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MEASUREMENT ERROR CAUSES SCALE-DEPENDENT THRESHOLD EROSION OF BIOLOGICAL SIGNALS IN ANIMAL MOVEMENT DATA

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Abstract. Recent advances in telemetry technology have created a wealth of tracking data available for many animal species moving over spatial scales from tens of meters to tens of thousands of kilometers. Increasingly, such data sets are being used for quantitative movement analyses aimed at extracting fundamental biological signals such as optimal searching behavior and scale-dependent foraging decisions. We show here that the location error inherent in various tracking technologies reduces the ability to detect patterns of behavior within movements. Our analyses endeavored to set out a series of initial ground rules for ecologists to help ensure that sampling noise is not misinterpreted as a real biological signal. We simulated animal movement tracks using specialized random walks known as Lévy flights at three spatial scales of investigation: 100-km, 10-km, and 1-km maximum daily step lengths. The locations generated in the simulations were then blurred using known error distributions associated with commonly applied tracking methods: the Global Positioning System (GPS), Argos polar-orbiting satellites, and light-level geolocation. Deviations from the idealized Lévy flight pattern were assessed for each track after incrementing levels of location error were applied at each spatial scale, with additional assessments of the effect of error on scale-dependent movement patterns measured using fractal mean dimension and first-passage time (FPT) analyses. The accuracy of parameter estimation (Lévy μ, fractal mean D, and variance in FPT) declined precipitously at threshold errors relative to each spatial scale. At 100-km maximum daily step lengths, error standard deviations of $\geq$10 km seriously eroded the biological patterns evident in the simulated tracks, with analogous thresholds at the 10-km and 1-km scales (error SD $\geq$ 1.3 km and 0.07 km, respectively). Temporal subsampling of the simulated tracks maintained some elements of the biological signals depending on error level and spatial scale. Failure to account for large errors relative to the scale of movement can produce substantial biases in the interpretation of movement patterns. This study provides researchers with a framework for understanding the limitations of their data and identifies how temporal subsampling can help to reduce the influence of spatial error on their conclusions.

Key words: Argos satellites; Fastloc; first-passage time; foraging; fractal dimension; geolocation; GPS; Lévy flight; radiotelemetry; random walk; spatial scale; VHF.

INTRODUCTION

A major aim in wildlife ecology is the identification and understanding of processes that shape animal movement because these patterns dictate a host of ecological attributes such as population distribution and abundance, metapopulation dynamics, disease prevalence and transmission, and community structure (With and Crist 1995, Keeling and Grenfell 1997, Hanski 1998, Turchin 1998, Morales and Ellner 2002, Johnson et al. 2006). From a conservation perspective, understanding movement patterns is particularly important for quantifying a population's predicted response to the alteration of habitat structure (Adler and Nuernberger 1994,

Schooley and Wiens 2004), given that one of the first consequences of habitat fragmentation is the disruption of the functional connectivity of population patches (Hansson 1991, With et al. 1999). It can be argued then that mobility, and the phenomena driving variation in this parameter, are key determinants of an individual's survival prospects and reproductive success (Cain 1985).

Keeping step with the increasing importance of quantifying mobility is the proliferation of technologies available for studying animal movement at a variety of spatial and allometric scales. Indeed, available techniques range from the simple, yet remarkably informative, application of unraveling thread for tracking the fine-scale movements of tortoises (Claussen et al. 1997; see Plate 1), to more complex methods that include the collection of temporal patterns in light intensity that provide coarse estimates of global position (Wilson et al. 1992, Hill 1994, Teo et al. 2004, Shaffer et al. 2005),

PLATE 1. (Left) An American mink (*Mustela vison*) in the United Kingdom carrying a very-high-frequency (VHF) radio collar and (right) a loggerhead turtle (*Caretta caretta*) in Greece carrying a state-of-the-art Global Positioning System (GPS) logger. Such devices form part of a broad range of tracking technologies available to ecologists. Photo credits: A. L. Harrington (mink) and G. Schofield (turtle).

very-high-frequency (VHF) radio tracking (Tew and Macdonald 1994, Dahle and Swenson 2003), advanced animal-borne sensors estimating tracks based on Doppler shift in frequency detected by satellite arrays (Keating et al. 1991, Priede and French 1991), harmonic radar transponders (Capaldi et al. 2000), dead-reckoning compass systems (Wilson et al. 1991), and the Global Positioning System, GPS (D'Eon and Delparte 2005). These techniques have been extremely effective in describing the often amazing feats of animal movement on land or in the seas (e.g., Craighead and Craighead 1987, Mate et al. 1997, Block et al. 2001, Weimerskirch et al. 2002, Sims et al. 2003, Wiig et al. 2003, Hays et al. 2004, Pennisi 2005), and tracking data sets are now being used increasingly in various quantitative movement analyses (e.g., Capaldi et al. 2000, Fritz et al. 2003, Pinaud and Weimerskirch 2005). Such analyses are essential to change the study of animal movement from primarily a descriptive exercise to one that can quantify the behavioral and ecological complexities of foraging and movement strategies at a variety of spatial scales.

Many have realized the importance of location error when interpreting animal tracks. For example, Hays et al. (2001) examined the effects of variable precision in Argos-based locations for migrating green turtles (*Chelonia mydas* Linnaeus) and showed that accurate travel speeds could be obtained if pairs of locations used to estimate speed were sufficiently far apart. More recently, Jerde and Visscher (2005) used Monte Carlo simulations to examine the influence of measurement error relative to distance between successive locations

(step length) derived from GPS collars, and demonstrated that estimates of turn angle and step length were accurate only when step lengths were large relative to measurement error. Likewise, Jonsen et al. (2005) used a Bayesian state–space model that incorporated known information on location error to improve the behavioral interpretation of foraging seal tracking data derived from Argos satellites. Tremblay et al. (2006) examined the effects of various interpolation algorithms on the location data from various marine species to determine the overall accuracy of interpolated locations relative to the precision of the tracking technology employed.

Our aim in this paper is to build on previous studies investigating the effects of measurement error on the biological signals derived from animal movement data. We achieve this by simulating a large number of idealized tracks at three spatial scales: 1-, 10- and 100-km maximum step lengths, and then blur the resulting locations with incrementing errors normally associated with GPS, Argos, and light-level geolocation technologies. The idealized tracks and their error-blurred versions are assessed quantitatively using three mathematical procedures that highlight different biological signals integrated by tracking data. Here, we apply incrementing measurement error to the simulated tracks and measure (1) the deviance from idealized Lévy random walks (Viswanathan et al. 2000), (2) the change in mean fractal dimension (Milne 1991), and (3) the change in search effort using first-passage time (FPT) analysis (Johnson et al. 1992) at each spatial scale under consideration. The outcomes of this study provide
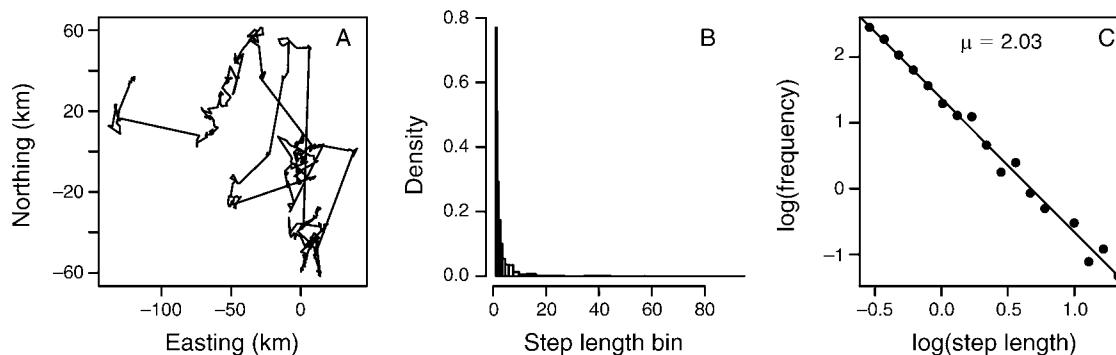
Fig. 1. (A) An example track simulated over 365 days using an idealized Lévy flight pattern with $\mu = 2$ (the power exponent) and maximum daily step length of 100 km. (B) The density (proportional frequency) histogram of step lengths with non-equidistant bins. (C) The relationship between log-transformed frequency (bin-width corrected) and log-transformed step length to estimate μ as the absolute value of the slope; in this particular example, μ was estimated at 2.03.

ecologists with a basic set of initial ground rules to apply to a range of movement analyses, regardless of the spatial scale or the specific tracking technology involved. In short, we show how noise introduced by location inaccuracies can be overcome to extract meaningful biological movement signals.

METHODS

Lévy flight patterns

Under the predictions of optimal foraging theory, an organism is expected to maximize the probability of detecting food patches by altering its movement path relative to the temporal and spatial configuration of the prey field (Stephens and Krebs 1986). When universal knowledge of the foraging environment is degraded by stochastic influences and complex prey behavior, a foraging organism is theorized to employ a suite of movement conventions that optimize encounter probability (Houston and McNamara 1999). Many different models have been proposed to examine these movement patterns, with recent attention focused on a category of random walks known as Lévy flights (Viswanathan et al. 2000, Bartumeus et al. 2005). These specialized random walks consist of clusters of relatively short step lengths (distance between successive locations over a defined period of time) connected by longer movements, with this pattern repeated at all scales, and the step lengths drawn from a probability distribution with a power-law tail (Bartumeus et al. 2005). A foraging organism employing a Lévy flight movement pattern maximizes its probability of detecting a food patch within complex landscapes where prey are sparsely or randomly distributed outside of the forager's sensory detection range (Viswanathan et al. 1999, 2000, Bartumeus et al. 2005).

Track simulation

We considered three spatial scales of movement where we set the maximum daily step length in increasing orders of magnitude: 1 km, 10 km, and 100 km. The distribution of step lengths was set to an idealized Lévy random walk:

$$\Pr(l) = \alpha l^{-\mu}$$

where $\Pr(l)$ is the probability density of having a step length l, α is a normalizing constant, and μ is the power exponent. For each spatial scale considered, a power-law distribution with $\mu = 2$ of daily step lengths was generated, given that modeling studies have determined that this exponent produces optimal Lévy flight search patterns (Viswanathan et al. 1999, 2000, da Luz et al. 2001). We simulated 1000 specialized random walks, each of 365 days, by drawing steps from this step length distribution and applying a random turn angle between 0 and 359 degrees. For each track, a histogram of step lengths was produced to determine μ (estimated from the slope of the relationship between the $\log_{10}$ of bin frequency and $\log_{10}$ of the step length bin). However, the estimation of μ is highly sensitive to the histogram binning procedure, so a transformation was applied to produce non-equidistant bins (Sims et al., 2007). First, the bin widths were set to increase exponentially relative to the number of bins (k) such that vector of bin widths $= 2^k$ (Viswanathan et al. 1996). Next, bin frequencies were divided by their bin width to normalize the probability density (Newman 2005, Pueyo 2006), and the $\log_{10}$ of this vector was plotted against the $\log_{10}$ of the bin widths to estimate μ. This procedure accounted correctly for increasing bin widths, avoided the weighting of excessive zero frequencies at high step lengths, and provided equidistant data points in the linear regression. An example of a simulated track, step length histogram, and the associated estimate of μ are shown in Fig. 1. More detailed descriptions of the track simulation and associated computer code are provided in the Appendix and Supplement.

Fractal dimension

The use of fractal geometry in ecology can provide useful insights into the landscape perception of foraging

animals (Crist et al. 1992, With 1994, Fritz et al. 2003) because it provides a single (quantified) value measuring the spatial (and temporal) complexity and heterogeneity of the resource field (Leduc et al. 1994). The fractal dimension (D) measures the tortuosity (crookedness) of movement paths (Milne 1991) such that $D = 1$ indicates a straight path and $D = 2$ indicates maximum tortuosity covering an entire plane (Milne 1997). Fractal D varies with the view of the path at different spatial scales, so it also provides information on changes in behavior at different spatial scales (Nams 1996, Nams and Bourgeois 2004). Given that we constructed our simulated paths to emulate a scale-invariant property (Lévy flight), our approach assumes that the simulated organisms view the habitat similarly over the entire range of spatial scales. As such, we hypothesized that the overall mean fractal D of our simulated tracks would become less tortuous with greater degrees of spatial error.

To measure fractal D for our simulated paths, we employed the mean fractal method of Nams (1996) that minimizes edge effects complicating the traditional divider method. This method measures the length of the path by randomly starting from any point and working the "divider" in both directions to estimate the fractal mean D (Nams 1996). Fractal mean D was calculated for each simulated track and a confidence interval was derived over all paths at each spatial scale.

First-passage time analysis

One informative method for measuring search effort along an animal's foraging pathway is to examine the allocation of time spent along the path. Paths that are more tortuous tend to increase the time along the path at various scales of assessment (Fauchald and Tveraa 2003). This reasoning gave rise to the method of first-passage time (FPT) analysis (Johnson et al. 1992), with FPT defined as the time required for an animal to cross a circle with a given radius (Johnson et al. 1992). When FPT analysis is applied to a random-walk path, the mean FPT increases exponentially with the radius of the circle, and the exponent is determined by the fractal dimension of the path itself (Johnson et al. 1992, Fauchald and Tveraa 2003).

For each simulated random walk, we interpolated equidistant points along the path (this step is necessary to calculate the relative variance in FPT by creating a series of intermittent steps within the range of the smallest radii considered) and then assessed the time required to cross a circle with radii (r), incrementing the radius to two times the maximum step length. The estimated relative variance, $\hat{S}_r$, in FPT was calculated as a function of r:

$$\hat{S}_r = \mathrm{Varlog}(t_r)$$

where t_r is the FPT for a circle of radius r. We considered r values ranging from 0.04 km to 2 × maximum step length (l_{max}) at increments of 0.10 × l_{max}. The log transformation makes $\hat{S}_r$ independent of the magnitude of the mean FPT (Fauchald and Tveraa 2003). Express-

ing $\hat{S}_r$ as a function of r therefore provides a means of identifying the spatial scales associated with an area-restricted search (ARS), which is defined as increases in turning rate and decreases in movement rate where resources are plentiful (Fauchald and Tveraa 2003, Pinaud and Weimerskirch 2005). All analyses were done using the R software package (R Development Core Team 2004), with specific code for the FPT analysis provided by D. Pinaud (Pinaud and Weimerskirch 2005).

Location errors

The numerous technologies available for remotely estimating the movement paths of free-ranging animals while foraging all have particular error magnitudes that have been estimated. We chose to examine three of the most commonly applied technologies to tracking animals and their associated errors at the different spatial scales of investigation.

GPS.—The Global Positioning System is a worldwide, satellite-based, radio-navigation system developed by the U.S. Department of Defense (DOD) (Dana 1989). A ground-based GPS receiver calculates the time it takes for individual signals to arrive from at least three satellites to the receiver to compute a two-dimensional, horizontal fix (latitude and longitude), given an assumed height. The detection of satellite signals of four satellites can determine three-dimensional positions and time, whereas five or more can provide position, time, redundancy, and the certainty of the greater position fix (Dana 1989). In May 2000, the DOD lifted the restrictions on the freely available service and its predictable accuracy is now estimated to be 22 m (horizontal). However, we used a suite of GPS errors ranging from 10 to 65 m (standard deviation in x and y coordinates), given that precision depends on terrain and the application of differential correction algorthims (Table 1).

Argos.—Platform Transmitter Terminals (PTT) provide Argos Doppler-shifted estimates of location by transmitting an ultra-high-frequency (UHF) pulse to Argos satellites (implemented in 1979 by collaborative French and American agencies; Argos 1989). PTTs deployed on animals automatically send a message at a predetermined rate to multiple low-earth-orbit satellites, and then these signals are relayed from satellite to a ground station that forwards the data to the Argos processing center. According to Argos, precision varies; thus locations are divided into quality classes. Error estimates are described as the standard deviation of a bivariate normal distribution, with the standard deviations for different location classes (LC) being: classes A/B, no estimate of accuracy; class 0, >1000 m; class 1, >350 to <1000 m; class 2, >150 to <350 m; and class 3, <150 m (Argos 1989). However, location quality has been assessed independently for certain foraging taxa (e.g., marine turtles; Hays et al. 2001), so we use the standard deviations per location class as defined in that study (Table 1).

TABLE 1. Common methods of tracking marine and terrestrial species with associated x- and y-coordinate error standard deviations calculated for example species.

Species	Method	SDx (km)	SDy (km)	Source
Moose (*Alces alces* Linnaeus)	GPS-differential	0.01–0.02	0.01–0.02	Rempel and Rodgers (1997), D'Eon and Delparte (2005)
Moose	GPS-3 dimensional, non-differential	0.0455	0.0455	Rempel et al. (1995)
Moose	GPS-2 dimensional, non-differential	0.0655	0.0655	Rempel et al. (1995)
Roving module (simulated animal)	GPS (various configurations)	0.007–0.090	0.007–0.090	Hulbert and French (2001)
Various mountain-dwelling ungulates	VHF telemetry	0.34	0.34	Haller et al. (2001)
Green turtle (*Chelonia mydas*)	Argos Class 3	0.12	0.32	Hays et al. (2001)
Green turtle	Argos Class 2	0.28	0.62	Hays et al. (2001)
Green turtle	Argos Class 1	1.03	1.62	Hays et al. (2001)
Green turtle	Argos Class 0	4.29	15.02	Hays et al. (2001)
Atlantic bluefin tuna (*Thunnus thynnus* Linnaeus)	Archival light geolocation with latitude SST derivation	60.0	60.0	Teo et al. (2004)
Laysan Albatross, Blackfooted Albatross (*Phoebastria immutabilis* Rothschild, *P. nigripes* Audubon)	Archival light geolocation with SST latitude correction	186.5	216. 5	Shaffer et al. (2005)

Note: Methods are Global Positioning System (GPS), Very High Frequency (VHF) telemetry, Argos satellite network Doppler-shift, and light-level geolocation with and without sea surface temperature (SST) correction.

Light geolocation.—Data loggers attached to foraging animals can be programmed to record light intensity at set time intervals, and these values are then used to calculate the time of sunrise and sunset for each day; these times indicate approximate latitude and longitude coordinates based on standard equations for solar navigation (Nautical Almanac Office 1991, Wilson et al. 1992). Geolocations are generally considered to be accurate within one degree of latitude (111 km), although they are often less accurate than this (Hill 1994). However, because latitude estimates are less accurate than longitude estimates, researchers use tag-recorded sea surface temperature (SST) compared with satellite remote-sensing SST images to improve accuracy of the latitudinal component of the light-level geo-locations. Various studies have estimated the precision of geolocation estimates derived from foraging animals (Bradshaw et al. 2002, Teo et al. 2004, Shaffer et al. 2005), and we used two of these derived from fish and bird studies with and without SST corrections (Table 1).

Of course, there are many examples of researchers using very-high-frequency (VHF) radio telemetry (see Plate 1) to determine the movement patterns of terrestrial and marine animals (e.g., Tew and Macdonald 1994, Bradshaw et al. 1997, Wilson et al. 2002, Dahle and Swenson 2003, Baubet et al. 2004), although the technique appears to be used less frequently in recent years with the advent of cheaper and more reliable satellite-based methods. The approach uses regular pulses of VHF radio signals transmitted from the animal and received by a directional antenna that is either held in the hand or mounted on a vehicle or aircraft. Although practical in some circumstances, the technique requires the receiver to be within line-of-sight and range of the transmitter (McDonald and Amlaner 1980), and the collection of sufficient data is often extremely labor

intensive (Kenward 2000). As such, the precision and accuracy of the locations received is highly variable depending on the terrain, vegetation cover, weather conditions, behavior of the individuals tracked, and level of researcher effort (McDonald and Amlaner 1980, Kenward 2000). We therefore chose not to examine explicitly the errors associated with VHF telemetry because the error range that we examined (from GPS to light-level geolocation) encompasses VHF telemetry-associated precision. Indeed, the latter's precision is known to be generally much lower than GPS technology (Bechtel et al. 2004), often with errors that well exceed 100 m (Haller et al. 2001, Baubet et al. 2004); see Table 1.

For each spatial scale of investigation, we applied the range of errors described (with corresponding interme-diate values) and recalculated the step lengths between successive blurred locations to determine their effects on the Lévy flight parameters. Lévy flights with $1 < \mu \le 3$ are super diffusive (Viswanathan et al. 1996), where Brownian motion (normal diffusion) emerges with $\mu > 3$ and anomalous diffusion occurs with $\mu \le 1$ (Bartumeus et al. 2005). As such, we determined the proportion of error-blurred tracks producing μ within the Lévy flight range, with the corresponding estimates of mean μ at the errors considered. Similarly, we examined the change in the average fractal mean D and the relationship between FPT $\hat{S}_r$ and spatial scale at various error levels.

Temporal subsampling

A previous study (Hays et al. 2001) found that accurate parameters describing the movement of free-ranging animals can be estimated even in the presence of spatial error when the temporal or spatial scale of investigation is adjusted accordingly. Accurate estimates of travel speed in migrating green turtles could be obtained with Argos locations of classes A, B, and 1–3
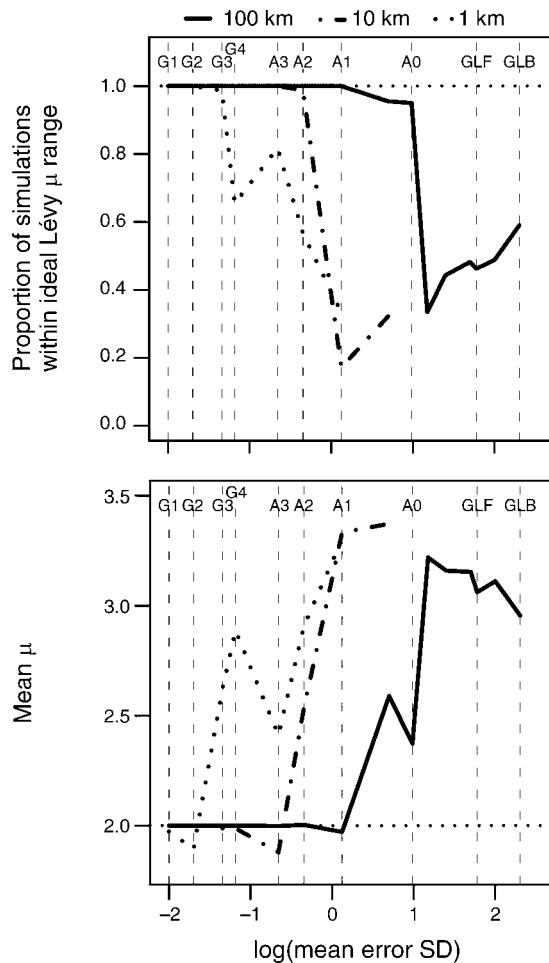
step lengths) and subsampled the locations derived from GPS; however, this provides the same results, albeit at a different spatial scale.

RESULTS

As hypothesized, increasing the degree of spatial error degraded the various biological signals as determined from the changes in the Lévy exponent μ, fractal mean D, and the variance in first-passage time at each spatial scale investigated. Interestingly, the accuracy of parameter estimation was reduced precipitously at various threshold standard deviations of location error. For the 100-km scale of investigation, the proportion of simulations falling within the Lévy flight interval of 1 < μ ≤ 3 declined markedly at spatial errors of Argos LC 0 (error SD ≅ 10 km) (Fig. 2). Likewise, the Lévy proportion dropped precipitously when errors exceeded Argos LC 1 (SD ≅ 1.3 km) and non-differential, two-dimensional GPS error (SD ≅ 0.07 km) at the 10-km and 1-km spatial scales of investigation, respectively (Fig. 2). These patterns were mimicked in the mean estimates of μ at the 100-km scale, with large increases
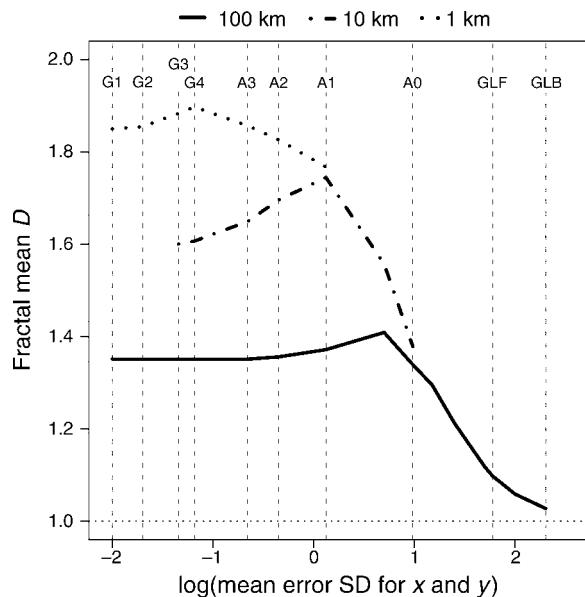
FIG. 2. The proportion of simulations resulting in Lévy μ estimates falling within the idealized range of 1–3 for increasing errors (log of the mean standard deviation error for x and y coordinates measured in km; top panel) at three spatial scales of investigation (100, 10, and 1 km). Also shown is the mean estimate of μ for incrementing location errors at each spatial scale (bottom panel). Location error classes are indicated by dashed vertical lines: G1 = 0.010 km GPS; G2 = 0.020 km GPS; G3 = 0.0455 km non-differential 3-D GPS; G4 = 0.0655 km non-differential 2-D GPS; A3 = Argos LC 3; A2 = Argos LC 2; A1 = Argos LC 1; A0 = Argos LC 0; GLF = 60 km geolocation (fish); GLB ≅ 200 km geolocation (bird). Refer to Table 1 for a detailed description of location error classes.

when consecutive pairs of locations were at least 90 km apart (Hays et al. 2001). Therefore, to investigate whether reducing the resolution of the simulated tracks would result in the maintenance of the biological signals inherent in error-blurred foraging patterns, we systematically subsampled the 100-km scale simulated tracks at increasing intervals (e.g., every two, three, four, and so on, days) and recalculated the Lévy flight statistics (μ and proportion of simulations where 1 < μ ≤ 3) at three levels of location error: Argos LC 0, geolocation (fish), and geolocation (birds). Of course, we could have chosen another spatial scale (e.g., 1-km maximum daily

FIG. 3. Average fractal mean dimension D (Nams 1996) as a function of increasing location error (log of the mean standard deviation error for x and y coordinates measured in km) at three spatial scales of investigation (100, 10, and 1 km). Maximum path tortuosity (crookedness) gives a fractal mean $D = 2$, and $D = 1$ indicates a straight path (Milne 1991). Location error classes are indicated by dashed vertical lines: G1 = 0.010 km GPS; G2 = 0.020 km GPS; G3 = 0.0455 km non-differential 3-D GPS; G4 = 0.0655 km non-differential 2-D GPS; A3 = Argos LC 3; A2 = Argos LC 2; A1 = Argos LC 1; A0 = Argos LC 0; GLF = 60 km geolocation (fish); GLB ≅ 200 km geolocation (bird). Refer to Table 1 for a detailed description of location error classes. The "true" fractal mean D 95% confidence intervals derived from the trajectories simulated without location error were 1.8044–1.8590, 1.5891–1.6051, and 1.3470–1.3549 for the 1-, 10-, and 100-km scales, respectively.
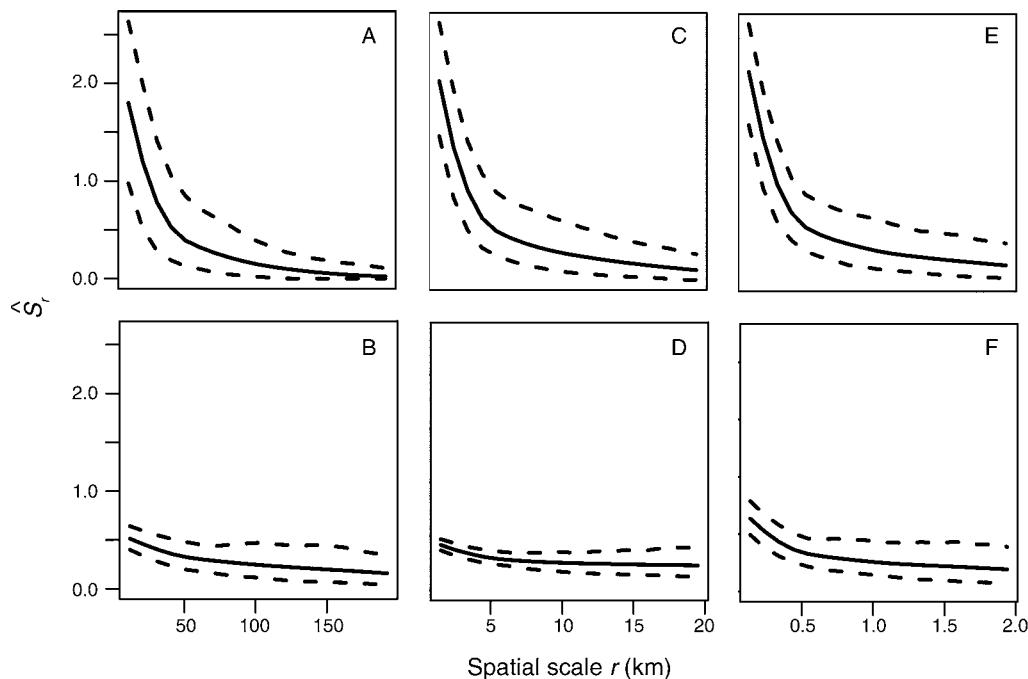
FIG. 4. The relationship between estimated relative variance, $\hat{S}_r$, in first-passage time (FPT) spatial scale, where r is the radius of the search FPT circles (mean [solid lines] and 95% confidence limits [dashed lines]; Fauchald and Tveraa 2003) for (A) no error at the 100-km maximum step length scale, (B) Argos LC 0 error at 100-km, (C) no error at 10-km, (D) Argos LC 1 error at 10-km, (E) no error at 1-km, and (F) non-differential 2-D GPS error at 1-km maximum step length.

above the theoretically optimal value of $\mu = 2$ at errors of Argos LC 0. However, mean μ increased noticeably at smaller errors than that indicated by the proportion within the Lévy range for the 10- and 1-km scales (Argos LC 2 and non-differential 3-D GPS, respectively; Fig. 2).

The average value of mean fractal D was also highly sensitive to location error, with deviations from the idealized non-error-blurred values declining precipitously as in the Lévy flight analysis. As such, the errors associated with Argos LC 0, Argos LC 1, and non-differential 2-D GPS induced large declines in mean fractal D at the 100-, 10-, and 1-km spatial scales, respectively (Fig. 3). Our investigation of the effects of these errors on the relationship between the log of variance in FPT vs. spatial scale indicated that, at each spatial scale, the errors at which we observed marked degradation in the biological signals quantified by the Lévy and mean fractal D analysis (Argos LC 0, Argos LC 1, and non-differential 2-D GPS for 100-, 10-, and 1-km scales, respectively) suppressed the overall variance in FPT (Fig. 4).

The temporal subsampling of the simulated tracks at the 100-km step length scale and various levels of location error demonstrated that this procedure can maintain the biological signals inherent in the data when subsampling is of a sufficiently high frequency. For example, when location errors are on the order of 10 km (Argos LC 0), step lengths that are recalculated over periods of three days (c.f. daily step lengths) result in the correction of μ

estimates toward the idealized value of 2 (Fig. 5). At greater levels of location error, subsampling at 10- and 14-day intervals improves, but does not completely correct, the estimation of Lévy μ at errors associated with geolocation of fish and birds, respectively (Fig. 5).

DISCUSSION

With the increasing application of quantitative techniques used to extract the spatial and temporal signals of optimal foraging behavior integrated by movement data, an assessment of the influence of location error on these conclusions is a fundamental first step in any movement analysis. As such, we provide an important evaluation of the effects of spatial error on the interpretation of search patterns based on Lévy flight, fractal dimension, and first-passage time analyses at various spatial scales. Our use of Lévy random walks to generate the simulated tracks on which the analysis was based should not be viewed as a prerequisite for the evaluation of location error in this context. Our approach of error-blurring simulated Lévy tracks was an efficient method of ascertaining error effects on behavior patterns with explicit macroscopic properties, rather than an evaluation of Lévy flight per se, although there is increasing evidence of Lévy behavior from a broad range of taxa (e.g., Viswanathan et al. 1996, 1999, Atkinson et al. 2002, Mårell et al. 2002, Ramos-Fernández et al. 2004).

Our results showed clear thresholds where the metrics relating to optimal search patterns were degraded at different spatial scales of investigation. At macroscales (100-km maximum daily step length), errors typically associated with Argos LC 0 (~10 km; Hays et al. 2001, Vincent et al. 2002) and above, resulted in a skewing of Lévy μ, average fractal mean D, and the relationship between the variance in first-passage time (FPT) and spatial scale (Figs. 2 and 3). At mesoscales (10-km maximum daily step length), errors greater than or equal to those of Argos LC 1 (~1 km; Hays et al. 2001) were sufficient to degrade the signals measured. Finally, at microscales (1-km maximum daily step lengths), errors of ~60 m (equivalent to non-differential GPS errors) had the same effect. For the Lévy μ metric, large errors typically resulted in large values (μ > 3) that would be erroneously interpreted as Brownian motion (Bartumeus et al. 2005, Sims et al. 2007) instead of optimal searching (μ ≅ 2). One also should be aware that small sample sizes (i.e., short duration of tracking data collected) might also influence the estimation of μ, even though the exponentially incrementing bin-width procedure corrects, to some extent, a surplus of zero counts in the upper step length bins.

Likewise, large location errors tended to reduce the mean fractal dimension toward values of $D = 1$ that indicate less tortuosity in movement paths. This may seem initially to be counterintuitive, given the expectation that tortuosity should increase with higher and higher location error. Fig. 3 demonstrates that initially, fractal D increases slightly with incrementing errors up to a threshold error, and then declines precipitously toward less and less tortuous movement patterns. We can explain this trend by the loss of the predominant small step lengths that exist when errors are small; in other words, high errors effectively remove the number of tight turns represented by small daily movements, leading to much less tortuous paths and the resulting decline in fractal D. The suppression of the variance in FPT suggests that the identification of the spatial scales where area-restricted searches (ARS) occur (Fauchald and Tveraa 2003, Pinaud and Weimerskirch 2005) would be difficult to detect with errors greater than or equal to those threshold values identified at each spatial scale. For example, errors that exceed the threshold values identified in this study are likely to remove the peaks in the relationship between the variance in FPT and scale that have been used to identify relocating behaviors in terrestrial species such as *Cervus elaphus* (Linnaeus) moving through areas of high predator density (Frair et al. 2005).

Previous studies have suggested that excessive error in locations can bias conclusions regarding the foraging dynamics of an organism. It has been shown that Wandering Albatrosses (*Diomedea exulans* Linnaeus) demonstrated less-tortuous movements than previously thought when higher-precision GPS technology was used in favor of Argos locations (Weimerskirch et al.
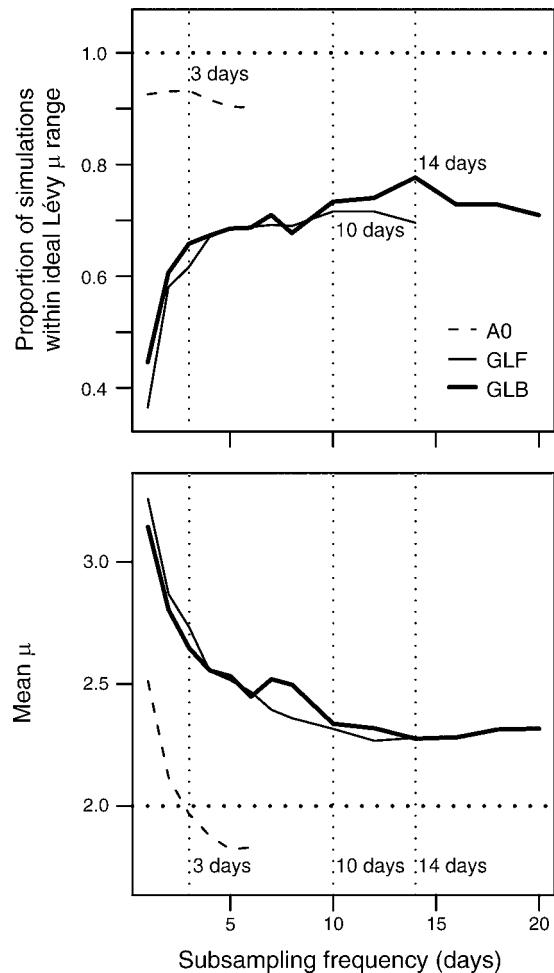

Fig. 5. The proportion of 100-km maximum step length simulations resulting in Lévy μ estimates falling within the idealized range of 1–3 for three levels of location error: A0, Argos LC 0; GLF, 60 km geolocation (fish); and GLB ≅ 200 km geolocation (bird) after subsampling the tracks at incrementing frequencies (top panel). Also shown is the mean estimate of μ for incrementing subsampling frequencies at the three levels of location error considered (bottom panel). Refer to Table 1 for a detailed description of location error classes.

1997, Fritz et al. 2003). More recently, Weimerskirch et al. (2005) concluded that prey encounter patterns of the same species followed a Lévy flight, although their μ estimate of 1.26 was not close to the optimal value (~2), leading the authors to conclude that prey encounter may not be optimal for albatrosses. Foraging routes in that study were determined from Argos locations and were subsequently filtered, but the error inherent in Argos locations may have biased the conclusions of optimality. Likewise, Austin et al. (2004) examined movement patterns of gray seals (*Halichoerus grypus* Fabricius) and found only trivial evidence for Lévy flight search patterns (Sims et al., *in press*) using Argos technology (tracks were filtered and based on location classes 3–0). They concluded that only 15% of the individuals tracked

had a frequency distribution of movement lengths fitting the negative power-law tail of a Lévy flight. It is arguable that this low percentage was detected simply by the influence of location error.

Temporal subsampling was a moderately effective means to account for some of the degradation in foraging signals associated with large location errors. For example, at the 100-km scale the sampling of locations at three-day intervals appeared to correct the Lévy flight characteristics when errors of Argos LC 0 are apparent. Interestingly though, subsampling to correct for larger errors (i.e., those associated with light-level geolocation) resulted in an improvement in the Lévy patterns, thus allowing detection of Lévy flights in animal tracks, but not in a complete correction (Fig. 5). Indeed, an increase in the subsampling frequency yields diminishing improvements in the proportion of simulations producing idealized Lévy flight characteristics, such that subsampling frequencies beyond five days provide little recovery of the true value of μ (Fig. 5). It also should be noted that temporal subsampling will explicitly change the scale of the analysis, such that scale-variant properties may be eliminated if excessive subsampling is required. Additionally, there is an inherent trade-off between the improvement in the quantification of the biological signal of interest (e.g., idealized Lévy flight) and the increased variance associated with smaller sample sizes that result from temporal subsampling. This can be observed directly in Fig. 5, where the proportion of movement paths with A0 location errors that fall within the idealized Lévy flight window declines after the optimal subsampling window of three days is surpassed. These findings, coupled with the requirement of extensive temporal data sets to offset high subsampling frequencies, suggests that only moderate improvements in the derivation of optimal foraging metrics with quantified limits can be made using this approach.

Importantly, we found that the high-precision locations provided by GPS technology can, in fact, result in rather substantial deviations from optimality measures when the spatial scale of an organism's normal daily movement is in the order of hundreds of meters. Many forms of GPS technology now exist to track marine and terrestrial species, such as the new Fastloc system (Wildtrack Telemetry Systems, Leeds, UK). These new systems will have their own particular error distributions, so it is important that users of these technologies appreciate and consider the spatial scales limiting the interpretations of fine-scale movement patterns.

CONCLUSION

The large number of tracking technologies available for quantifying animal movement patterns provides a wealth of choice to biologists seeking to examine the factors driving individual and population behavior within a changing environment. However, coupled with this choice is the responsibility of taking account of the precision of the chosen method relative to the spatial scale of movement of the study organism. We have shown, like others before us (e.g., Jerde and Visscher 2005), that failure to account for large errors relative to the scale of movement can impart large biases in the interpretation of optimality in foraging dynamics and searching behavior. Additionally, we have demonstrated that relevant biological signals can be extracted from relatively noisy data, provided the measurement errors are less than approximately one order of magnitude of the maximum observed step length. As such, we hope that our conclusions will assist researchers in the choice of the appropriate technology for monitoring their system of interest and will provide mechanisms for analyzing their data to extract the most meaningful biological signals.

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APPENDIX

Methodological details (*Ecological Archives* A017-025-A1).

SUPPLEMENT

Computer code (R language) to derive a power-law tail probability density function and to simulate tracks (*Ecological Archives* A017-025-S1).