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## Original Article

# The ideal free antelope: foraging dispersions

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The theory of ideal free distributions seeks to predict the dispersions of organisms given heterogeneous resource landscapes and density dependent fitness. Behavioral ecologists usually test this theory by examining outcomes, particularly whether the equilibrium fraction of animals in each alternative site equals the fraction of resource there (proportional settlement). Population ecologists instead focus on the relevant process: how does dispersion relate to resource distributions and is it density dependent? Isodar analysis is a process-focused method that assesses the relative roles of quantitative and qualitative factors in shaping density dependent settlement. Here, we apply isodar analysis to the dispersions of wild Thomson's gazelles foraging on natural swards in Kenya. Frequent and detailed mapping of resource levels allowed us to delineate rich and poor regions, and to record the densities of foraging females in each region throughout an annual cycle. Whereas quantitative differences attracted more foragers into the rich region at low ambient densities, the poor region became increasingly favored at higher densities, implying the competing influence of a qualitative factor. Additional regressions suggested that this factor involved predation risk through the following scenario. Intakes were found to increase with proximity to ruminating conspecifics. The latter favored poor regions perhaps for improved predator detection. High wet season food abundance both increased gazelle densities and decreased the costs of foraging in the poor region next to vigilant ruminators. Low dry season food levels resulted in lower gazelle densities, and higher costs of foraging in the poor region despite shared vigilance burdens.

**Key words:** foraging, gazelles, Kenya, ideal free distribution, isodars, predation.

## INTRODUCTION

One of the early canons of behavioral ecology was that mating system evolution is constrained by the dispersion of species members, which in turn is determined by the spatial distributions of key resources (Crook 1964; Verner and Willson 1966; Lack 1968; Orians 1969; Jarman 1974; Emlen and Oring 1977). Although the first part of this proposition has received extensive support theoretically, experimentally, and in the field (see Shuster and Wade 2003; Davies et al. 2012), there was initially no general theory for the second. Early mating system models thus largely focused on specific ecological contexts.

The publication of the theory of ideal free distributions (IFDs) by Fretwell and Lucas (1969) raised hopes that this second part of the canon had been clarified. Ideal free settlement involves 3 key components. First, settlers on heterogeneous habitats are able to accurately compare resource levels in available subregions and pick the 1 yielding the highest fitness. Second, settlement is density dependent: that is, each additional immigrant to a patch reduces the fitness of everyone on that patch, eventually making settlement on poorer patches more profitable than further crowding into a rich one. And third, such density dependent settlement usually leads to

an equilibration of fitness across patches so that it no longer pays for any settler to relocate.

In the ensuing 2 decades, animal behavior journals hosted many publications extending IFD theory and testing its predictions. One widely tested version assumed that resources in a patch were continually used and replenished, and the total in any patch was divided equally between settlers. As a result, fitness on a patch depended on the reciprocal of the number of settlers there. These assumptions led to the prediction that, in an ideal world at equilibrium, the fraction of settlers on a patch should equal the fraction of resource on that patch. This was called the “input matching rule” (Parker 1978) or more recently “proportional settlement.” Other settlement permutations involved unequal competitors, territorial defense of resources, and pre-emptive settlement (Sutherland and Parker 1985; Parker and Sutherland 1986; Pulliam and Danielson 1991; Sutherland and Parker 1992).

The initial enthusiasm for IFD theory has steadily ebbed in the animal behavior literature (see review in Emlen et al. 2003, Appendix A). Most tests of the predictions, both in the laboratory and the field, exhibited “undermatching,” that is, too few settlers on the richer patches compared with proportional settlement predictions. In addition, the failure of study systems to meet the many assumptions of the IFD (e.g., accurate omniscience about resource distributions, cost-free movement between patches, equal

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physiological needs, etc.) discouraged many researchers from applying the theory. Despite recent theoretical advances suggesting that the IFD is more robust and widely applicable than originally thought (Cosner 2005; Cantrell et al. 2008; Křivan et al. 2008; Cantrell et al. 2010; Matsumura et al. 2010; Cantrell et al. 2012; Cosner et al. 2012), the topic currently receives only rare attention in the behavior literature.

In contrast, IFD theory has continued to thrive in the population and community ecology literature. The 3 core assumptions of IFD theory are widely invoked in models of habitat partitioning and community diversity (Rosenzweig 1987, 1991). Population ecologists have also invoked them in studies of habitat selection. In particular, Morris (Morris 1987, 1989, 1992) developed a method called “isodar analysis” to demonstrate and characterize density-dependent settlement. In contrast to the behavior literature, which often invokes proportional settlement as a test of IFD theory, Morris argued that complete use of a patch’s resource by settlers was unlikely (Morris 1994). Instead of modeling competition as a  $1/N$  process, Morris assumed that each successive settler in a patch depresses average fitness by an equal amount. Density dependence then becomes a linear process, not a hyperbolic one, and proportional settlement is almost never predicted.

Isodar analysis typically compares settlement on a pair of accessible habitats that differ in amounts or exploitability of resource, and assumes that fitness has equilibrated (the third IFD assumption). It then examines how the equilibrations are achieved as overall settler densities vary. Patterns are detected by regressing the settler densities on the presumed more suitable habitat against simultaneous densities on the alternative habitat. If the settlers ignore the differences in resource and settle randomly, the regression may be significant but it will have a slope of unity and an intercept of zero. If the differences in resource are quantitative and the settlers do attend to them, but there is no density dependence, the regression line will be vertical or horizontal depending on which habitat has the larger amount of resource. If settlement on quantitatively different habitats is density dependent, the regression intercept will differ significantly from zero, in favor of the richer habitat, and the slope will be significantly different from zero. Qualitative differences between the 2 habitats in how residents are affected by changes in ambient densities show up as regression slopes that differ significantly from unity. If 1 habitat is both quantitatively superior and its qualitative factors are least affected by density changes, the isodar slope will be greater than 1; if 1 is quantitatively superior but the qualitative factors in the other are less affected by density changes, the slope will be less than 1. In the latter case, the relative suitability of the 2 habitats decreases with increasing population density, and there can even be a “crossover” density below which the quantitatively superior habitat is more favored (and populated) and above which the roles are reversed (Morris 1988). Other types of outcome are possible (Morris 1988, 1992, 1994, 2002; Morris and MacEachern 2010). Whereas most tests of IFD theory in the behavioral literature compare 1 or a few observed dispersions to specific predictions, such as proportional settlement, isodar analysis amalgamates a dozen or more dispersions at different population densities and then looks for any general pattern.

Although isodar analysis is widely used by ecologists (see lists of studied species in Dexter et al. 2011) and Ramp and Coulson 2002), we could find no examples of its use in the animal behavior literature. (If bird journals are included, the paper by Fernandez-Juricic (2001) would be the sole exception). One reason for this disparity may be ecologists’ focus on discrete habitat selection, whereas most

mating system models, a frequent focus for behavioral ecologists, deal with dispersions within continuously varying single habitats. Behavioral ecologists may also have been dissuaded by ecologists’ claims that isodars are best suited to coarse-scale settlement (like habitat selection), whereas other analytic methods, such as resource selection functions, should be used for fine-scale and within-habitat studies (McLoughlin et al. 2010). However, this bias seems as much a reflection of the different questions that ecologists and behavioral researchers tend to ask. In behavioral ecology, we often want to know how a species distributes itself within a given, albeit heterogeneous habitat, as this sets the stage for consequent mating system and social evolution.

In this paper, we report our attempt to use isodar analysis to characterize short-term within-habitat dispersion of foraging female Thomson’s gazelles (*Eudorcas thomsonii*). The mating system in this species is considered an example of male resource-defense polygyny given the heterogeneous dispersion of foraging females over a spatially variable but continuous resource (Jarman 1974; Walther et al. 1983; Estes 1991). This species is particularly suited for testing IFD models as it avoids many of the violations of IFD assumptions that have plagued other studies. Unlike sympatric impalas (*Aepyceros melampus*), kin affiliation plays no detectable role in Thomson’s gazelles, and herd structure is typically diffuse. Physical interference and dominance interactions between adjacent foragers are rare at best, and at the within-habitat scale considered here, travel costs between successive feeding patches are minimal. The relevant resource is a 2-dimensional short-grass sward whose heterogeneities are easily mapped on a regular basis. In our site, all gazelles were highly visible and also easily mapped; unlike many other studies on mammalian dispersions, we did not have to estimate densities from feces, tracks, trapping, or other indirect evidence. Dividing the study site into contiguous rich and poor regions of equal area, we recorded simultaneous densities in the 2 regions on multiple occasions, and submitted these data to isodar analysis. The specific questions being asked were: 1) are foraging female gazelles distributing themselves in a density dependent manner; 2) do quantitative differences in region resources play a role in that density dependence; and 3) do qualitative differences between regions affect equilibrium dispersions? We then used concurrently collected data on gazelle bite rates, time budgets, recent predations, infant densities, and dispersion of ruminating individuals to try to make sense of the isodar results.

## METHODS

### Study site and seasons

The overall study was conducted on a 528-ha boot-shaped block of plains nestled between the Olare Orok and Ntiakitiak Rivers, and straddling the boundary of Kenya’s Maasai Mara National Reserve with the Koyiaki Group Ranch (approx. center of site: 35.15290°E, 1.333278°S). Because of persistent water in the adjacent rivers, significant numbers of Thomson’s gazelles were present on the site throughout our study. As the site was continuous with similar grasslands on 2 sides, there was frequent flux of herbivores into and out of it. The grassland was dominated by *Themeda triandra* kept to 5–15 cm heights by local herbivores and occasional burning by the resident Maasai. More details on the site’s plant community and gazelle dietary preferences can be found in Bradbury et al. (1996).

Besides Thomson’s gazelles, Grant’s gazelles (*Nanger granti*), topi (*Damaliscus korrigum*), and impalas were present all year but largely foraged on the higher grass levels and browse at

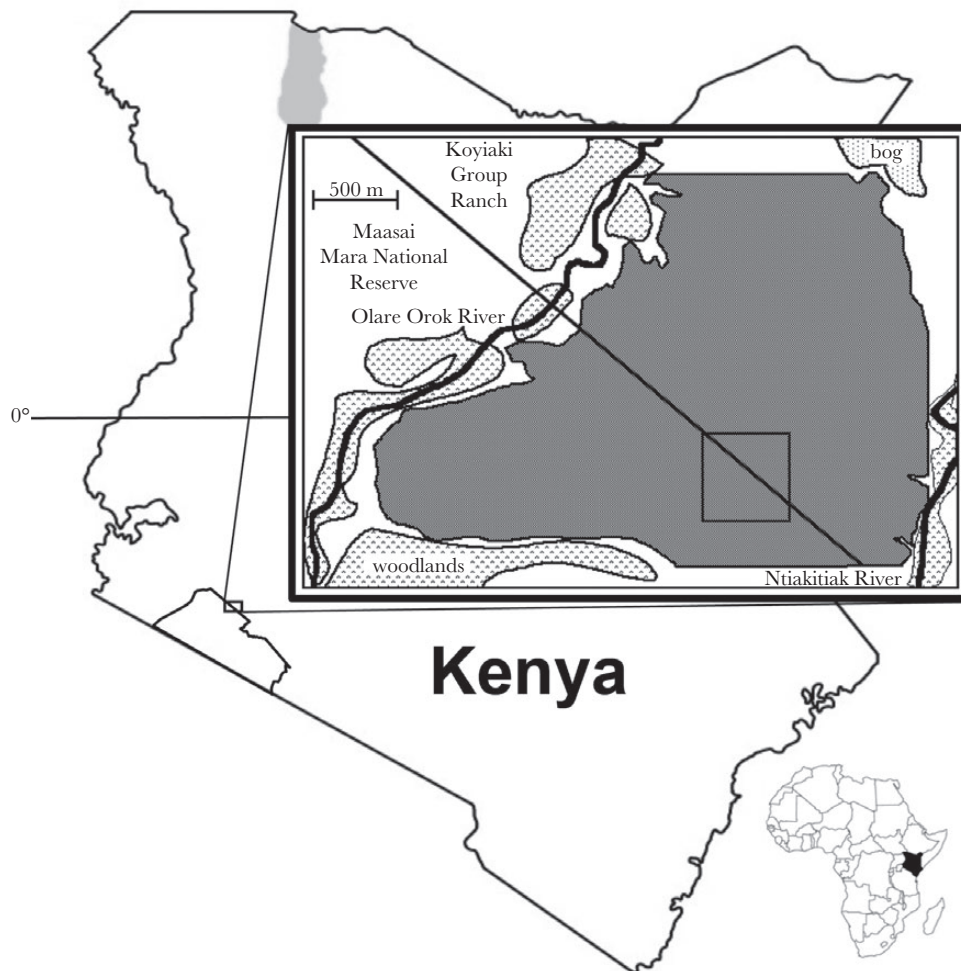
the fringes of the study area. Managed herds of Maasai cattle (*Bos primigenius*) were grazed in part of the overall area at intervals, but most often the Maasai just herded the cattle from their nearby manyatta to zones of higher grass heights. Zebra (*Equus quagga*) and wildebeest (*Connochaetes gnou*) were present in the dry season, but again tended to graze in peripheral zones with a higher grass level than that favored by the gazelles. Gazelle predators on the site included lions (*Panthera leo*), spotted hyenas (*Crocuta crocuta*), cheetahs (*Acinonyx jubatus*), wild dogs (*Lycaon pictus*), black-backed jackals (*Canis mesomelas*), and olive baboons (*Papio anubis*).

The field study spanned a 1-year period beginning August 1989. Several months were spent perfecting techniques and defining the area boundaries. The subsequent field data on gazelle dispersions and foraging can be divided into 4 blocks: during the end of the 1989 dry season (Oct-mid-Dec) and first part of the subsequent rainy season (late Dec-Feb 1990), we sampled throughout the entire 528-ha study area. These results constitute our “global” samples. For the remainder of that rainy season (Mar–May), and the first part of the next dry season (June–July), we collected more intensive data within a 25 ha “central” quadrat near the middle of the global site (see Figure 1). The total numbers of Thomson’s gazelles at any one time ranged from 154–750 on the global site and 4–241 on

the central one. Having both global and central samples allowed us to determine the degree to which isodar results depended on scale.

### Resource mapping

Heterogeneities in resource abundance were mapped every 14 days in the global site and every 5 days in the central site. For each mapping, we drove a vehicle outfitted with 2 separately filtered radiometers, an Etak navigational device, and a portable computer along a gridded route (Clifton et al. 1994). Radiometric values were then converted to g of dry green biomass/m<sup>2</sup> (hereafter DGBM) and g protein/m<sup>2</sup> using regressions based on clipped samples taken on the same days (Clifton and Clifton 1991). We here focus on DGBM, which is the most widely used index of nutritional value in savannah ungulate field studies (McNaughton 1979). Because the radiometric samples had frequent overlaps, we used them to estimate DGBM values at points in standard rectangular coordinate grids using spline interpolation routines in MATLAB (v. R2014b, The Mathworks, Inc). The standard grids had 29083 points (15-m separations) for the global site and 2601 points (10-m separations) for the central site. For days between resource mappings, we generated equivalent maps using point-to-point linear interpolations based on the number of days since the last sample relative to the days between actual samples.



**Figure 1**

Map of study area in western Kenya. Boot-shaped global study site of 528 ha shown in gray and partially bordered by rivers and woodlands, but also continuous with open plains on 2 sides. Central site of 25 ha is shown as rectangle in lower central region of global site.

We initially used contour routines in Matlab to divide each resource map into 2 regions of equal area where all points inside the “rich” region had DGBM values equal to or greater than that value, and all points in the “poor” had values less than that isopleth. However, we found that simply using the median DGBM value in the relevant gridded map to define good and poor gave similar results with only a 0.03% difference in assignments. The median was thus used in the analysis here.

### Gazelle mapping

Gazelles were mapped from the roof of our research vehicle parked at a sufficient distance to avoid any disturbance to the gazelles. Two military rangefinders (Sokkiaha 50 cm base and Wild Heerbrugg 80-cm base) were rigged with calibrated resistors on their range adjustments to provide distance information, and mounted on a tripod with another calibrated resistor to provide azimuth. Outputs from these devices were combined with that from the car navigator to compute study area coordinates for each mapped gazelle. Calibrations of this system showed accuracies of 1 m over ranges of 100–700 m and even better when closer. Although adult female dispersions were the primary focus of the study, all Thomson’s gazelles present on the site were mapped. Additional inputs to the computer included an animal’s sex, state (standing or lying down), age (adult or infant), and whether it was selected for a subsequent foraging behavior sample. Each complete mapping of all gazelles in the current study site is called a “herd scan.”

Gazelles could sleep anywhere inside or outside the study area and began moving to foraging sites soon after dawn. Barring disturbances such as predations, we undertook our first herd scans at 7:00. In the global site, a second herd scan was usually performed at 13:00. Central sample herd scans were performed every half hour from 7:00 to 12:00. Herd scans were undertaken at an average interval of 6 days in the global site and 4 days in the central one.

Forager proximities were extracted from each herd scan using a Delaunay tessellation (Matlab). The harmonic mean distance between each standing female and the neighboring standing females connected to it by a single Delaunay link was used as a measure of individual spacing between foragers. Other distances recorded for each standing female were that to the nearest standing neighbor, that to the nearest ruminating or resting female, and that to the nearest ruminating or resting individual of either sex.

### Isodar analysis

DGBM values under each mapped gazelle were estimated by interpolation using that day’s resource map (Matlab). These values were then compared with the median DGBM for that day: those individuals standing on less than the median were assigned to the poor region and the rest to the rich. Counts were converted to local densities to allow pooling across sites when appropriate. To compute isodars, we regressed densities from the quantitatively more favorable zone (here the rich region) on the contemporaneous densities in the poor. Because both variables were measured the same way, both likely contributed to variation around any pattern in choice of foraging region. Errors in the abscissa bias slope estimates of Model I regressions (such as ordinary least squares, hereafter OLS) to values less than the true value (Sokal and Rohlf 1995). There are 2 solutions to this problem. One is to estimate the relevant errors and correct the OLS slope estimate accordingly (Angleton and Bonham 1995; Carroll and Ruppert 1996; Robinson 2005; Smith 2009). The second is to use Model II regressions (Legendre and

Legendre 1998). Unfortunately, there are over 20 alternative Model II protocols to choose from, and each has its own limitations and biases (McArdle 1988; Leng et al. 2007; Ludbrook 2010). The most popular Model II protocol, geometric mean regression (also called the reduced major axis method), tends to produce slope estimates biased toward unity, the bias increasing as sample sizes and the correlation between the regression variables decrease (McArdle 1988; Jolicoeur 1990; Smith 2009). It is also very sensitive to outliers.

We performed both OLS and geometric mean regressions on our data, hoping the truth would lie somewhere between their estimates. The OLS analyses were run in JMP Pro (v. 11.0.0, Cary, NC; SAS Institute, Inc.), and the geometric mean regressions in Matlab using routines provided by Edward Peltzer (<http://www.mbari.org/staff/etp3/regress.htm>). We also tried to quantify any OLS bias by estimating the magnitude of measurement and sampling errors relative to overall abscissa variance. These 2 components are argued to be the main sources of bias in OLS regressions (Carroll and Ruppert 1996; Smith 2009). Sampling errors were likely small in our study as we mapped every animal in every herd scan and generally obtained large sample sizes. Our main measurement error was deemed to be incorrect assignment of standing females to a region. Although the assignment criterion was clear, inaccuracies in mapping animal locations and estimating underlying DGBM could jointly result in assignment errors. The probability of an error depended on the accuracy of our animal mapping, the local interdigitation of the 2 regions, and the gradient of DGBM around the mapped animal. We estimated the combined effects of these factors by computing the minimum distance between each standing female’s mapped location and the nearest contour line for the median DGBM on that day (Matlab). We then computed the difference in abscissa variance if all females within a specified distance of a contour line had been assigned a region in error, and also how slope estimates changed when these samples were deleted.

The regression analyses provided estimates and 95% confidence intervals (CIs) for slopes and intercepts that we then compared with 3 different hypothetical models. The first, random settlement, predicted an intercept of zero and a slope of 1. We thus examined whether these values fell within the confidence limits for the observed data. The second hypothetical model was proportional settlement. To test this, we first estimated the fraction of total DGBM in each region at the time of a herd scan, and multiplied this fraction by the overall density of standing females to obtain the predicted densities in each region. These were then regressed against each other to obtain slopes and intercepts predicted for proportional settlement. Given large differences between the sites in the range of DGBM values, we performed separate regressions for each site. The slopes and intercepts for observed versus predicted OLS regressions were compared using Ancova in JMP Pro. The high variable correlations in the proportional settlement datasets meant that OLS and geometric mean regressions would give equivalent results (Legendre and Legendre 1998). For contrasts between proportional settlement parameters and geometric mean estimates, we just used the OLS values for the former. As our final hypothesis testing, we compared the observed slopes from each regression method to a value of one to identify which of the alternative dispersion patterns delineated by (Morris 1987) typified the gazelle data.

### Focal forager samples

Between successive herd scans, we conducted focal forager samples of 10 min each. Subjects were chosen using a spatially stratified

random process to increase chances that samples were obtained in both regions. For each sample, one observer mapped the focal animal's location every minute, whereas a second recorded every bite, step, head raising, or lowering, and nonforaging activities. The same team members performed the same sampling roles throughout the study. Four exclusive states were distinguished: 1) "foraging" began when the focal animal put its head down and/or began walking; 2) "standing" began when the animal stopped moving and kept its head raised for 5 or more seconds; 3) "resting" began when a gazelle lay down or began ruminating; and 4) an "other activities" state included agonistic interactions, grooming, running, predator inspection, or drinking. The foraging state was further subdivided into bouts and interbouts: the former began with the first bite and ended when the animal raised its head or 5 s elapsed without an additional bite.

A number of foraging parameters were then computed for each focal sample. The total times spent in each state were converted to time budget fractions, and event counts were converted into rates by dividing the total number of each type of event by 1) the 10-min sample duration (gross rate), 2) the total time spent in a foraging state (rate/min foraging), and 3) the summed time spent in foraging bouts (within-bout rate). Rates were least for the first measure, greatest for the last, and intermediate for the second. The DGBM under each mapped location in the focal animal's trajectory was estimated using interpolation from the relevant resource map, and the mean used as a foraging parameter.

Spacing parameters for the focal foragers were based on a herd scan just prior to the focal sample. For the central samples, we completed 1–2 focal samples between each successive herd scan on a given day. Focal samples in the global site were sometimes collected on the same day as the most recent herd scan or on the next morning. To obtain spacing data for global focal samples, we mapped all gazelles within 50 m of each other starting with the next focal individual just prior to a focal sample. For both central and global maps, we extracted the spacing parameters outlined earlier from Delaunay tessellations.

Additional parameters tabulated were season, site, the fraction of females resting or ruminating during the relevant herd scan, the overall mean DGBM level in the study site on the day of the sample, mean sward height, mean fraction of dry grass biomass that was green, the densities of males and females within a convex hull for herd scans or in a 25-ha circle (global) or square (central) centered on the focal animal for behavior samples, the time of the sample relative to the peak numbers of ruminator (usually 10:00), whether any distracting disturbances such as passage of a predator or human occurred during the sample, and whether 1 or more predations on ungulates had occurred 1) on the same day as the focal sample and 2) on the prior day. Predations were recorded on a daily survey across the entire study area. Given that on 63% of sample days, no infants were seen on the study site, we recoded infant abundance into low (<3) and high (otherwise).

### Fitness measures

Isodar analysis assumes that settlers have equilibrated between alternatives such that fitness is equal everywhere. We thus sought a suitable proxy for fitness so that we could compare mean values across regions. We here follow several other authors (Fortin et al. 2002; Courant and Fortin 2012; Morris 2014) by assuming that gazelles maximize fitness by maximizing instantaneous food intake rates. Intake rates were estimated as the product of bite rate and bite mass (Spalinger and Hobbs 1992). The 3 bite rates outlined

above were multiplied by bite mass estimates to compute gross intake/min, intake/min foraging, and within-bout intake rates. As outlined in our prior publication, bite mass in the wet season can be estimated as: bite mass (g DGBM/bite) = 0.0106 (DGBM under the forager in g/m<sup>2</sup>)<sup>0.2306</sup> (Bradbury et al. 1996). For the dry season, we used published linear regressions of Thomson's gazelle bite masses on calibrated swards of native Serengeti grasses (Wilmshurst et al. 1999): bite mass (g DGBM/bite) = 0.023 + 0.0001 × DGBM under the forager in g/m<sup>2</sup>. Although different equations were used for the 2 seasons, and different functional responses to varying food densities were invoked (Spalinger and Hobbs 1992; Bradbury et al. 1996), plots of estimated intakes against the full range of DGBM densities under our focal animals show a single narrow ellipse of points with no seasonal breaks, and a steady linear increase in intakes as underlying DGBM increased. To test for fitness equilibration, we used matched pair *t*-tests to determine whether daily average intakes were equal in the 2 regions.

### Parameter regressions

We undertook 2 sets of analyses to identify parameter correlates of observed patterns. The first regressed the fraction of standing females that were located in the rich region on the within-herd scan means of possibly relevant contextual parameters across herd scans. The second set regressed intake measures on possibly relevant contextual parameters across focal animal samples. We first used generalized regression routines (adaptive lasso with AIC criteria in JMP Pro) to remove the least correlated parameters. We then examined subsets of the remaining parameters to find those biologically reasonable models with the lowest AICc values (Burnham and Anderson 2002; Anderson 2008). The distributions of parameters were transformed when needed to ensure normally distributed regression residuals.

## RESULTS

### Isodar analyses

Table 1 summarizes the estimated slopes, intercepts, and 95% CIs from our isodar regressions. Results are listed both for the entire data set and for the individual seasons. Figure 2 shows the isodar plot for the full data set fitted with a geometric mean regression line. All of the OLS regressions had slopes significantly greater than 0; it is not possible to perform similar tests on geometric mean slopes. The OLS analyses all found significantly positive intercepts and slopes significantly less than 1. The geometric mean isodars for the pooled and dry season data also estimated slopes less than 1 and their upper confidence limits only barely included a value of 1. Both methods indicated steeper slopes in the wet season, but an OLS Ancova did not find a significant difference ( $t = 1.53$ ,  $df = 321$ , and  $P = 0.127$ ).

Although CIs for all 3 OLS regressions excluded the intercept of zero and slope of one predicted for random settlement, the higher slope estimates and large CIs for the geometric mean regressions could only exclude an intercept of zero for the dry season. Table 2 summarizes the contrasts between the observed isodars and those predicted given proportional settlement for each site separately. In both sites, the slope of the proportional settlement line is significantly steeper than that of the observed dispersions whether contrasted through OLS Ancova or comparison of confidence limits generated by either regression method. In both sites, the OLS lines for observed and proportional settlement cross at low densities

**Table 1**  
Isodar regression statistics for Thomson's gazelles

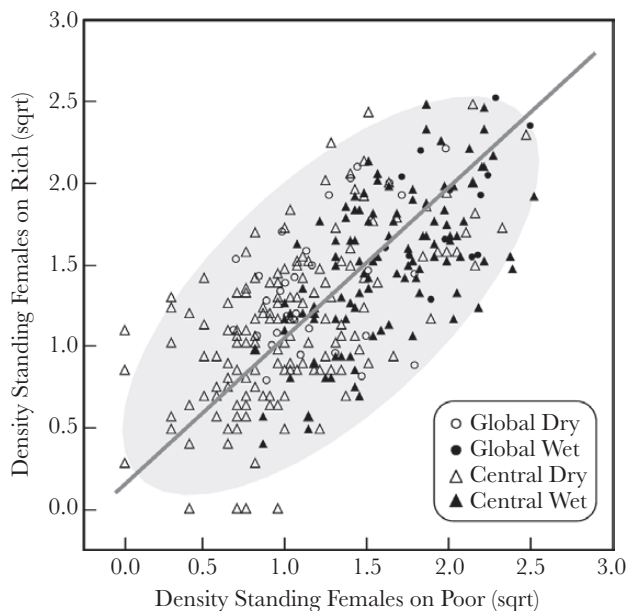
Model parameters	Pooled seasons	Dry season	Wet season
Model I (ordinary least squares):			
Intercept	0.48 (0.37, 0.59) <sup>a</sup>	0.53 (0.40, 0.66)	0.30 (0.02, 0.57)
Slope	0.65 (0.58, 0.73)	0.61 (0.49, 0.72)	0.76 (0.60, 0.92)
<i>n</i>	321	198	123
<i>r</i> <sup>c</sup>	0.683	0.598	0.650
<i>P</i>	<0.0001	<0.0001	<0.0001
Model II (geometric mean):			
Intercept	0.09 (-0.02, 0.21)	0.16 (0.10, 0.29)	-0.30 (-0.58, -0.03)
Slope	0.96 (0.87, 1.04)	0.95 (0.83, 1.07)	1.15 (0.97, 1.33)
<i>n</i>	318 <sup>b</sup>	195	121
<i>r</i> <sup>c</sup>	0.675	0.601	0.630

Table values based on square-root transformation of densities before regression.

<sup>a</sup>Parameter estimates followed by 95% CIs in parentheses.

<sup>b</sup>Several outliers removed before Model II analyses.

<sup>c</sup>Pearson correlation.



**Figure 2**

Isodar plot for herd scans after converting counts to densities, pooling sites, and seasons and applying a square-root transform to ensure normally distributed residuals. Several outliers were removed before using Model II (geometric mean) regression to fit line to data. Shaded area is 95% bivariate normal ellipse.

(8–10% of the total abscissa range above the minimum for untransformed abscissa axes): below these points, the gazelles exhibit overmatching, but over most of the abscissa range, they undermatch proportional settlement predictions.

OLS slopes in Tables 1 and 2 range from 62% to 68% of geometric mean estimates. For this difference to be solely due to OLS bias, our combined measurement and sampling errors must be 32–36% of the overall variance in the abscissa variable (McArdle 1988; Carroll and Ruppert 1996; Smith 2009). Of the 24041 mapped locations of standing females, only 0.6% were within 1 m of the nearest median contour line, 3% were within 2 m, and 7% were within 3 m. Our estimated mapping error was 1 m or less. If we reassigned all females within 3 m of a contour line to the opposite region, the abscissa variance was only changed by 0.9%

and the ordinate by 0.5%. The slope estimates using either method of regression were unchanged. If all females located within 3 m of a contour were deleted from the data set, both regression slopes decreased (the geometric mean value by 4% and the OLS value by 11%). Were erroneous assignments generating OLS bias, we would have expected the OLS slope to increase with their deletion. It appears that assignment errors are an unlikely cause of the lower OLS slopes when compared with the geometric mean ones.

Taken together, the evidence suggests that the true isodar slopes and intercepts lay somewhere between the OLS and geometric mean estimates. If so, the true isodars had significantly positive intercepts and positive slopes significantly less than 1 whether data were pooled, divided by season, or divided by site. Positive intercepts and slopes less than unity fit Morris' (Morris 1988) "convergent" pattern in which suitability of the 2 regions becomes more similar as densities increase. In addition, it leads to the possibility of crossovers such that the role of most favored and consequently most populated region can switch as densities rise and fall. We take up further evidence for this phenomenon below.

## Equilibration

Values of mean daily intake rates matched for the 2 regions were consistently and significantly higher in the rich region (gross intake: rich region 25% higher,  $t = 4.91$ ,  $P < 0.0001$ ; intake/min foraging: rich region 18% higher,  $t = 4.92$ ,  $P < 0.0001$ ; within-bout intake: rich region 16% higher,  $t = 7.48$ ,  $P < 0.0001$ ). Similar outcomes are obtained when sites or seasons are analyzed separately. If settlement were random, intake rates should reflect the relative abundances of DGBM in each region; in our samples, the rich region contained an average 38% more DGBM than the poor. If settlement were proportional, rates should be equal (difference of 0%). Our gross intake rates thus fall about a third of the way from random toward proportional settlement expectations, whereas the within-bout rates are a bit more than half-way between the 2 hypothetical predictions. Although some density dependence is clearly at work, it is incomplete if resource intake is the only relevant fitness component.

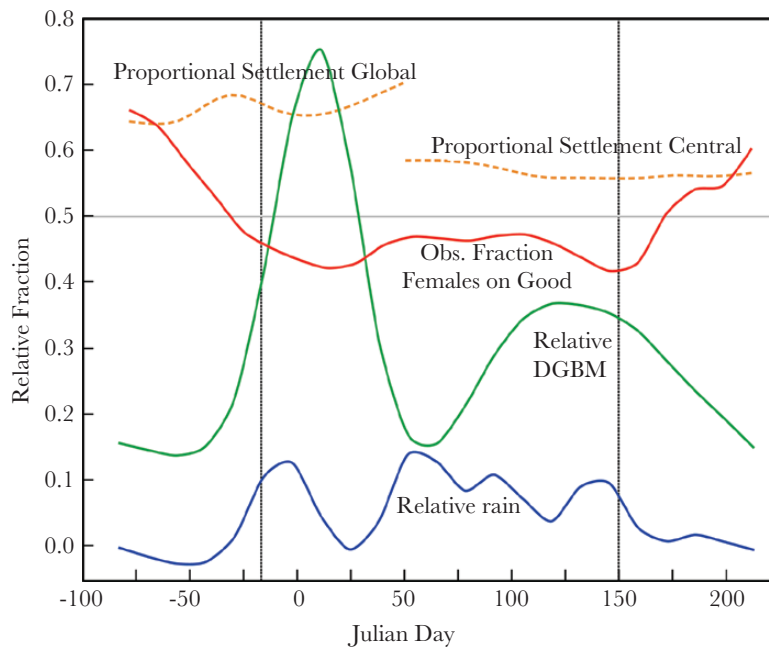
## Correlates of isodar patterns

Figure 3 shows the overall trends for rainfall, median DGBM, and the fractions of standing females in the rich region predicted given proportional settlement and actually observed. There is a clear shift

**Table 2**  
**Contrasts between observed and proportional settlement isodar parameters**

Parameter	Regression model	Estimate (CI)	<i>t</i>	<i>P</i>
<b>(A) Global site (<i>n</i> = 45)</b>				
Variable correlation (Pearson <i>r</i> )	Proportional settlement OLS	0.97 (0.94, 0.98)	25.80	<0.0001
	Observed OLS	0.62 (0.40, 0.77)	5.22	<0.0001
Intercepts	Proportional settlement OLS	-0.14 (-0.28, 0.01)	-1.85	0.0715
	Observed OLS	0.71 (0.39, 1.04)	4.43	<0.0001
Slopes	Observed geometric mean	0.23 (-0.01, 0.47)	—	—
	Proportional settlement OLS	1.50 (1.38, 1.62)	25.81	<0.0001
	Observed OLS	0.56 (0.34, 0.78)	5.22	<0.0001
Observed geometric mean	0.90 (0.66, 1.14)	—	—	
Intercept difference	OLS Ancova	0.20 (0.14, 0.25)	6.80	<0.0001
Slope difference	OLS Ancova	0.47 (0.32, 0.62)	6.40	<0.0001
<b>(B) Central site (<i>n</i> = 259)</b>				
Variable correlation (Pearson <i>r</i> )	Proportional settlement OLS	0.97 (0.94, 0.98)	201.0	<0.0001
	Observed OLS	0.67 (0.60, 0.73)	14.60	<0.0001
Intercepts	Proportional settlement OLS	0.02 (0.01, 0.03)	2.92	0.0036
	Observed OLS	0.47 (0.36, 0.59)	7.98	<0.0001
Slopes	Observed geometric mean	0.09 (-0.04, 0.22)	—	—
	Proportional settlement OLS	1.12 (1.11, 1.13)	213.8	<0.0001
	Observed OLS	0.65 (0.56, 0.74)	14.59	<0.0001
Observed geometric mean	0.96 (0.87, 1.06)	—	—	
Intercept difference	Ancova	0.06 (0.04, 0.08)	4.95	<0.0001
Slope difference	Ancova	0.23 (0.19, 0.28)	9.70	<0.0001

Probabilities for OLS regressions compare correlation, intercept, and slope parameter estimates to value of 0. Ancova compares slopes and intercepts of OLS regression for proportional settlement with OLS regression for observed data. Geometric mean slope and intercepts cannot be tested against 0 value. All densities were square-root transformed before analysis to ensure normal residuals.



**Figure 3**  
 Seasonal phenology showing spline-smoothed plots of rainfall (blue), median DGBM (green), predicted fraction of standing females in the rich region given proportional settlement (dashed orange), and observed fraction in the rich region (red). Rain and DGBM are shown relative to maximum values. Julian day was set to 0 for 1 January, 1990. Horizontal line indicates crossover threshold for standing female dispersions. Two vertical dotted lines indicate transitions between dry seasons (left and right sections) and wet season (middle section). Dispersions are clearly undermatched relative to proportional settlement for most of the year. The slight overmatching in middle dry seasons (ends of plot) is real and not an artifact of smoothing.

in the observed distribution of standing females from the rich to the poor region at the onset of the rainy season, and a later shift back at the onset of the next dry season. Not shown in the figure is a nearly 2-fold increase in overall densities of standing females in the wet season (dry season mean: 2.89/ha, wet season mean: 5.58/

ha; *t* = 9.97, *df* = 319, and *P* < 0.0001). Thus, the potential for crossovers predicted by the isodar analysis is clearly realized at the seasonal level. Not visible given the smoothing of the trend lines are other transitions across this threshold: an average 20% of successive herd scans crossed the 50% line in one direction or the other.

Clearly other factors than the gross seasonal changes were affecting foraging female dispersions.

We thus regressed the fraction of standing females in the rich region on a large suite of likely contextual parameters. For this analysis, we pooled sites and seasons but included these variables in the initial model. The final model is summarized in Table 3 ( $r = 0.540$ ,  $n = 281$ , and  $P < 0.0001$ ). A greater fraction of standing females was found in the rich region when more resting females were also situated there, when there had been 1 or more predations on the prior day, and when a greater fraction of females were standing. Higher female densities and abundant infants shifted standing females back into the poor region. The fraction of standing females in the rich region was also slightly higher on average in the central site than in the global one. Note that once the other variables were included, neither season nor median DGBM were entered into the final model.

The strongest effect was that of the fraction of resting females located in the rich region. There are several possible reasons for the positive correlation between these 2 measures ( $r = 0.425$ ,  $n = 281$ , and  $P < 0.0001$ ). However, a matched pairs test across all herd scans showed that the fraction of resting females in the rich region was consistently less than the concurrent fraction of standing females there (resting female mean: 0.468, standing female mean: 0.514,  $t = 3.00$ ,  $df = 280$ , and 2-tailed  $P = 0.003$ ). However, this contrast ignores any seasonal effects. As the isodar results imply, the fraction of standing females in the rich region decreased with seasonal shifts in ambient densities. The fraction of resting females in the rich region followed the same seasonal shifts, but while the slopes of the relevant linear regressions were statistically similar, the intercept for standing females was significantly higher than that for resting ones (Ancova: intercept difference:  $t = 2.74$ ,  $P = 0.0064$ ; slope difference:  $t = 0.09$ ,  $P = 0.93$ ).

### Correlates of intake rates

Initial regressions indicated that sites should be pooled for this analysis, but seasons analyzed separately. Table 4 summarizes the final models. Because intakes were in part based on underlying DGBM, we did not include either median DGBM or DGBM under the focal animal for the models listed in Table 4. We did do a second series including each DGBM measure, but other than showing the expected positive effect of DGBM on intakes, the other results were unchanged. Note that some parameters were kept in the model even though their slope estimates were not significantly different from zero because their deletion from the model resulted in a large

**Table 3**  
Best multiple regression model of fraction of standing females in the rich region on concurrent parameters

Parameter <sup>a</sup>	Estimate	SE	<i>t</i>	<i>P</i>
Fraction resting females on rich	0.23	0.03	7.24	<0.0001
Predation on prior day	0.04	0.01	4.31	<0.0001
Female density	-0.06	0.02	-3.97	<0.0001
Fraction females standing	0.04	0.02	1.75	0.0821
Site (central higher)	0.03	0.02	1.55	0.1214
Infant abundance	-0.03	0.02	-1.44	0.1502

<sup>a</sup>Parameters submitted initially but not recruited into the final model: season, same day predation, median DGBM, mean grass height, mean fraction of dry biomass that is green, mean proximity to nearby forgers, and mean proximity to resting female. Herd scans in which no females were resting anywhere were excluded before analysis.

increase in the AICc value. In the dry season, a higher fraction of dry sward biomass that was green strongly enhanced all 3 intake measures. Time spent with the head raised and/or in activities other than foraging reduced intake rates with the expected strongest depression on gross intake and the least on within-bout intake. Increased female densities reduced intakes, but so did greater distances between a forager and the nearest other foragers or the nearest resting/ruminating individual. Whereas predations on the prior day or earlier on the same day induced higher intake rates, disturbances during the focal sample reduced them. Male density had a very marginal positive effect on female intakes, perhaps by augmenting the nearest neighbor benefits, or alternatively, forcing females to make up time lost due to male harassment.

In the wet season, fraction green was only significant for gross intake. Time spent with the head raised and/or activities other than foraging again reduced intake rates. Parturition peaked in the early wet season, and the more infants that were present, the higher were female intake rates. Unlike the dry season results, higher male densities and predations on the same or prior days each inhibited intake rates. Higher average sward height also reduced intakes. As with the dry season, the closer a focal forager was to a resting individual, the higher its intake. This was particularly true for within bout rates. However, proximity to other foragers did not appear to affect wet season intakes significantly, although the slight positive effect of female density may have substituted for this effect.

### DISCUSSION

If we accept that the true slopes and intercepts in our isodar analyses fell between the OLS and geometric mean estimates, we can infer that our foraging gazelle dispersions were nonrandom and density-dependent, and that quantitative differences in resource levels played an important role in that process. However, the results also point to the existence of qualitative differences between the 2 regions that tended to work against the quantitative ones, especially at higher ambient densities. The consequence was a persistent undermatching relative to proportional settlement expectations despite higher mean intakes in the rich region. The lack of intake equilibration across regions suggests that factors in addition to food intake are contributing to fitness; might these be the qualitative ones suggested by the isodar results?

The most likely other fitness factor is predation risk. One or more predations occurred on a third of the days during our study, and just over half of the identifiable victims were Thomson's gazelles. It would clearly pay for foraging gazelles to be wary, particularly when recent predations indicated nearby predators. Based on this presumption, and combining the results of Tables 3 and 4, we propose the following interpretation of our results. Head-up time was a major constraint on gross intakes in both seasons. Proximity to resting females provided a significant enhancement of intakes in both seasons. Proximity to nearest foraging neighbors also enhanced intake in the dry season, when overall densities were low but not in the more densely populated wet season. Resting females rarely sleep, but being more vulnerable when lying down, keep their heads up while they ruminate. They thus can act as sentinels for nearby foragers, which can then spend more time with their own heads down. For reasons that are unclear from our samples, the fraction of resting females in the rich region is regularly less than the concurrent fraction of foraging females there. Surveillance visibility might be a factor, although even at peak values, our sward heights were less than 30 cm and more typically 5–12 cm. Whatever



**Table 4**  
**Best models of multiple regression analyses of three intake measures on concurrent parameters**

Season	Parameter <sup>a</sup>	Gross intake rate		Intake/min foraging		Within-bout rate		
		<i>t</i>	<i>P</i>	<i>t</i>	<i>P</i>	<i>t</i>	<i>P</i>	
Dry	Fraction green	7.65	<0.0001	4.58	<0.0001	9.18	<0.0001	
	% Time in head-up	-6.24	<0.0001	-3.71	<0.0001	-1.52	0.1308	
	% Time in Other	-6.51	<0.0001	-3.73	0.0004	-2.84	0.0051	
	Female density	-3.29	0.0012	-3.79	<0.0001	-4.49	<0.0001	
	Standing female proximity	2.73	0.0071	2.48	0.0005	2.46	0.0015	
	Resting female proximity	2.27	0.0249	2.83	0.0012	1.96	0.0513	
	Same day predation	2.26	0.0253	2.30	0.0055	2.36	0.0196	
	Prior day predation	—	—	—	2.08	0.0396	—	
	Disturbance in sample	—	—	—	—	-2.17	0.0317	
	Male density	—	—	1.53	0.1268	—	—	
	Overall <i>r</i> <sup>2</sup>	0.500	0.396	0.427	—	—	—	
	Overall <i>P</i>	<0.0001	<0.0001	<0.0001	—	—	—	
	Wet	% Time in head-up	-6.66	<0.0001	-4.22	<0.0001	—	—
		% Time in other	-5.68	<0.0001	-1.93	0.0548	—	—
Infant abundance		5.04	<0.0001	5.53	<0.0001	7.48	<0.0001	
Prior day predation		-3.05	0.0027	-2.66	0.0087	-3.85	0.0002	
Fraction green		2.42	0.0167	—	—	—	—	
Male density		-1.82	0.0703	-2.07	0.0397	-2.06	0.0414	
Resting female proximity		0.73	0.4562	1.07	0.2857	2.01	0.0458	
Grass height		—	—	-2.05	0.0425	-1.55	0.1237	
Same day predation		—	—	-1.85	0.0659	-2.18	0.0311	
Female density		—	—	1.55	0.1231	—	—	
Overall <i>r</i> <sup>2</sup>		0.447	0.338	0.341	—	—	—	
Overall <i>P</i>		<0.0001	<0.0001	<0.0001	—	—	—	

<sup>a</sup>All parameters listed in the text were included in initial models. Those not listed in the table proved insignificant for all 3 intake rates. Parameters that were not significant for 1 or more rates but significant for others are shown here as blanks. Dry season focal sample  $n = 166$ , Wet season  $n = 169$ .

the reason, a propensity for resting females to favor the poor region provides an incentive for foragers to settle there. Although this would reduce the DGBM being foraged, the loss might be partially made up by increased head-down time. This loss is likely smaller in the wet season than in the dry. There may also be a reduced predation risk near ruminators because the latter are likely to spot approaching predators earlier than preoccupied foragers.

This hypothesis would explain a number of other findings. The observation in Table 3 that the major correlate of the fraction of foraging females in the rich region is the fraction of resting females there fits well. Further support comes from the lesser but positive effect of the fraction of females that are standing: when fewer females are lying down, there is less incentive to forage in the poor region. This, however, likely reflects a push-pull between the 2 states: if most individuals want to forage and favor the rich region, the few ruminators may have to follow them into the rich area or lose any “selfish herd” benefits. Similarly, if most animals have filled their stomachs and want to ruminate, remaining foragers may have to accompany the majority into the poor region. This may explain why the 2 fractions remain correlated across a wide range of ambient densities. It also fits the observed seasonal shifts: because median DGBM levels are nearly 50% higher in the wet season, foragers should be able to fill their stomachs sooner each morning, resulting in a greater fraction of ruminators in wet season herd scans. This is in fact the case: the average fraction of resting females is 15% higher in the wet season than in the dry ( $t = 3.13$ ,  $df = 260$ , and  $P = 0.0019$ ).

Other parameters that were significant in Tables 3 and 4 can be explained without undermining this hypothesis. Recent predations in the dry season resulted in higher intakes later in the same or next day (Table 4), and to accomplish this, foragers were more likely to be found in the rich region (Table 3). In the resource abundant wet season, makeup of intake lost to recent predation disruptions is less

an issue, and here gazelles can afford to respond to recent predations by increasing wariness at the expense of intakes (Table 4). Most infants are born in the early wet season when the fractions of females resting in the poor region are highest (Table 3), but because the many lactating females must eat more, intakes increase when infants are abundant (Table 4). Increased female density was associated with fewer foragers in the rich region (Table 3), and generally depressed mean intakes in the dry season (Table 4). Male density (but not female density) reduced intakes in the wet season, likely due to higher harassment of females when more males were present. The fraction of dry biomass that was green played a major role for all intake rates in the dry season, but only affected gross intakes in the wet. This parameter likely affects both the fraction of grass at a given feeding station that is acceptable, and the ability to spot the next feeding station when search is a critical constraint on intake (Bradbury et al. 1996).

The major alternative to the above hypothesis is that foraging females have some reason to shift to the poor region during the wet season but move back again during dry periods. Resting females would then be dragged along to avoid isolation (China et al. 2008). One possible cause of such shifts is suggested by the work of Wilmshurst et al. (1999, 2000) who argued that savannah ungulates in general, and Thomson’s gazelles in particular, should avoid higher biomass swards because of a tradeoff between intake rates and digestibility. Although stomachs can be filled faster when feeding on high underlying biomasses, these tend to be less digestible and the longer time required to extract energy and nutrients could actually reduce net daily intakes. To identify the optimal biomass density for Thomson’s gazelles, they provisioned 2 captive subadults with wild grasses of varying dry biomass content and 2 different heights. Their method for provisioning elicited wet season functional responses. The resulting predicted optimum, 25-g dry

biomass/m<sup>2</sup>, corresponds to 21 g/m<sup>2</sup> of our wet season DGBM. This value is far below what we observed our gazelles eating: the median wet season DGBM selected by foragers in the poor region was twice the predicted optimum, and that for those in the rich region was 3 times that value. Either the model was improperly cast, or the calibrations used to predict the optimum did not fit our study site. It is easy to see that a moderate change in the model's bite rate dynamics would shift the predicted optimum to higher values, even to values higher than our study animals experienced. It is thus instructive that regressing the DGBM values selected by our foraging females against median DGBM on the sampling day showed a highly linear relationship ( $r = 0.886$  and slope = 1.04), with a daily coefficient of variation in selected DGBM of only 16%. At least over the range of DGBM values experienced by our study populations, there is no evidence of avoidance of high biomass swards. We should also note that if this alternative hypothesis were valid for our site, it would be difficult to explain why the fraction of resting females in the rich region was consistently less than the concurrent fraction of foraging females there.

Isodars have been profitably applied to a variety of bird and mammal species. Convergent isodars in which quantitative and qualitative factors interact differently with ambient density have been reported in cowbirds (Jensen and Cully 2005), urban passerines (Fernandez-Juricic 2001), a variety of rodents (Ovadia and Abramsky 1995; Hansson 1996; Shenbrot 2004), bandicoots (Dexter et al. 2011), feral horses (van Beest et al. 2014), and chital deer (Vijayan et al. 2012). Although crossovers were expected in several of these species, they have only been demonstrated in chital deer. This study on Thomson's gazelles would thus be only the second example in a terrestrial vertebrate field system.

Although the principle of isodar analysis seems superior to classical IFD tests, we encountered 1 problem in practice. Morris (1987) argued that uncertainty in variable causalities and the presence of error in both variables favor the use of Model II regressions for isodar analyses. Despite this early admonition, the subsequent isodar literature remains split between OLS and geometric mean methods. The latter protocol is only recommended when sample sizes are greater than 20 and variable correlation is at least 0.6 (Jolicoeur 1990). These warnings seem to have been ignored in a number of published isodar studies. Our sample sizes were many times the recommended numbers, but our variable correlations were only slightly above the threshold, making some bias likely. This is why we performed both types of regressions and hoped the true values were intermediate.

A related issue concerns the kinds of errors that bias OLS slope estimates. Carroll and Ruppert (1996) and Smith (2009) divide the overall error variance in each regression variable into measurement, sampling, and "natural" error. The latter arises in part from sampled animals not following the "rule" that one is trying to extract using isodars. In our case, animals standing in either region but not foraging were likely not attending to local resource or competitor densities. Mapped foragers may have been moving across poor regions to get to the next feeding station in the rich region. This "noise" does not lead to abscissa bias, but it does affect the resultant slopes and residuals. It is not clear to us which method best handles this source of variation. What we can say is that our OLS results provided clear predictions about phenomena, such as convergence and crossovers, that were later verified, whereas the geometric mean results sometimes left us unable to exclude even random settlement.

A recent study of Soay sheep dispersions concluded that "although the IFD model has proved useful in investigations of animal distribution both in its original and in modified form ..., it may be inappropriate for investigating the distribution of foraging ungulates across a heterogeneous and dynamic food resource" (Jones et al. 2006). We would differ with this conclusion and argue that the isodar "form" of IFD modeling is quite applicable to foraging ungulates and can provide major insights into how these animals disperse and why. Proportional settlement was not observed, as is so often the case, but density dependence and its modulation by both quantitative and qualitative factors were convincingly demonstrated. Clearly, direct field manipulations are now needed to test our suggestion that resting females play a qualitative role in shaping the forager dispersions of Thomson's gazelles, but this all fits nicely within the isodar version of IFD theory.

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