

# Moving beyond Curve Fitting: Using Complementary Data to Assess Alternative Explanations for Long Movements of Three Vulture Species

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Submitted February 20, 2014; Accepted July 14, 2014; Electronically published January 8, 2015

Online enhancements: appendixes.

**ABSTRACT:** Animal movements exhibit an almost universal pattern of fat-tailed step-size distributions, mixing short and very long steps. The Lévy flight foraging hypothesis (LFFH) suggests a single optimal food search strategy to explain this pattern, yet mixed movement distributions are biologically more plausible and often convincingly fit movement data. To confront alternative explanations for these patterns, we tracked vultures of three species in two very different ecosystems using high-resolution global positioning system/accelerometer tags accompanied by behavioral, genetic, and morphological data. The Lévy distribution fitted the data sets reasonably well, matching expectations based on their sparsely distributed food resources; yet the fit of mixed models was considerably better, suggesting distinct movement modes operating at three different scales. Specifically, long-range forays (LRFs)—rare, short-term, large-scale circular journeys that greatly exceed the typical foraging range and contribute to the tail-fatness of the movement distribution in all three species—do not match an optimal foraging strategy suggested by the LFFH. We also found no support for preferred weather conditions or population genetic structure as alternative explanations, so the hypothesis that LRFs represent failed breeding dispersal attempts to find mates remains our most plausible explanation at this time. We conclude that inference about the mechanisms underlying animal movements should be confronted with complementary data, and suggest that mixed behavioral modes likely explain commonly observed fat-tailed movement distributions.

**Keywords:** movement ecology, Lévy flight foraging hypothesis, sex-biased dispersal, fat-tailed step-size distribution, wildlife biotelemetry, 3-D accelerometers.

## Introduction

Movement of organisms plays a key role in a wide range of evolutionary and ecological processes and receives increasing attention (Holyoak et al. 2008; Nathan et al. 2008a; Giuggioli and Bartumeus 2010). Long-range movements may be infrequent during an individual's lifetime, but such movements are of particular interest as key drivers of metapopulation dynamics, colonization, population spread, and biological invasions (Nathan et al. 2008b). Movement patterns are typically shaped by complex interactions among various internal and external factors. Yet our ability to dissect the different factors and identify the underlying mechanisms are often hampered by methodological limitations (Nathan et al. 2008a, 2012).

Long-range movements, well beyond the spatial scale of typical movements, occur in many animals, giving rise to probability density functions of observed step sizes with fatter tails than Gaussian or Exponential distributions. Consequently, distributions generated from Lévy flights or composite Brownian walks commonly provide better fits to step-size data (Bartumeus et al. 2005; Sims et al. 2008; Santos et al. 2009; Bazazi et al. 2012; Humphries et al. 2012; Jansen et al. 2012). The generality of fat-tailed distributions across a large variety of animals, environments, and movement types (Viswanathan et al. 1999; Sims et al. 2008; James et al. 2011; Humphries et al. 2012) has led to formulation of the Lévy flight foraging hypothesis (LFFH). The LFFH asserts that Lévy-like step-size distributions reflect an optimal search strategy in which a forager switches between exponentially bounded (Brownian) and highly directional (ballistic) movement modes, thus allowing for both efficient short-step local searches and

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Am. Nat. 2015. Vol. 185, pp. E44–E54. © 2015 by The University of Chicago. 0003-0147/2015/18502-55305\$15.00. All rights reserved.

DOI: 10.1086/679314

long-step displacement far beyond the intensively searched zone (Viswanathan et al. 1999; Lomholt et al. 2008; Bénichou et al. 2011; Bazazi et al. 2012). The ongoing debate on the LFFH refers to various methodological concerns (Edwards et al. 2007; Edwards 2011; James et al. 2011) and to the validity of the model for real-life conditions, where external factors affect the search pattern (Benhamou 2007; Reynolds 2008; Petrovskii et al. 2011; Jansen et al. 2012; Palyulin et al. 2014). Some of the LFFH's initial prerequisites have now been relaxed (e.g., resource distribution; Lomholt et al. 2008) and applied for study systems ranging from albatrosses to *Escherichia coli* (Bénichou et al. 2011). Recently, however, it was suggested that the LFFH reflects intrinsic behavior in the absence of external information (Bazazi et al. 2012; Salvador et al. 2014).

The need to carefully infer mechanisms from patterns is well established in ecology (Levin 1992). A good fit of an observed step-size distribution for a fat-tailed function might not necessarily entail support for the LFFH (Benhamou 2007; James et al. 2011; Jansen et al. 2012), because other mechanisms, separately or jointly, can give rise to the same pattern (Benhamou 2007; Petrovskii et al. 2011; Jansen et al. 2012). To date, studies arguing for (or against) the LFFH have seldom provided independent evidence to support (or refute) this hypothesis (but see Humphries et al. 2012). The active debate on this topic emphasized the need to develop in-depth understanding of the mechanisms and motivation underlying animal movements in general (Nathan et al. 2008a) and fat-tailed step-size distributions in particular. Here we propose that this challenge can be addressed by analyzing independent data sets complementary to the movement data in a manner that examines evidence for or against alternative mechanisms. We illustrate this approach by focusing on a particular type of long-range movement known as long-range forays (LRFs), which effectively contribute to the fatness of step-size distributions.

LRFs are relatively short-term spatially extended movements in which individuals depart from their regular foraging area, travel to remote locations, and return to the original core area (here we document LRFs of a few hundred kilometers over periods of days to weeks, but both temporal and spatial scale may differ significantly among study systems). LRFs are typically studied in the context of foraging, suggested to reflect an adaptive exploratory strategy (Conradt et al. 2003) for exploiting remote food patches (e.g., Viswanathan et al. 1999; Reynolds 2008; Humphries et al. 2012; López-López et al. 2013) and possibly other resources. Nevertheless, LRFs might also be part of fundamentally different movement phenomena, such as migration and dispersal. LRFs resemble migratory journeys in having a loop pattern and differ in lacking intraspecific synchronization and distinct temporal struc-

ture characterizing migration; these differences, however, are not sufficient to discriminate LRFs from migration, because LRFs might reflect age- and sex-biased (partial) migration (Lundberg 1988). The lack of intraspecific synchronization, in turn, is typical of both LRFs and dispersal events, but successful dispersal generates a unidirectional path from a natal or breeding site to a new breeding location (Greenwood and Harvey 1982) rather than a loop pattern. Individuals returning to their original natal/breeding site after failed dispersal attempt, however, could generate a similar loop pattern.

Old World vultures are obligate scavengers that cover vast areas while searching for spatiotemporally unpredictable sparsely distributed carcasses. Vultures use thermals and orographic winds for energetically inexpensive soaring flight (Mundy et al. 1992; Ruxton and Houston 2004) and rely on social information sharing for food finding (Jackson et al. 2008; Monsarrat et al. 2013). Recently, vultures were suggested as yet another example of the LFFH, with long movements interpreted as an adaptive search for scarce resources (López-López et al. 2013): fixed time intervals, rather than reorientation steps used in this analysis, however, confound interpretation of the results. Natal dispersal of vultures, like other raptors, is well known (Kenward et al. 2001; Le Gouar et al. 2008). Adult vultures are typically considered local residents, and their long-range movements, and particularly LRFs, have been scarcely documented and investigated.

The goal of this study is to explore movement patterns in free-ranging vultures, particularly long-range movements and LRFs, and to assess potential underlying mechanisms. In testing the LFFH, we fitted several models (single and mixed-probability density functions) to the observed step-sized distributions of movement data from adults of three vulture species tracked in two very different ecosystems, all of which were found to perform LRFs. To elucidate possible mechanisms underlying this distinct behavior, we focused on our largest and most inclusive data set and used complementary behavioral, morphological, genetic, and meteorological data to assess the evidence for or against the following mechanisms that could generate LRFs: (i) optimal foraging behavior, (ii) sexual dimorphism in wing loading, (iii) meteorological conditions favoring soaring flight, (iv) genetic differentiation, and (v) search for mates and other conspecifics.

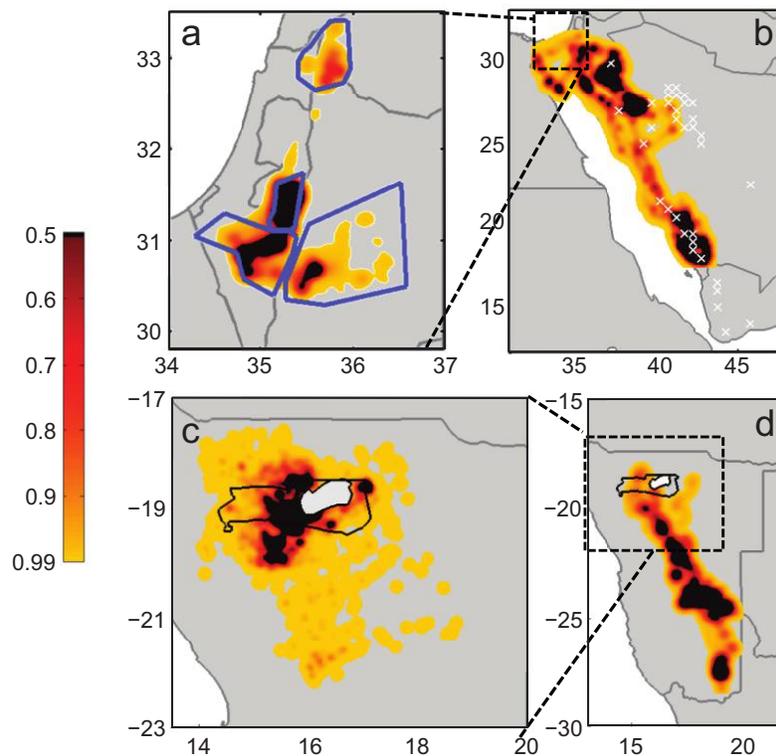
## Material and Methods

### *Field Work (Vulture Trapping and Data Collection)*

Eurasian griffon vultures (*Gyps fulvus*, Hablitzl 1783; EGVs) were tracked in Israel and surrounding countries. Their activity concentrated mostly in four subregions that differ

substantially in terrain structure and food availability: the Judean and Negev deserts in southern Israel (where supplementary food is provided), the northeastern parts of the country and southwestern Jordan (Dana nature reserve district; fig. 1a). Each EGV typically foraged and roosted mostly in one of these subregions with rather infrequent crossings among them. During the field seasons of 2008–2011, 53 adult birds were captured using walk-in traps located in the Judean and Negev deserts (31°N, 35°E) and equipped with high-resolution global positioning system (GPS) and accelerometer (ACC) tags (hereafter GPS-ACC tags). Contrasting with the intensive management system in Israel, the white-backed vultures (*Gyps africanus* Salvadori, 1865; WBV) and lappet-faced vultures (*Torgos tracheliotus* Forster, 1796; LfV) that we studied in Namibia foraged for carcasses of free-ranging ungulates in a more natural setup within and outside the Etosha National Park (19°S, 15°E). These species were trapped at the park using leg-hold traps around bait carcasses during two field seasons in 2008 and 2009, and 19 GPS-ACC tags were deployed on adult birds (five of which were on LfVs).

The GPS-ACC tags (160 g; E-OBS, Munich, Germany) were fitted in a backpack configuration and set to a 12-h duty cycle starting at 7:00 a.m. to correspond with the vulture diurnal activity pattern. Samples were taken every 10 min using two independent sensors: (i) a GPS device, providing the three-dimensional position, and the ground speed for each data point; (ii) an ACC measuring acceleration in three perpendicular axes, in bouts of 16–24 s at a frequency of 3.3 Hz for each axis. The ACC data allow estimation of energy expenditure using the overall dynamic body acceleration index (ODBA; Green et al. 2009). In addition, when combined with the corresponding GPS data and analyzed using a supervised, artificial neural network machine-learning algorithm trained with field data, the ACC data allow identification of vultures' behavior, specifically of feeding events. Collected GPS-ACC data were stored onboard until downloaded through UHF communication to a handheld receiver. For additional information regarding the study system, fieldwork, and sampling protocols, see previous publications (Nathan et al.



**Figure 1:** Kernel density estimation for all Eurasian griffon vultures (EGVs) in Israel (*a* and *b*) and for all lappet-faced vultures and white-backed vultures in Namibia (*c* and *d*). Color bars indicate increasing usage density, and X- and Y-axes show latitude and longitude, respectively, in degrees. Note the different spatial scales. Left panels (*a*, *c*) are for all non-long-range-foray (LRF) movements within home ranges, and right panels (*b*, *d*) are LRF movements. Blue polygons (*a*) indicate EGV subregions of activity, and white X symbols (*b*) indicate grid cell of known EGV colonies. The Etosha saltpan and the borders of Etosha National Park are shown by black polygons (*c*).

2012; Spiegel et al. 2013a, 2013b) and appendix A (apps. A and B are available online).

*Wing Morphology Measurements.* During the last two seasons, wing measurements were taken from GPS-tagged EGVs by photographing the spread wing against a scaling board. Wing area was determined using ImageJ software (<http://rsb.info.nih.gov/ij/>) and used to calculate wing loading given the mass (converted to weight) measurement of the same day for each individual.

*Data Analysis (Movement, Genetic, Climatic, and Behavioral Data)*

Because LFVs and WBVs shared the same region and had similar daily movement distances (Spiegel et al. 2013a) that differed substantially from the EGV movements, their tracks were combined to a single data set (hereafter, LFV-WBV). LRFs were defined as movements exceeding a minimal threshold value between mode roost location and the most distant roost (see in fig. A1; figs. A1, A2 are available online). LRFs were found in all three species and included directional outbound “commuting phase” away from the regular home range, a relatively short “wandering phase” in a remote area, and an inbound commuting phase. The EGV and LFV-WBV data sets were split into two subsets: LRF days only and non-LRF days. The utilization-distribution function was estimated separately for these two subsets using Worton’s (1989) kernel methods for these two subsets (fig. 1). For EGVs, the monthly frequency of crossings among all four subregions was compared against crossings to a fifth subregion that include all LRF roosts, covering southeastern Jordan, Sinai, and western Saudi Arabia.

*Step-Size Distributions.* Step sizes between reorientations were calculated for each data set and subset using the nonlocal turning method that defines reorientations as turns where the cumulative change of direction from the previous turning event exceeds  $\theta = 60^\circ$ . This method is commonly used because it provides a more reliable identification than local turns (Reynolds et al. 2007; Plank et al. 2013). Sensitivity analysis for the range  $40^\circ < \theta < 90^\circ$  ensured selected value did not affect our model-fitting results (table B2; tables B1–B6 are available online). Minimal step size was set to 25 m to account for GPS position errors (López-López et al. 2013), and maximal step size was set to 500 km, which is above the maximal observed daily travel distance (482 km). Five alternative models were fitted for both data sets and subsets (LRFs and non-LRFs): truncated exponential distribution (TEXP); truncated Pareto distribution (Lévy walk; TP), and three different composite Brownian walk models composed of two (CBW2),

three (CBW3), and four (CBW4) weighted exponential distributions. Parameter values were obtained through numerical solution of the maximum likelihood estimation function, following the procedures described in Jansen et al. (2012). Weighted Akaike information criterion (wAIC) was used to rank the information loss by the different models (Burnham and Anderson 2002; Jansen et al. 2012; Plank et al. 2013), and goodness-of-fit was estimated for the best model using a G-test with William’s correction and an initial bin size of 1 km (Sokal and Rohlf 1995; see Edwards 2011 for detailed binning and testing protocol).

*Weather Data Annotation.* To test whether the seasonal patterns of LRF departures were coordinated with favorable soaring conditions, we analyzed the weather conditions encountered by EGVs along their LRF commuting flights. Data from the European Centre for Medium-Range Weather Forecasts (ECMWF) was incorporated using the Environmental-Data Automated Track Annotation (Env-DATA) system (Dodge et al. 2013). Thermal uplift ( $\omega^*$ ) and tailwind assistance were calculated for GPS fixes of flying vultures with respect to vulture’s current step heading direction (Shamoun-Baranes et al. 2007). Conditions encountered en route (all LRFs occurred during September–January) were contrasted with “pseudo-LRFs” (generated by time-shifting actual LRFs to randomly selected departure dates in spring and summer; see app. A).

*Genetic Work.* We tested for genetic differences between LRF and other individuals using 11 neutral markers (microsatellites) obtained in 2011 for 125 EGV individuals in our Israeli system. Genetic differences would help support an explanation that LRFs are related to partial migration or a different origin for individuals performing this behavior. The data set included nontracked EGVs (IL,  $n = 105$ ) and GPS-tracked individuals that did (LRF,  $n = 7$ ) or did not perform LRFs during their tracking duration (non-LRF,  $n = 13$ ). EGVs from Spain were used as an outgroup (SP,  $n = 16$ ). See appendix A for further information on DNA extraction, sex determination, microsatellite selection, and data analysis tools.

*Behavioral and Energy Expenditure Analyses.* To explore possible mechanisms underlying LRF behavior, we compared several measures described below of individual EGVs among four different classes: LRF birds during (i) the LRF commuting phase (combining both outbound and inbound parts), (ii) the LRF wandering phase, (iii) a 2-week period starting after the bird returned from an LRF, and (iv) a randomly selected non-LRF bird during the same dates of the wandering phase. Specifically, we compared daily travel distance and a proxy for energy balance estimated by dividing feeding frequency (energy input, pro-

portion of days with feeding events; measured in events  $\text{day}^{-1}$ ) by mean daily ODBA (energy output; measured in units of  $g$ ). We also examined differences in roost fidelity—the probability of a vulture to return in two consecutive nights to the same roost site (defined as grid cells of  $0.03^\circ$ ; i.e.,  $\sim 9\text{-km}^2$  area). Comparisons were done through a one-way ANOVA with the Tukey-Kramer correction for multiple comparisons post hoc tests.

### Results

For the EGV data set, GPS-ACC data were retrieved from 47 EGVs (22 males, 24 females, 1 unknown sex; i.e., female fraction = 0.52) with mean ( $\pm$ SE) tracks of  $339 \pm 36$  days (range, 30–1,264 days) reflecting a total of 507,711 GPS data points and 15,966 vulture-days. Females were more likely to leave the study area, resulting in shorter tracks ( $268 \pm 55$  vs.  $421 \pm 66$  days,  $T_{44} = 2.19$ ,  $P = .033$ ). In Namibia, tracks longer than 14 days were obtained for three male LFVs (track durations: 160, 377, and 512 days) and 10 WBVs ( $254 \pm 56$  days; range, 47–534 days; 5 males, 4 females, 1 unknown sex) reflecting a total of 245,889 GPS data points collected over 3,479 days.

#### LRFs

EGV activity in the study region is concentrated in a few connected but distinct sub-regions in the mountainous parts of Israel and southwestern Jordan (fig. 1*a*). Five EGVs (four females) made six LRFs to the northern and western parts of Saudi Arabia (the southern parts of Asir Ridge), reaching as far as  $1,094 \pm 283$  km from the home range center ( $337\text{--}1,724$  km). These forays started with an outbound commuting phase of a long directional flight heading southeast to the destination area, lasting  $9.2 \pm 2.3$  days (2–17 days). At the destination area, individuals traveled around for  $46.0 \pm 9.1$  days (8–66 days) during the wandering phase, before the inbound commuting phase of  $8.5 \pm 2.5$  days (2–17 days). One additional female made two LRFs to Sinai (Egypt), where she circled the entire peninsula in a 6-day journey and repeated a very similar track 10 days after returning home (fig. 1*b*). Another tagged female was trapped in December 2010 in Saudi Arabia, presumably  $\sim 700$  km from the center of its home range, but the GPS-ACC data were not obtained. None of these EGVs was breeding during the LRF year. Wing tag observations or GPS tracks suggest that during the year preceding the LRF at least four birds bred in Israel, and at least one bird bred in Israel in the year following the LRF.

Activity areas of adult LFV and WBV were more scattered across the plains of northern Namibia, often reaching as far as central Namibia (fig. 1*c*). Two WBVs undertook

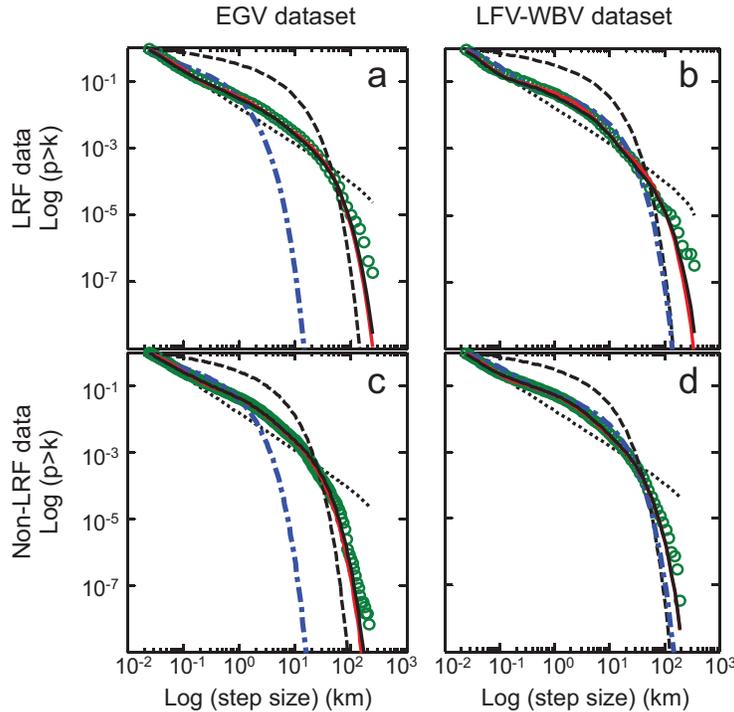
LRFs, commuting as far as 650 km to southern Namibia and wandering around for 71 and 31 days before return (fig. 1*d*). One LFV commuted south for  $\sim 7$  days and reached an area  $\sim 1,000$  km from its home range center. After 6 days, it commuted back to its home range in 4 days. The same individual repeated a similar LRF journey twice more at 3-week intervals. Altogether, LRFs accounted for 384 and 191 days (2.8% and 5.5% of the overall tracking period) in the EGV and LFV-WBV data sets, respectively. The GPS tracks are deposited in <https://www.movebank.org/> data depository (doi: 10.5441/001/1.8c56f72s).

#### Step-Size Distributions

A total of 4,531 steps out of 165,306 and 2,071 steps out of 44,198 were performed during LRFs in the EGV and LFV-WBV data sets, respectively, with step size ranging from 25 m (set as minimal step) to 291 and 456 km. Table B1 summarizes the values for selected parameters and the fit of the models. CBW4 provided the best fit in all cases ( $wAIC = 1$  vs. 0 for all alternative models), followed by CBW3 with slightly lower AIC values (fig. 2), and goodness-of-fit comparison found no significant difference between this model and all but one of the observed data sets (table B1). CBW2 and TP distribution (Lévy walk) ranked third and fourth, but TP was better in the LRF subset of LFV-WBV (fig. 2*b*). TEXP always gave the worst fit. Because the higher ranking of CBW4 over CBW3 is due to better fits at smaller rather than larger scales (see fitted movement scales in table B1), in the interests of simplicity and because of our focus on processes causing fat-tails, we center our discussion around the CBW3 fits to our data. Identifying typical movement scales ( $1/\lambda$  for CBWs) reveals that vulture's movement is a mixture of three different spatial scales: small scale movements with mean step size of 46–83 m for the different subsets, an intermediate scale with a mean of 2.1–4.6 km, and a large scale with a mean of 12.1–31.6 km. The CBW4 identified the same three scales but gave a better fit by adding another movement scale of less than 1 km (table B1). The distinct signature of the LRF subsets of both data sets was apparent in the high mean values of the two larger-scale movements (or three for CBW4) compared with the non-LRF subsets (e.g., for the largest scale, EGV: 21.5 vs. 12.1 km; LFV-WBV: 31.6 vs. 17.8 km) and the overall high mean step length of 5.6 and 7.5 km vs. 3.5 and 4.2 km, respectively.

#### Seasonality and Weather

Seasonal patterns of EGV LRFs differed markedly from those of other subregional crossings (fig. 3*a*). Although



**Figure 2:** Model fit for vultures' empirical step-size distributions (green circles). A truncated exponential probability density function (dashed black line), truncated Pareto probability density function (dotted black line), two composite Brownian walks (blue dash-dotted line), three composite Brownian walks (red solid line), and four composite Brownian walks (solid black line) are shown. EGV, Eurasian griffin vulture; LFV, lappet-faced vulture; LRF, long-range foray; WBV, white-backed vulture.

the latter occurred mostly during the summer months (with a peak in June) and were very infrequent during winter, when some of the tagged EGVs incubated their egg, LRF events occurred during the fall and early winter (September–January), with departures mostly during October and return flights until February. Tailwind assistance was similar for observed and “pseudo-LRF” events ( $0.62 \pm 0.56$  vs.  $2.34 \pm 1.35$  km h<sup>-1</sup>,  $T_6 = -1.48$ ,  $P = .19$ ; fig. 3*b*). Because summer in the region is dry and hot, thermal uplift was lower during observed LRF events compared to pseudo ones ( $1.31 \pm 0.12$  vs.  $1.75 \pm 0.10$  m s<sup>-1</sup>,  $T_6 = -3.32$ ,  $P = .016$ ; fig. 3*c*), suggesting that the LRFs commenced despite unfavorable soaring conditions.

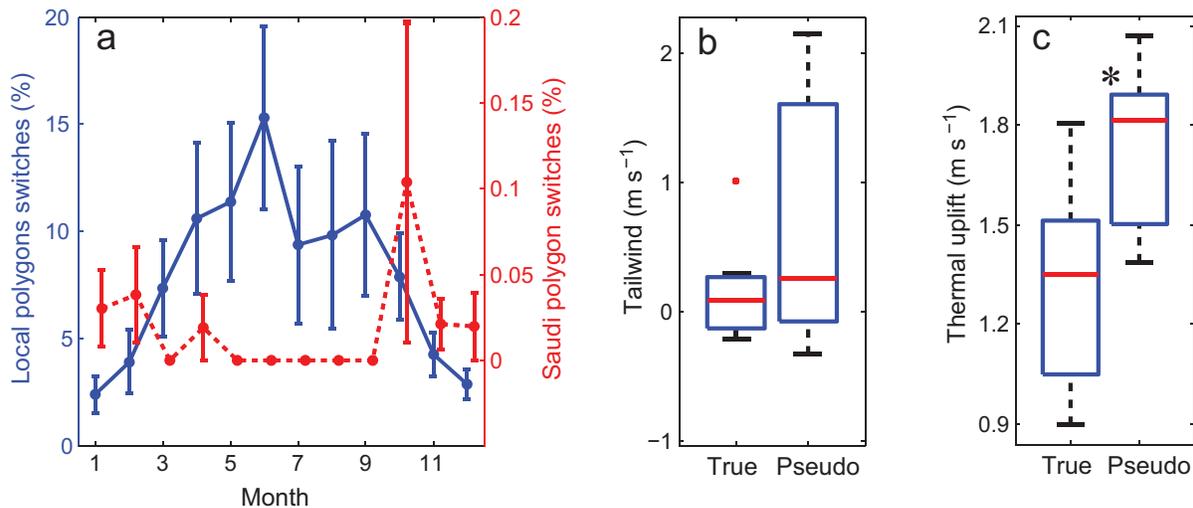
#### Genetic Analysis

Microsatellite analysis revealed no significant genetic structure for EGVs among vultures arranged in three different groups (LRF, non-LRF, and IL; see genetic diversities in Israel and Spain; tables B3 and B4, respectively), which suggests that LRF individuals do not differ from other vultures sampled in Israel (table B5). This result is also supported by the principal component analysis, in which the first three axes explain 58.0% of the genetic variation

(21.6%, 19.7%, and 16.7% for X, Y, and Z, respectively) and no spatial aggregation of individuals within or between groups is observed (see fig. A2).

#### Behavioral Analysis

For the EGV data set, the daily travel distance was significantly higher during LRF commuting and wandering compared with the after-return period or non-LRF individuals ( $F_{3,22} = 15.7$ ,  $P < .001$ ; fig. 4*a*), emphasizing the uniqueness of LRFs in comparison to regular movements. The energy balance proxy was lower during the commuting phase compared with all other categories, although the difference from the LRF wandering phase is not significant ( $F_{3,22} = 4.9$ ,  $P = .001$ ; fig. 4*c*). Because lower values indicate higher energy expenditure in relation to feeding frequency, these results suggest that vultures experience unfavorable energetic balance during LRFs, in addition to the longer time spent airborne. By definition, the probability of two consecutive nights in the same roost is zero during the commuting phase (except for a few rare cases of back-tracking during commuting). However, this probability was also very low during the LRF wandering phase ( $F_{3,22} = 11.4$  sin,  $P = .001$ ; fig. 4*e*), suggesting that EGVs



**Figure 3:** Seasonal dynamics and the effect of climatic conditions on long-range forays (LRFs) of Eurasian griffon vultures. *a*, The proportions of crossings among subregions (fig. 1*a*) in each month are shown by the solid blue line, whereas the proportions of crossing to the LRF subregion are shown by the dashed red line (see text for details). Error bars represent SE of intraspecific (or between events) variation. In contrast to subregional crossings that were most frequent in the summer, LRFs occurred mostly during fall and early winter. Tailwind assistance (*b*) and thermal uplift strength (*c*) across the LRF track are compared between two cases: during the LRF outbound commuting phase (True), and during randomly selected dates at the same locations (Pseudo). Boxes are the lower and upper quartiles, the median is shown by the red line, whiskers indicate the range of 1.5 interquartile distances, and the red cross indicates one outlier. The asterisk indicates a significant difference.

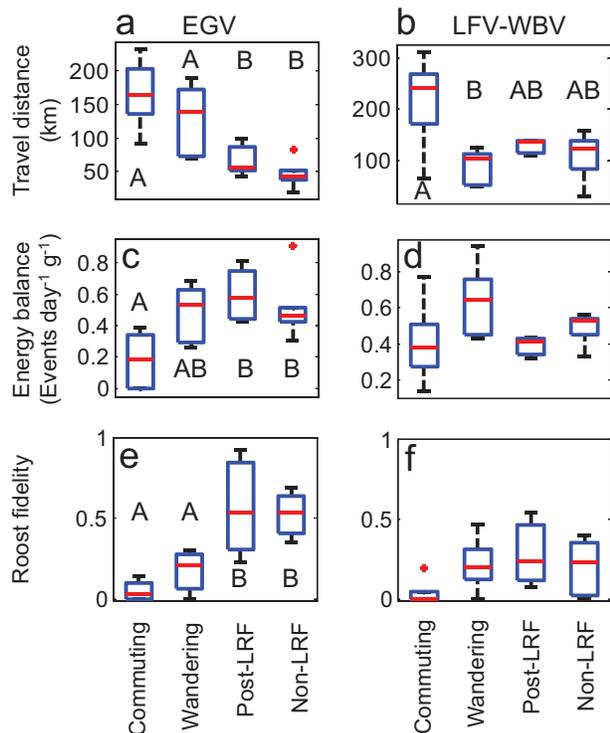
also alternate between roosts more frequently during LRF while wandering in the destination area, as opposed to the high roost fidelity in the home range. For the LRV-WBV data set, daily travel distance during LRF commuting was higher than in other phases, although post hoc comparison suggests that this difference is significant only when compared with the wandering phase ( $F_{3,14} = 4.5$ ,  $P = .02$ ; fig. 4*b*). None of the differences in energy balance or roost use were significant for this data set ( $F_{3,14} = 1.9$ ,  $P = .16$ ; fig. 4*d*;  $F_{3,14} = 2.0$ ,  $P = .15$ ; fig. 4*f*).

#### Wing Morphology

Wing loading data were obtained for 8 female and 15 male EGVs, including 3 of the LRF individuals. Wing area did not differ between sexes ( $0.792 \pm 0.019$  vs.  $0.791 \pm 0.011$  m<sup>2</sup>,  $T_{df=13} = 0.14$ ,  $P = .4$ ), but females were heavier ( $8.51 \pm 0.19$  vs.  $7.85 \pm 0.16$  kg;  $T_{df=13} = 2.9$ ,  $P < .01$ ), hence had a significantly higher (8%) wing loading ( $10.77 \pm 0.30$  vs.  $9.96 \pm 0.20$  kg m<sup>-2</sup>;  $T_{df=13} = 2.3$ ,  $P = .039$ ). Although the sample size of LRF EGVs is too small for a proper comparison, these birds had wing loading of 11.5, 11.3, and 10.6 kg m<sup>-2</sup>, which are typical values for this species.

#### Discussion

Analyses of extensive high-resolution GPS tracking data sets obtained from free-ranging adult vultures in two very different ecosystems reveal that vulture movements produce a fat-tailed step-size distribution (fig. 2). In all three species, we found evidence for long-range forays (LRFs; fig. 1) that contribute significantly to the fatness of these step-size distributions (table B1). These LRFs were in the form of rather infrequent return trips that include directional outbound commuting phase away from the regular home range, a relatively short wandering phase in a remote area, and an inbound commuting phase. Using independent complementary behavioral, morphological, genetic, and meteorological data, we rejected the following alternative mechanisms as explanations for LRFs: (i) optimal foraging was rejected, because LRF individuals flew longer distances, expended more energy, and ate less frequently (fig. 4); (ii) wing-loading measurements do not support morphological differences facilitating LRF behavior; (iii) wind conditions and thermal availability during LRF events were less favorable for soaring compared to other parts of the year (fig. 3); (iv) genetic analysis suggests that LRF individuals cannot be regarded as immigrants and are genetically indistinguishable from non-LRF individuals (fig. A2). In contrast, female sex bias, distinct seasonal pattern, and frequent roost alternation during LRFs wan-



**Figure 4:** Comparison of vulture behavior during and after long-range forays (LRFs) for the Eurasian griffon vulture (EGV) and the lapet-faced vulture and white-backed vulture (LFV-WBV) data sets. The upper panels (*a*, *b*) represent the daily travel distance. The middle panels (*c*, *d*) show a proxy of energy balance (feeding frequency divided by overall dynamic body acceleration index; see text). The lower panels (*e*, *f*) represent the probability of using the same roost for two consecutive nights. Each metric is calculated for two distinct phases of LRF (commuting and wandering), compared with the post-LRF period calculated for 2 weeks immediately after return, and to a randomly selected non-LRF individual during the same period of the LRF wandering phase (non-LRF). Error bars represent SE, and capital letters are statistically different groups using one-way ANOVA with correction for multiple comparisons.

dering phase suggest that female EGVs search for a mate at remote colonies before the breeding season; hence their LRFs might represent unsuccessful breeding dispersal attempts.

#### *LRFs and Their Explanations in Vultures and Other Animals*

Vultures are known for their large home ranges and long daily movements (Mundy et al. 1992; Monsarrat et al. 2013; Lambertucci et al. 2014). Yet, the LRFs described here are essentially different from the typical day-to-day behavior. Similar LRFs to those reported here have been documented for adult EGVs in Spain and France (García-Ripollés et al. 2011; Monsarrat et al. 2013) and for LRFV

and WBV in southern and Eastern Africa (Kendall and Virani 2012) and also for other animals, including wolves in Canada (Mech and Cluff 2011) and female loggerhead turtles in Greece (Schofield et al. 2010). Although Conradt et al. (2003) discussed infrequent dispersal LRF behavior in butterflies, most studies have considered LRFs as movements aimed to obtain favorable resources (e.g., Pinaud and Weimerskirch 2005; García-Ripollés et al. 2011; López-López et al. 2013). However, the underlying assumption that these LRFs are beneficial in terms of energetic intake rate has rarely been tested (Humphries et al. 2012). Here we explore a few alternative mechanisms by using various complementary data sets.

Although all of the above-mentioned LRF-like examples refer to adult animals, there are also examples of similar long movement executed by juveniles, including immature birds of several vulture species (e.g., WBVs, black and bearded vultures; Gavashelishvili et al. 2012; Margalida et al. 2013; Phipps et al. 2013). Similarly, in an ongoing study of EGVs in Israel, we find that almost all juveniles perform long migratory movements to wintering grounds in Eastern Africa or Southern Saudi Arabia, possibly to explore potential natal dispersal sites. These movements resemble the LRFs of adults in their spatial scale and in the timing of departure, but not in duration and frequency. This suggests that adults performing LRFs might have previous information on vulture colonies at these remote areas. Thus, in contrast to a “true navigation” context (navigation in unfamiliar areas), LRFs might represent a memory-based navigation. This is supported also by the observed similar (and high) directionality during both outbound and inbound commuting phases and by the documented examples of reoccurring LRFs to the same destinations. Indeed, all LRF wandering phases occurred within hotspots of EGV breeding colonies at Saudi Arabia (fig. 1*b*; Jennins 2010). It is possible that the two LRFs around the Sinai Peninsula (by the same bird, 3 weeks apart) may represent incomplete attempts to cross the Gulf of Suez on the way to known sites in eastern Africa.

Vultures are known to form mixed-aged flocks (Mundy et al. 1992), and in two cases we documented joint flight of two GPS-tagged EGVs, an adult and a juvenile, for some part of the LRF commuting. Therefore, it might be possible that LRFs are part of a postfledging “training” in which adult (female) vultures escort young birds on exploratory forays across large spatial scales (van de Castele and Matthysen 2006), yet such advanced behavior has not yet been described in any vulture species. LRFs might also represent investment in sampling habitat suitability in remote areas as a strategy for coping with environmental unpredictability (Stephens and Krebs 1986; Klaassen et al. 2006), or a search for a unique resource (e.g., a salt or a nutrient) missing in the regular diet (Stephens and Krebs 1986), but

these alternative explanations do not match such features of LRF as the observed sex bias and seasonality.

The variation in the spatial extension and wandering phase duration (a few days to 2 months) between different LRFs might suggest that different forays have different motivations. Yet this finding does not rule out the hypothesis that vultures (females in EGVs) commute to remote colonies in search of potential mates, presumably to commence a breeding cycle in these sites. Although this hypothesis cannot be exhaustively tested with the available data, it is supported by three lines of evidence. First, in contrast to other subregional movements that peak during the summer when soaring conditions are most favorable, LRF individuals departed mostly during fall and travelled vast areas during winter, when such conditions are much less favorable (fig. 3). Second, in contrast to the high roost fidelity characterizing EGVs in their home range, LRF individuals have frequently altered their roost during the LRF wandering phase (fig. 4e), possibly in search of receptive males. It is possible that some of the departing female EGVs have settled at the destination site, turning these journeys into successful breeding dispersal events (Greenwood and Harvey 1982). Such incidences cannot be detected by tracking devices used in this study, which require short-range UHF download, but this suggestion could explain the shorter tracking durations and higher loss rate of tagged females. In this scenario, females that failed to establish a breeding pair at the remote area are expected to return to their home range, where abundant food resources are provided in artificial feeding stations, thus turning unsuccessful breeding dispersal attempts into LRFs. The rarity of LRF events might be explained by the high costs associated with this behavior, which include direct energetic costs, cost of missed breeding opportunities, and risks associated with leaving a familiar home range.

Interestingly, despite apparent balanced sex ratio and sex-indifferent survival in the EGV population (Schohat et al. 2012), this hypothesis concurs with the relatively low number of breeding attempts (compared with the population size), the low breeding success of EGV in Israel, and the unexplained observations of the rather frequent unattended egg laying in the well monitored Gamla breeding colony. The evidence for reciprocal LRFs, in which EGV from Saudi Arabia, where colonies also suffer from massive reductions (Jennins 2010), visit Israel, may also support this hypothesis (see app. A). The scenario proposed here (which is based on incomplete evidence) calls for further investigation of the effective male shortage in Israel and Jordan (e.g., fertility tests and more elaborate drug tests of supplied carcasses) and the fate of adult EGVs undertaking long-range movements. Although complementary data are more limited for the LRVs and WBVs, the se-

quence of three LRFs performed by the same LRV within 2 months is also likely to reflect social motivation rather than other explanations.

Overall, despite their infrequency, LRF movements might be disproportionately important for various ecological processes at the population level and explain the wide-scale connectivity among broadly spaced vulture populations reported here and elsewhere (Le Gouar et al. 2007). LRFs also highlight the importance of developing large-scale conservation plans to preserve the decreasing vulture populations. Because EGV routinely cross international borders, especially during LRFs (Egypt, Israel, Jordan, and Saudi Arabia), effective conservation plans that account for their movement scale demand comprehensive international collaborations.

#### *Animal Movement Distribution as a Product of Mixed Behaviors*

The fact that the LRFs we observed appear to contrast optimal foraging expectations (regardless of the validity of the mate-search hypothesis) highlights the need to proceed beyond phenomenological curve fitting toward more mechanistic analyses of movement. Studies addressing the question of whether animal movement conforms to Lévy walk or other fat-tailed distributions and the adequacy of different curve-fitting methodologies statistics (Edwards 2011; James et al. 2011) should explicitly acknowledge the fundamental difficulty of inferring mechanisms from patterns. In the spirit of Karl Popper in solving the inverse problem of identifying the mechanisms that produced a particular set of observed data, one can only disprove possible explanations that do not fit the facts well and identify the best explanation for the observed data among the ensemble under study, recognizing that many other mechanisms might also be acting in concert.

In this vein, we argue that LFFH-like expectations, that a single mechanism could explain movements at multiple scales covered by a fat-tailed step-size distribution, should be confronted by alternative explanations that fat-tailed step-size distributions are derived from multiple mechanisms operating at different spatial scales (Benhamou 2007; Jansen et al. 2012), with the most plausible mechanism(s) at each scale awaiting identification. Investigating such alternative explanations requires the use of evidence independent of the movement track to contrast scale-invariant single-mechanism hypotheses (such as LFFH) with hypotheses arguing for multiple mechanisms operating across different scales. The LFFH may still serve as an adaptive template for intrinsic motives governing reorientations (or stops) in search without any extrinsic information (Bazazi et al. 2012; Salvador et al. 2014). Overall, the required paradigm shift advocated in this study for

animal movement research resembles the shift undertaken over the last decade in plant dispersal research, which moved from phenomenological approaches that assumed a single dispersal vector to mechanistic approaches that incorporated the joint and often sequential operation of multiple vectors (Nathan et al. 2008*b*).

### Acknowledgments

We thank the Namibian Ministry of Environment and Tourism, the Israeli Nature Protection Authority, and the Hebrew University ethics committee for study permits and the Etosha Ecological Institute for logistical support. We are grateful to many people who helped during fieldwork, including S. Bellan, W. Kilian, S. Kötting, M. Küsters, G. Shatumbu, W. Turner, and W. Versfeld (Namibia); A. Atar, A. Basbusa-Rashaide, O. Goelman, Y. Miller, Y. Sinai, O. Yahalomi, A. Zabari, and D. Zackai (Israel). G. Bohrer, S. Dodge, and the Movebank personnel helped with environmental data annotation; Y. Bartan, N. Horvitz, and other members of the Movement Ecology Laboratory helped at various phases of the research; and Elena Kmetova (Green Balkans) provided feather samples. We acknowledge funding from the National Institutes of Health (GM083863 to W.M.G.), from the US-Israel Bi-national Science Foundation (BSF) and the special BSF Multiplier Grant Award from the Rosalinde and Arthur Gilbert Foundation (BSF 255/2008 to R.N. and W.M.G.), from the Golda Meir postdoctoral fellowship of the Hebrew University of Jerusalem (to A.C.-C.), from the Eshkol fellowship of the Israeli Ministry of Science and Rothschild fellowship (to O.S.), and from the Adelina and Massimo Della Pergola Chair of Life Sciences and the Minerva Center for Movement Ecology (to R.N.).

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