs in many cases tend to avoid landing until the carcass is approached by WBVs.

*GPS Tracking.* We captured two LFVs and 12 WBVs during the first field season and four LFVs and 14 WBVs during the second field season. Overall, 19 GPS tags were deployed (five on LFV and 14 on WBV), and data was downloaded from 16 birds. Three LFVs (track durations: 160, 377, and 512 days) and 10 WBVs (track duration:  $254 \pm 56$  days, range 47–534 days) were included in the analysis and three tracks shorter than 14 days were excluded. These data are available through the Movebank project (<https://www.movebank.org/>). Five rare events of long-range forays (long directional flights to remote areas) by two individuals were also excluded from further analysis since they probably represent a different ecological situation with other motivations and movement patterns (Nathan et al. 2012). Generally, as summarized in table 1, the two species differ in their movement properties (e.g., flight elevation and speed), although some aspects were similar (e.g., DDT and DMD).

### Modeling

*The Effect of Detection Range and Movement Pattern on Search Efficiency.* Overall, the model results (fig. 2) agree with the empirical findings that despite their lower abundance, LFVs are first to arrive at around one-half of the carcasses and find around 1.5 times more carcasses for a given time interval. The simulations of the wildtype community (LFV<sub>var0</sub> vs. WBV<sub>var0</sub>) showed that proportions of carcasses found first by LFV are  $0.556 \pm 0.019$  and that LFVs found twice as many carcasses as WBV (ratio of  $2.09 \pm 0.07$ ).

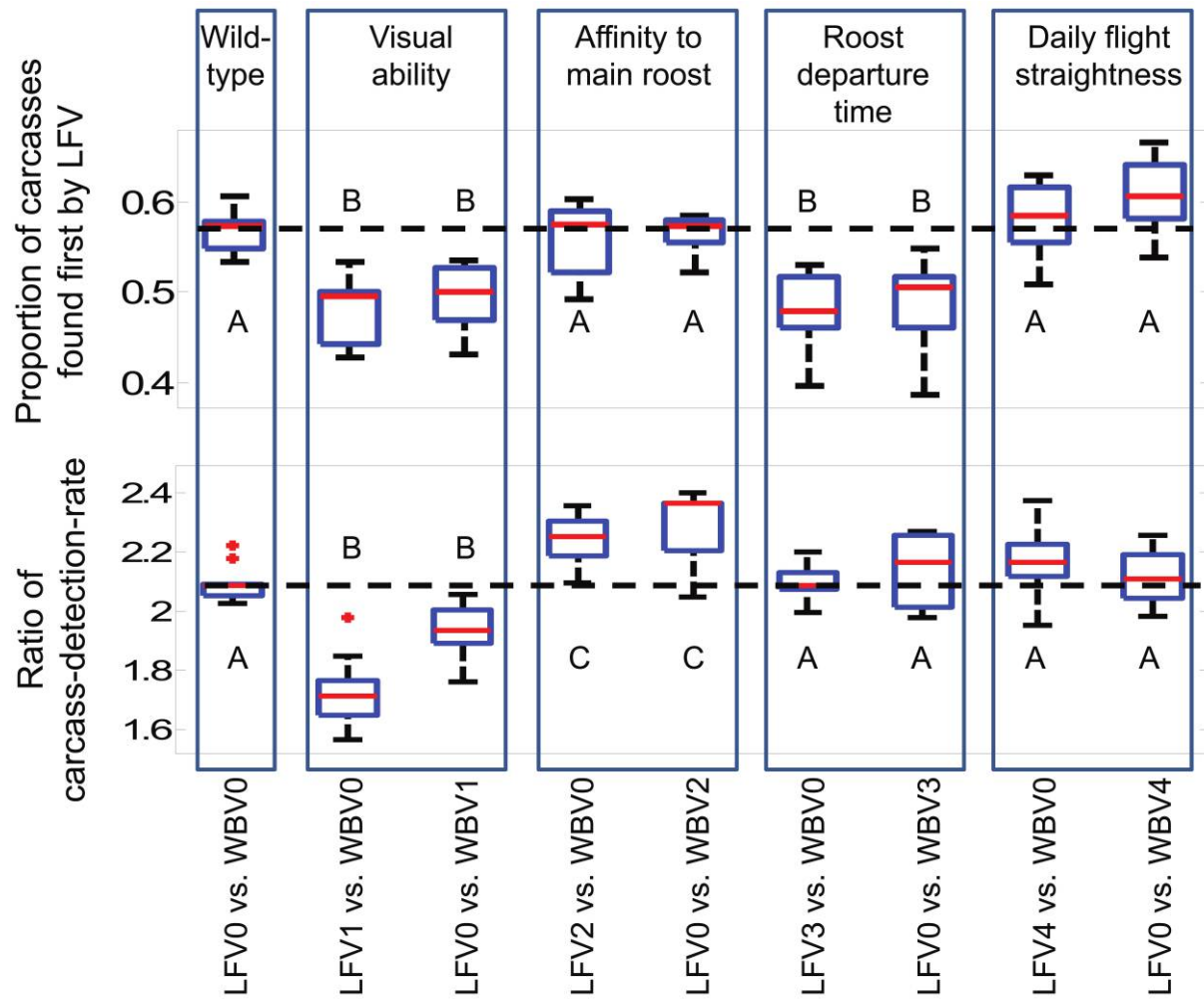
Simulation results of the different variants compared with the wildtypes provided the means to evaluate the relative impact of specific properties. The first-to-find measure of search efficiency was affected only by changes in the visual ability and roost departure time (fig. 2, upper panel). Enhancing WBV detection range (WBV<sub>var1</sub>) or reducing LFV detection range (LFV<sub>var1</sub>) had the same effect: the proportion of carcasses found first by LFVs was reduced since it took them more time to find the carcasses. Delayed LFV departure (LFV<sub>var3</sub>) or earlier WBV departure (WBV<sub>var3</sub>) significantly reduced LFV advantage, as expected. None of the other properties had significant effect on this measure.

The ratio between the two species in the carcass-detection rate measure was affected by the detection range, with variants eliminating LFV visual advantage (LFV<sub>var1</sub> and WBV<sub>var1</sub>) showing the expected decrease in search performance (fig. 2 lower panel). Modifying roost affinity (and consequently the area covered during routine foraging)

positively affected the ratio of carcass-detection rate. Both the increase in the LFV foraging area (LFV<sub>var2</sub>'s roost affinity is similar to that of WBV<sub>var0</sub> and lower than LFV<sub>var0</sub>'s affinity) and the reduction of the WBV foraging area (WBV<sub>var2</sub>) allowed LFVs to encounter relatively more carcasses than WBVs compared to the wildtype. Thus, the higher search efficiency of LFVs is not facilitated by their tendency to forage locally, as previously suggested (Kruuk 1967; Pennycuick 1972). Rather, it appears to exist despite this disadvantage. Modifying roost departure time did not affect the ratio of carcass-detection rate compared to the wildtype. Interestingly, the finding that flight straightness had no effect on the two measures of carcass search efficiency implies that this basic property of the movement path is not responsible for the observed difference. Presumably the magnitude of the difference between species (0.608 vs. 0.632) with respect to the long detection distances is not sufficient to impact search performance.

*The Effect of Roosts' Spatial Arrangement on Search Efficiency.* The simulations showed that the spatial arrangement of roost sites strongly influenced both measures of search efficiency (fig. 3). Fewer roosts lead to less efficient search (individuals start their search from fewer points), and individuals' affinity to their roosts (leading to underrepresentation of remote areas) reinforces this trend. For a given population size, fewer roosts also implies more individuals per roost, further reducing search efficiency and strengthening the advantage of a species with more roosts. This is evident for both species and both search efficiency measures (fig. 3A, 3C), with the exception of the low first-to-find measure values for simulations with only a few WBV roosts (fig. 3A). This exception is due to very high WBVs concentration at these roosts (with up to 216 birds per roost), enhancing WBV chances to find a carcass in the vicinity of the roosts and negatively affecting the number of carcasses found by both species.

The effect of spatial arrangement of roosts on the two search efficiency measures is examined by plotting the simulation results for these measures against increasing LFV : WBV ratios of roost numbers. We found positive trends for both measures, implying that the higher search efficiency of the LFV is more pronounced when there are relatively more roosts for this species compared to the WBV (fig. 3B, 3D). The power law function provides a reasonable fit for the first-to-find measure ( $\log_{10} Y = 0.154 \times \log_{10} X - 0.673$ ,  $R^2 = 0.36$ ,  $P < .0001$ ) and a much better fit for the carcass-detection rate measure ( $\log_{10} Y = 0.151 \times \log_{10} X + 0.288$ ,  $R^2 = 0.79$ ,  $P < .0001$ ), where our simulation results nicely fit the empirical results. For the first-to-find measure, however, our model seems to underestimate the empirical results (fig. 3B). This disagreement can be attributed to two properties of the



**Figure 2:** Simulating the effect of detection range and movement properties on the differences between white-backed vultures (WBVs) and lappet-faced vultures (LFVs) in two measures of search efficiency. The first-to-find measure (*upper panel*), calculated as the proportion of carcasses found first by an LFV out of all carcasses found by both species (e.g., a proportion of 0.57 suggests that more than half of the discovered carcasses are found first by an LFV). The carcass-detection rate measure (*lower panel*) is calculated as the ratio of the mean number of carcasses detected by each species (LFV : WBV; e.g., a ratio of 2 suggests that an LFV finds twofold more carcasses than a WBV during a run). Each column represents the results of 10 simulated communities, and each community consists of 24 LFVs and 216 WBVs of the variant specified (denoted as the species initials and variant serial number). The first column presents results for the two wildtypes (var0; LFV<sub>var0</sub> vs. WBV<sub>var0</sub> in the main text), which provides a reference for all other columns (variants) with the wildtype median value extended horizontally (dashed line) to facilitate comparisons. Variants differ from the wildtype of the species in one of the following properties: detection range (var1), affinity to the main roost (var2), roost departure time (var3), and daily flight straightness (var4). Boxes are the twenty-fifth and seventy-fifth percentiles crossed by the median. Capital letters indicate the significance of the differences from the wildtypes after Bonferroni adjustment: modifying a specific property does not significantly alter (A), significantly reduces (B), or significantly increases (C) the relative search efficiency of LFV compared to the wildtype performance.

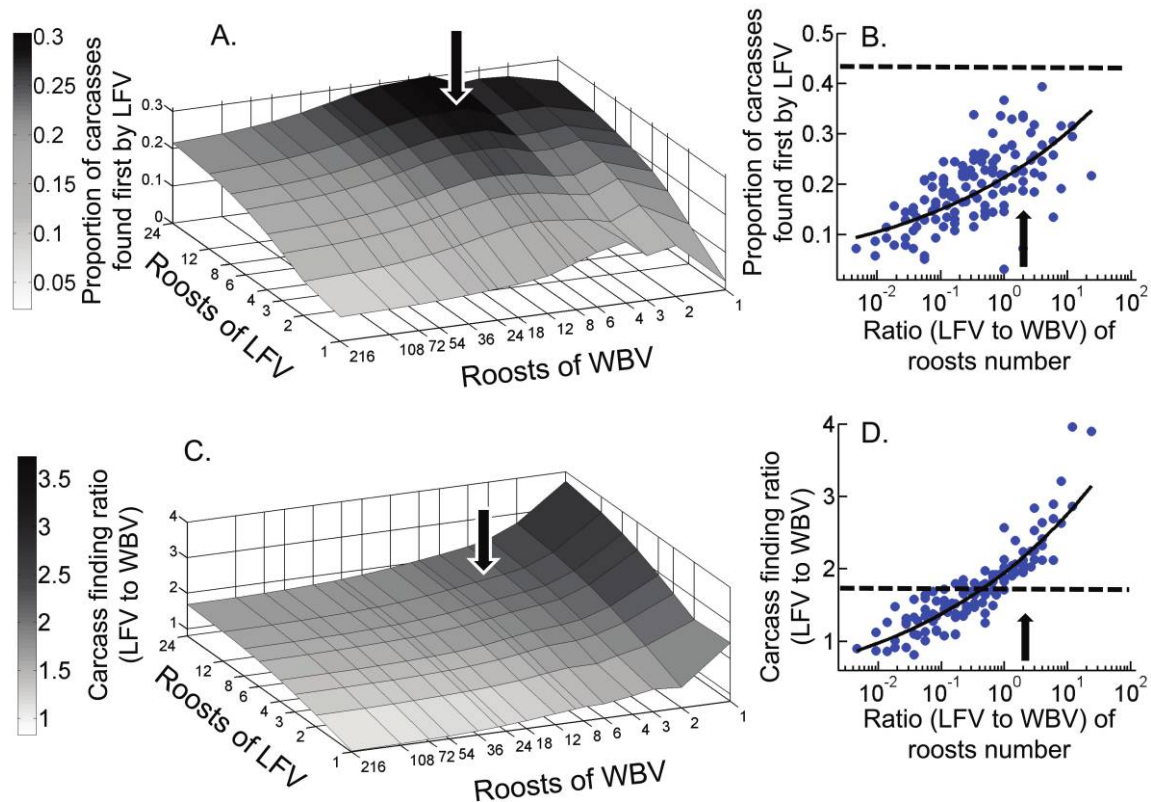
model. First, the procedure of calculating this measure: we consider only one (the first) of potentially multiple repeated detections of a carcass in the same location as a carcass detection event, thereby masking the advantage of LFVs in earlier detection of local carcasses. Second, whereas main roosts of both species are randomly located in our model, empirical evidence suggest LFV roosts might

be uniformly distributed (Pennycuik 1976), further facilitating early carcass discover by this species, and leading to the higher observed values of the first-to-find measure.

### Discussion

Our results show a significant difference in search efficiency between two species of vultures using the same





**Figure 3:** Comparisons of the effects of the number of roosts on the difference between white-backed vultures (WBVs) and lappet-faced vultures (LFVs) in two measures of search efficiency: the first to find (A, B) and the carcass detection rate (C, D). A and C show the results for communities of 24 LFVs and 216 WBVs with different combinations of roosts per species (and bird number per roost). For example, a value of 12 in the LFV axis means that the 24 LFVs are divided into 12 different roosts with 2 birds each. B and D show the results ranked by the LFV : WBV roost ratios. For example, a ratio of 6 reflects all scenarios where the number of roosts used by the 24 LFVs is sixfold the number of roosts used by the 216 WBVs. The dashed lines in B and D represents the empirical value for both measures. The black arrows point to the presumed natural situation in the study site, with roughly 2 LFVs and ~36 WBVs per roost, yielding an LFV : WBV roost ratio of 1.6.

resources and similar foraging tactics. At the individual level, these differences may be attributed to interspecific differences in morphology that affect both the perceptual and motion abilities, as related to eye size effects on detection range, and to wing loading effects on the duration of daytime available for soaring search flight. These differences can also be attributed to behavioral differences influencing efficiency through their effect on movement pattern and magnitude of central place foraging. Whereas most of these differences have already been reported in the literature (Huey et al. 1984; Bell 1991; Bartumeus et al. 2005; Pearce-Duvel et al. 2011), the effect of a searcher's spatial dispersion (resulting from different roosting behavior in our system) on search efficiency at the species level has been largely ignored (but see relevant discussion in Pennycuik 1972, 1976). Overall, our results emphasize the importance of an integrative empirical-modeling approach to address questions on search efficiency.

On the empirical side, we combined experimental carcass deployment with GPS tracking to explore the factors that potentially underlie the interspecific variation in different measures of search efficiency between lappet-faced and white-backed vultures. Both methods clearly confirmed previous evidence (Kruuk 1967; Pennycuik 1972) for higher search efficiency of LFVs compared to that of the considerably more numerous WBVs. We emphasize that our food supply experiments were limited to carcasses of large ungulates, selected to examine the most pronounced competition between the two species. Hence, the observed differences in search efficiency are unlikely to reflect differences in dietary preferences (e.g., carcass size) between the two species. On the modeling side, the results of our simulation model contradict the commonly held explanation asserting that LFVs search more efficiently because they intensively search a rather restricted area (Kruuk 1967; Pennycuik 1972; Houston 1975): a variant

LFV searching over larger areas has a significantly higher carcass-detection rate than the wildtype, and vice versa for a locally searching WBV variant. This implies that local search is in fact disadvantageous and that LFVs search more efficiently than WBVs despite this disadvantage. Thus, the higher search efficiency of LFVs should be attributed to other behavioral or morphological characters. We found that the higher search efficiency of LFVs can be attributed to their higher visual ability due to their ~1.4-fold larger eyes (leading to longer detection distances; see app. A), and to their tendency to depart from the roost earlier than WBVs presumably due to their lower wing loading (allowing them to use weaker thermals; Pennycuik 1972, 1976). Surprisingly, differences in the shape of the species movement patterns were not pronounced and had no significant explanatory power.

A growing number of studies focus on the statistical properties of the movement path (e.g., the distribution of step sizes) as strong determinants of the search efficiency (e.g., Bartumeus et al. 2005; Benhamou 2007; Edwards et al. 2007; Sims et al. 2008). It should be noted that the difference in path straightness of the two species was relatively small (0.608 vs. 0.632). Perhaps the similarity of these values represents the outcome of selection for an efficient search, given the properties of resource availability in the study ecosystem. Thus, our finding that movement-related differences between the two species do not explain the differences in search efficiency should not imply that the statistical analysis of movement paths is not worth pursuing; rather, it calls for considering not only path statistics but also relevant information about the morphology, ecology, and behavior of the study species.

#### *Social Information and Fitness Consequences of Search Efficiency*

Locating resources is only the first step in a sequence of events leading to resource consumption and consequent fitness gains. Our results show that LFVs are superior in finding the carcasses, yet in many cases LFVs avoid landing at the carcass site (fig. 1). Furthermore, it is common to see vultures of both species waiting in the vicinity of the carcass for a long while before approaching. This behavior probably reflects a trade-off between energy gain and risk avoidance, as vultures are vulnerable on the ground where they face predation or, at least, injury by mammalian scavengers (Kendall et al. 2012). These risks are particularly important in our study site where anthrax mortalities subsidize the mammalian scavengers and sustain a very dense jackal population (and presumably other species; Bellan et al. 2012). The WBVs forage in large groups and therefore gain “safety by numbers” during the handling phase of the carcass where they frequently mob other species (e.g.,

jackals), whereas the LFVs that forage in pairs must wait for the WBVs to aggregate before landing or approaching the carcass. Therefore, in contrast to other ecological situations, where higher search efficiency may lead to enhanced food consumption (e.g., Dias et al. 2009) and even to competitive exclusion of inferior species (Carrete et al. 2010), such exclusion is unlikely to be the case in our study system. In fact, if landing itself is fraught with danger, a LFV that finds first a carcass may benefit by accelerating recruitment of other (mostly white-backed) vultures to the site to ensure sufficient vulture numbers at the site to satisfy needs. Field observations of LFVs stretching out their legs while soaring above a carcass were proposed to represent a behavior aimed at slowing down (Pennycuik 1972; Mundy et al. 1992). Alternatively, leg-stretching behavior might be hypothesized to act as a signal for attracting other vultures to the carcass below.

In an attempt to explain his finding that LFVs first-to-find rates are higher than expected, based on their proportions in a vulture community, Kruuk (1967) suggested that LFVs search for carcasses directly, whereas the more numerous *Gyps* vultures (including WBV) rely on watching other vultures. This argument brings up social foraging and information sharing, typical of many vulture species (Houston 1974; Buckley 1996; Jackson et al. 2008) as important determinants of differential search efficiency among vulture species. Our simulation did not incorporate any mechanisms of information sharing or social foraging, mostly because the empirical quantification of such mechanisms is challenging, and partially because we did not find evidence for possible mechanisms, such as coordinated directional departure from the roost, in this study system. Moreover, most mechanisms of information sharing (e.g., local enhancement and information centers) facilitate recruitment to a previously discovered carcass, which would enhance carcass-detection rates but not the first-to-find rates. Thus, Kruuk’s argument fails to explain why WBVs, which are claimed to be more efficient in following informed vultures, are in fact inferior to LFV in carcass-detection rates. In addition, whereas Kruuk did not address the question of how LFVs directly search for carcasses, our study suggests some specific morphological features and behaviors that make LFVs more efficient in early detection of carcasses than other vulture species.

The discrepancy between LFV higher efficiency despite lack of apparent adaptive advantage and WBV inferior carcass-detection rate despite higher sociality might be explained by existing niche segregation between the two species: LFV diet includes both large and small items, whereas WBV specializes on large carcasses (Pennycuik 1972; Houston 1974, 1975; Mundy et al. 1992). Therefore, LFV search efficiency could be an adaptation to finding smaller items, whereas WBV lower carcass-detection rate might

be an incidental, and a consequence of the fact that finding larger carcasses is a much easier task that does not require the adaptations that LFVs have evolved to be efficient searchers. Alternatively LFVs' wider niche might be the consequence, rather than the cause, of their higher carcass-detection rate. Overall, deeper understanding of the co-evolutionary relationships between search efficiency and current niche utilization (a chicken and egg problem) requires more detailed data on LFV evolutionary history—of sensory traits such as visual acuity and behaviors shaping home range size, for example—than are available at this time.

#### *Methodological Limitations*

Our use of GPS tracks to estimate the carcass-detection rate measure of search efficiency relies on the assumption that carcass consumption events occur at similar frequencies in the two species. The above-mentioned diet differences, might also explain this result since LFVs' wider diet may reflect more frequent feeding opportunities. Nevertheless, both species rely on soaring flight that is energetically inexpensive compared to other (nonresting) behaviors (Ruxton and Houston 2004), and takeoff, in contrast, is energetically expensive, especially in the flat terrain of our study region. As discussed above, landing (on the ground) is also dangerous in terms of predation or injury. Thus, vultures probably limit day stops to those with some expected gain, presumably mostly related to resource consumption events.

Our model is simplistic in many ways, including the use of a spatially homogeneous landscape and ignoring many sources of variation, such as seasonal patterns and intraspecific variation. Moreover, the effects of flight speed and elevation are not included in the model. These two properties are the most pronounced differences between the two species, but they counteract each other with respect to angular velocity, which is similar for both species (and actually slightly higher for LFV; see "Methods"). Since both species fly high above the ground, calculated angular velocities are very low in comparison to empirically quantified abilities of raptors to cope with velocities of up to  $70^\circ \text{ s}^{-1}$  (Land 1999; Jones et al. 2007), suggesting that the issue of the smearing of the picture on the retina is not a limiting factor for our study system. Nevertheless, both flight speed and elevation might affect search efficiency in other ways. Flight elevation is likely to affect finding probability independent of its effect on angular velocity by imposing a trade-off between in-depth viewing (lower elevations increase visual resolution of particular objects) and wider coverage (higher elevations enabling larger areas to be scanned). Similarly, if the carcass-finding probability is limited by cognitive abilities and not only by visual

mechanics, LFVs' slower flight speed might be more beneficial for finding items. LFVs compensate for reduced distances associated with lower speed by allocating more search time, allowing them to cover the same distances daily.

#### *Applied Implications of Search Efficiency Differences*

The remarkable differences in search efficiency between species consuming similar resources may lead to dependency and to a producer-scrounger game where one species relies on the other for helping to find its food. In fact, it was suggested that *Gyps* vultures rely on other birds for carcass finding both at the intraspecific (Kruuk 1967) and interspecific levels, whereas WBVs rely on white-headed vultures (in places where this species occurs) and to a lesser degree on LFVs (Houston 1975). Our results support this hypothesis and stress the unique roles the two species play in the sequence of events leading to carcass consumption. A priori LFVs are more prone to local extinction because of their smaller population size. Indeed, this species is classified "vulnerable" by the International Union for Conservation of Nature, due to declining populations and local extinctions in many parts of their distribution area (Shimelis et al. 2005). The dependency of WBVs on LFVs for finding resources suggests that the disappearance of the latter may impair the fitness of the former in these areas.

These findings emphasize that effective conservation efforts should be based on good knowledge of the role of local species in the community and on identifying the key species whose removal might generate cascading effects. Conservation efforts could also be improved by better understanding the key morphological traits and behaviors underlying the functional role of different species in a community. The strength of the study reported here is in linking a field assessment of interspecific variation in species search efficiency with the model-based exploration of the factors responsible for these differences. This combination of empirical and modeling work facilitates our understanding of the factors influencing search efficiency and highlights the need for studying foraging behavior of free-ranging animals in their natural settings in order to fully understand animal search patterns. Following the general principles of the movement ecology paradigm (Nathan et al. 2008), we thus advocate combining theoretical and empirical studies of animal foraging to consider the internal constraints imposed by a searcher's morphology and behavior on its perceptual range and search time allocation, as well as the effect of spatial dispersion on searchers.

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### APPENDIX A

#### Assessment of Visual Acuity and Carcass Detection Range

Interspecific differences in the detection range of the resources may have profound effect on the search efficiency (Jones et al. 2007; Scharf et al. 2009). We parameterized detection range values used in the model through calculations of visual acuity, defined as the ability to distinguish between two adjacent points, using morphological eye measurements. Given that the two species are functionally and phylogenetically closely related, we assumed that their visual acuity should scale along the same allometric curve of body to eye size. Checking this assumption requires an ocular study that is beyond the scope of this study.

Corneal diameters were measured from close-up photographs of captured individuals. The results showed that LFV ( $n = 6$ ) have larger corneal diameter than WBV ( $n = 10$ ), with values of  $16.97 \pm 0.94$  mm (mean  $\pm$  SE) and  $12.50 \pm 0.46$  mm, respectively. Additionally, we found that the eye shape of the two species is similar with a ratio of approximately 1.4 between corneal width and height. The mean corneal diameter (CD) values for each species

were translated to axial length (AL), using Hall's and Ross's (2007) formula for diurnal animals:

$$AL = CD \times 10^{-0.22},$$

implying axial length of  $28.14 \pm 1.55$  and  $20.71 \pm 0.75$  mm for LFV and WBV, respectively. These values were used to calculate the visual acuity (VA) using Kiltie's (2000) allometric function:

$$VA = 10^{(1.42 \times \log_{10}(AL) - 0.11)},$$

found to be  $88.9 \pm 7.2$  cycles  $m^{-1}$  for LFV and  $57.5 \pm 2.9$  for WBV. These values of visual acuity indicate that LFV can see a 2-m object from  $10,178 \pm 821$  m and WBV from  $6,594 \pm 340$  m. Since the carcass distance in the model is a two-dimensional projection, the detection ranges listed above were corrected to account for species-specific mean flight elevations (431.2 and 506.2 m above ground, respectively), leading to a reduction of a few meters in the calculated detection distance. Hence, detection range values of 10,173 m for LFV and 6,579 m for WBV were used for the model. Although the actual detection range is probably considerably overestimated, our measure is valid for comparing the relative acuity of the two species.

### APPENDIX B

#### Comparing Movement Properties between Species Using the Ratio Estimate Technique

The use of a simple  $t$ -test is not appropriate for comparison between the two species in the various movement properties mentioned in the main text because significant differences among individuals in tracking duration are not accounted for. Therefore, we compared the two species using a modified  $t$ -test, called the ratio estimate (Cochran 1977), where tracking duration determines the relative weight of each individual. This prevents the unwanted situation where samples with shorter tracking duration (and therefore less reliability) are overrepresented.

In the following paragraph we provide the detailed procedure and an example where daily displacement is compared between species following Cochran's (1977) procedure. First, we wish to estimate the ratio for each case,  $R = \mu_x/\mu_y$ , where  $\mu_x$  and  $\mu_y$  are two expectations of the two random variables  $X$  and  $Y$ .

Let  $(x_1, y_1), (x_2, y_2), \dots, (x_n, y_n)$  be a random sample of  $n$  observations from the joint distribution of  $X$  and  $Y$ . Ratio  $R$  can be estimated by the ratio of the sample means of  $X$  and  $Y$ :

$$\hat{R} = \frac{\bar{x}_n}{\bar{y}_n} = \frac{(1/n) \sum_{i=1}^n x_i}{(1/n) \sum_{i=1}^n y_i} = \frac{\sum_{i=1}^n x_i}{\sum_{i=1}^n y_i}.$$

Using Fisher's asymptotic variance approach, we get an estimate for the variance of  $\hat{R}$ :

$$\hat{\text{Var}}(\hat{R}) \cong \frac{n}{(n-1)(\sum_{i=1}^n y_i)^2} \times \left[ \sum_{i=1}^n x_i^2 + \hat{R}^2 \sum_{i=1}^n y_i^2 - 2\hat{R} \sum_{i=1}^n x_i y_i \right]$$

and

$$\hat{\text{SE}}(\hat{R}) = \sqrt{\hat{\text{Var}}(\hat{R})}$$

Comparing the ratios between two cases ( $R_1$  and  $R_2$ ) is done by a  $t$ -statistic with  $df$  degrees of freedom:

$$t = \frac{(\hat{R}_1 - \hat{R}_2)}{\sqrt{(\hat{\text{Var}}(\hat{R}_1) + \hat{\text{Var}}(\hat{R}_2))}}$$

and the number of degrees of freedom is approximated using Welsh method. Let

$$c = \frac{\hat{\text{Var}}(\hat{R}_1)}{\hat{\text{Var}}(\hat{R}_1) + \hat{\text{Var}}(\hat{R}_2)}$$

$$df \approx \frac{1}{\left[ \frac{c^2}{n_1 - 1} \right] + \left[ \frac{(1 - c)^2}{n_2 - 1} \right]}$$

Note that contrary to the common case where the degrees of freedom depend only on the  $n_1$  and  $n_2$  and on the number of estimated parameters, here the degrees of freedom depend on  $\text{Var}(\hat{R})$  and may have different noninteger values for different comparisons of using the same group sizes.

In our example the ratios are the mean daily displacement for each species (notated by  $R_T$  for *Torgos* and  $R_G$  for *Gyps*), with  $x_i$  being the sum of daily displacements (in km) for the  $i$ th individual out of  $n$  and  $y_i$  being the number of tracking days for this individual.

For *Torgos*:

$$n_T = 3, \sum_{i=1}^3 x_i = 31,626.51 \text{ km},$$

$$\sum_{i=1}^3 y_i = 947 \text{ days},$$

$$\hat{R}_T = \frac{\sum x_i}{\sum y_i} = \frac{31,626.51}{947} = 33.39 \text{ km} \times \text{day}^{-1},$$

$$\hat{\text{Var}}(\hat{R}_T) \cong 68.13.$$

And for *Gyps*:

$$n_G = 10, \sum_{i=1}^{10} x_i = 94,589.89 \text{ km},$$

$$\sum_{i=1}^{10} y_i = 2,138 \text{ days},$$

$$\hat{R}_G = 44.24 \text{ km} \times \text{day}^{-1},$$

$$\hat{\text{Var}}(\hat{R}_G) \cong 7.219,$$

$$t = \frac{(\hat{R}_T - \hat{R}_G)}{\sqrt{(\hat{\text{Var}}(\hat{R}_T) + \hat{\text{Var}}(\hat{R}_G))}}$$

$$= \frac{(33.39 - 44.24)}{\sqrt{(68.13 + 7.219)}}$$

$$= \frac{-10.84}{8.68} = -1.249,$$

$$df = \frac{1}{\frac{[(68.13)/(68.13+7.219)]^2}{(3-1)} + \frac{[(7.219)/(68.13+7.219)]^2}{(10-1)}} = 2.44,$$

$$\text{Pr}(t_{2.44} < -1.249) = 0.1689.$$

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