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▶ To cite this version:

Guillaume Péron. Reproductive skews of territorial species in heterogeneous landscapes. Oikos, 2023, 2023 (2), pp.e09627. 10.1111/oik.09627 . hal-03824494

HAL Id: hal-03824494 https://hal.science/hal-03824494

Submitted on 5 Dec 2023 $\,$

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Reproductive skews of territorial species in heterogeneous landscapes

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Abstract (modified from published versions...): I investigated the reproductive skew resulting from the way the variation in social status and resource availability interact to shape the spatial distribution of territories and the resulting inequality in reproductive output in territorial species. Lifetime reproductive success data from 46 species indicated a common pattern in both social and solitary species, namely the emergence of a few high performers amidst a majority of mediocre performers. This first result indicated that reproductive skews are not a unique properties of social species, even if most models of reproductive skews are currently based on within-group social processes. I thus devised a I also used an alternative theoretical model that worked for solitary species, in which the socio-spatial distribution emerged from interactions between immediate neighbors only. Using the model, I predicted a correlation between three statistics of the reproductive skew (the skewness, the Gini coefficient of inequalities, and Hill's index of heavy-tailed distribution) and the degree of spatial autocorrelation in territory quality. I retrieved these three correlations when comparing the reproductive skews of the 46 species. The distribution of lifetime reproductive success was more skewed but also more egalitarian in homogeneous than heterogeneous landscapes, after controlling for the allometric effect of the body mass. In the proposed model, the increase in egalitarian properties of the LRS distribution in heterogeneous landscapes comes from the fact that some individuals "hide" behind their neighbors and secure a better territory than if the distribution was despotic. This work emphasizes that the shape of the distribution of fitness components conveys information besides the mean and the variance, and the potential for nontrivial effects to emerge from simple movement heuristics.

Additional Keywords: ideal despotic distribution; heavy-tailed distribution; Pareto; peer of a peer; socio-spatial structure

1 Introduction

2 Populations of territorial species (Maher and Lott 1995) often exhibit a match between measures of 3 individual quality, e.g., body mass, and measures of territory quality, e.g., resource density (Ens and 4 Goss-Custard 1984, Komdeur 1992, Nystrom 1997, Pryke et al. 2001, Candolin and Voigt 2001, Balbontín and Ferrer 2008, Sergio et al. 2009). Such patterns if they are perfect are termed ideal despotic 5 distributions (Fretwell 1972). Under an ideal despotic distribution, the best individuals cumulate their 6 7 intrinsic advantage and the benefits of a good territory, potentially over multiple breeding attempts. 8 This can yield major heterogeneities in lifetime reproductive success, i.e., a few high performers and 9 many mediocre performers (Hochachka 2006, Balbontín and Ferrer 2008), which is often referred to as 10 reproductive skews in the behavioral ecology literature (Johnstone 2000). However, over iteroparous 11 lifetimes and in the context of life-history tradeoffs, the influence of stochasticity, i.e., luck, oftentimes 12 trumps the effect of fixed individual and environmental variation on reproductive skews (Tuljapurkar et al. 2020, Broekman et al. 2020). In addition, the ideal despotic model is well-known for lacking realism. 13 14 Indeed, the model ignores that information and access to territories are constrained by distance, which 15 hinders the ability of individuals to perfectly match their intrinsic quality and the quality of their 16 territory (Ens and Goss-Custard 1984, Hemelrijk 1999).

17 Territoriality and the emerging socio-spatial structure are not the only drivers of reproductive skews. Indeed, group-living species provide many examples where the main skew-generating 18 19 mechanism corresponds to a within-group process rather than to cross-territory variation (Johnstone 20 2000). Within groups, dominant individuals may monopolize resources and mating opportunities 21 (Murray et al. 2007, Spong et al. 2008, Saltzman et al. 2009, Josi et al. 2021). This observation further 22 challenges the ideal despotic model because in most group-living species, dominants cannot be 23 despotic, they have to make concessions to promote the continued attachment of group mates 24 (Johnstone 2000, Montana et al. 2022). Without concessions, subordinates leave the group (Datta 1988, 25 Buston and Zink 2009). Despite these concessions, the reproductive skews of group-living species are very similar to the reproductive skews of solitary, territorial species (Fig. 1). This suggests that a 26 27 modulating mechanism also occurs in territorial species, i.e., the aforementioned spatial constraints.

28

29 Fig. 1: Comparison of the reproductive skew in solitary, territorial species (grey) and in group-living species

30 (white). The three skew metrics (skewness, Gini coefficient, and Hill's tail index) are explained in the method

31 section. The data sources are presented in Appendix S1 and the method section.



32

33 To further explore how spatial constraints influence the reproductive skew of territorial species, 34 I performed a comparative analysis across terrestrial vertebrates of the relationship between landscape 35 configuration and three measures of the shape of the distribution of lifetime reproductive success: the skewness, the Gini coefficient of inequality, and Hill's tail index (see methods). Next, I devised a 36 37 theoretical scenario designed to explain the patterns that I found in the comparative analysis. Individuals had a fixed individual quality, representing the effect of the genotype and the conditions 38 39 experienced during early life (Albon et al. 1987, Lindstrom 1999, Spagopoulou et al. 2019). They 40 scrounged for the best territory by way of a series of dyadic interactions between immediate neighbors. At each time step, neighbors switched positions whenever their territory and individual qualities did 41 42 not match (Fig. 2a). This simple model corresponds to observations in many species, such as owls (McGinn et al. 2022), gamebirds (Eason and Hannon 1994) and songbirds (Naguib et al. 2004), and also 43 44 agrees with the general common sense that individuals first interact with their immediate neighbors. 45 The main reason why I expected some nontrivial effects to emerge from the above-described simple movement heuristic is that some territories become effectively invisible to potential challengers, or at 46 47 least less accessible than if there was no constraint on who can interact with whom (Figs. 2b-2c). More 48 precisely, a low-quality individual may find itself protected by a shield of high-quality neighbors (Fig. 49 2b). An average individual may secure an above-average territory provided it is hidden behind low-50 quality neighbors (Fig. 2c). The frequency of these situations and the number of individuals that benefit 51 from them expectedly depends on the grain of the landscape. A homogeneous landscape with very 52 clinal changes in territory quality expectedly facilitates the sorting of individual and territory qualities. 53 Individuals would progress in a consistent direction until they hit a wall. This wall could however 54 potentially shield many individuals behind it, leading to the emergence of modules of individuals that 55 interact among themselves but are shielded from interaction with individuals from other modules. By 56 contrast, in a grainy landscape, the sorting of individual and territory qualities is already hindered at 57 small spatial scales. Therefore, homogeneous landscapes should generate more skewed and heavier-

- 58 tailed distributions of lifetime reproductive success than heterogeneous landscapes, but also more
- 59 egalitarian properties, as more individuals benefit from the shielding effect, and as the socio-spatial
- 60 structure is increasingly modular.
- 61 **Fig. 2**: Theoretical model. (a) Neighbors switch position whenever the difference in individual quality (shades of
- 62 blue) does not match the difference in territory quality (shades of orange). Here, individual C takes over the
- 63 territory of individual A. (b) and (c) Two situations in which individual A secures a better territory than C even
- 64 though C is of better individual quality than A.



65

66 Material and methods

67 Econometrics to quantify the reproductive skew

The *Gini coefficient* sums all the pairwise differences between individual LRS values. Denoting *n* the total number of records, x_i and x_j the LRS (or other aspect of performance) of individuals *i* and *j*, and \bar{x} the mean LRS, the Gini coefficient is $G = \frac{1}{2n^2\bar{x}}\sum_i \sum_j |x_j - x_i|$. It takes value 0 if all individuals perform the same, and value 1 if only one individual has a positive reproductive output. I used Davidson's (2009) formula for the standard error of *G*. The main issue with the Gini coefficient is the presence of \bar{x} at the denominator. In practice, the computation is more stable if the data are manipulated so that the minimum performance value is set to 1 instead of 0.

The *skewness* quantifies the asymmetry of the distribution and in particular the frequency and magnitude of records that are above the modal LRS value. It is positive when there is an excess of high performing individuals compared to a symmetric distribution that would have the same variance. Because vertebrate LRS datasets are typically zero-inflated, i.e., the modal value is 0, they almost always exhibit a positive skewness (Tuljapurkar et al. 2020). Importantly, the skewness should not be computed from samples <20 records. Even if its point estimate depends on the first three moments of the distribution only, its standard error depends on the first six moments (Fisher 1930).

To focus on the very best performers only, and quantify how far from the rest of the population they sat and how frequent they were, I selected *Hill's tail index* (Hill 1975). Based on the theoretical distribution $L(x)x^{-\alpha}$ where L(x) is any slowly varying function, and α is Hill's index, the estimator is $\hat{a}^{(k)} = k/\sum_{i=1}^{k} \log\left(\frac{x_{n-i+1}}{x_{n-k}}\right)$, where the records $x_1, ..., x_n$ are sorted in increasing order, *k* is a threshold after which 86 the tail behavior occurs, and log as usual denotes the natural logarithm (base *e*). The standard error is 87 $\hat{\alpha}^{(k)}/\sqrt{k}$. A large α indicates a light-tailed distribution with rare high-performers and/or relatively low 88 extremes. A small α indicates a heavy-tailed distribution with several high-performers and/or very 89 extreme performances. The threshold k can be set arbitrarily but should be optimized instead. I chose 90 the "AMSE" method to compute the optimal threshold (Caeiro and Gomes 2016). This method 91 minimizes a criterion based on the third order Taylor decomposition of the mean squared error in $1/\alpha$. 92 Empirically, this method was stable in small datasets and yielded results consistent with the visual 93 aspect of the distributions. I used the package tea for R (Ossberger 2020), which also lists many 94 alternative tail indexes and threshold optimization methods.

95 Literature search for lifetime reproductive success (LRS) data

96 I only considered vertebrates. In addition, I excluded aquatic species, fish-eating species, and capital 97 breeders with long-distance migration, because I was going to use the terrestrial vegetation of the 98 breeding area to quantify the landscape configuration. Datasets had to document 20 individuals or 99 more.

100 Searching for published LRS data poses a challenge because the search term "lifetime reproductive 101 success" is frequently used in the ecology and evolution literature. For the present study, no attempt 102 was made to put together an exhaustive list of all the LRS data ever collected. To be included, the data 103 had to (i) be publicly available as a downloadable electronic document or as an histogram that I could 104 digitalize without requesting additional information from the authors; and (ii) appear in one of the three 105 sources below. This ad hoc procedure yielded a total of 71 sex-specific datasets from 25 birds, 20 mammals, and 1 reptile. The relatively large number of species (46), their large taxonomic diversity, the 106 107 large array of sampled biomes and natural histories, large array of publication dates, and the fact that I 108 retrieved all the datasets that I a priori listed before launching the search, all suggest a representative 109 sample (Appendix S1).

110 The search was divided in three parts. First, I searched the Dryad data repository (datadryad.org) on 111 July 1, 2020 with the search term "lifetime reproductive success". The search returned 98 results of 112 which 12 met the above criteria. These studies were published between 2012 and 2020. Second I mined 113 the two reference books of the field (Clutton-Brock 1988, Newton 1989), obtaining 14 studies that met the above criteria. In order to also sample datasets published between 1989 and 2012, I used 114 115 webofknowledge.com and Google Scholar, last checking on July 1, 2020. To divide the task into 116 manageable segments, and to filter out the vast majority of studies that mention lifetime reproductive 117 success but do not provide field records of it, I combined the search term "lifetime reproductive success" 118 with the name of specific taxa. These taxa either had lifestyles that make the collection of LRS data 119 possible, or I deemed them to represent reference taxa likely to be mentioned by studies into other taxa: "kestrel", "tit or titmice", "flycatcher", "owl", "bat", "deer", "macaque", "chimpanzee", "mouse", and "meerkat". For each of the taxa names, I considered the first 20 results as sorted by the search engines with default sorting criterion, as well as the cited and citing literature (first 20 citing articles). I then used the title, abstract, and supplementary material titles of the articles to determine whether the articles contained publicly available LRS data. This yielded 33 studies that also met the above criteria. I acknowledge the possibility of observer and popularity biases in this procedure, but the final result suggests a representative sample nonetheless.

Although the definition of LRS is the number of offspring that fledge (for birds) or reach weaning age (for mammals), I included four datasets of lifetime production of recruits and one dataset of lifetime mating success. Another potential source of spurious variation, for socially monogamous species, was that some authors were able to perform a genetic test of paternity to sort out the extra-pair paternities, whereas most authors compiled the number of socially affiliated offspring. In this study, I did not detect any difference between the two approaches.

Lastly, I defined two broad categories of social organization: "solitary" or "group-living". I considered 133 134 the social organization during the breeding period. I used the information provided in the source 135 studies and references therein. Typical solitary species were those that defend an exclusive territory, mostly forage alone, and only associate with their current mate and recent dependent offspring. Typical 136 137 group-living species were those in which group mates are not always closely related to each other and 138 male or female offspring (or both) stay in the natal group after weaning or fledging. A few species proved hard to categorize. I categorized polar bear (Ursus maritimus) as group-living because of routine 139 140 dyadic contacts between individuals and of physical competition between males for access to oestrous 141 females; however this species is traditionally categorized as solitary. Four bird species may nest in loose colonies or alone, and may forage in groups or alone when breeding. I classified two of these as solitary 142 143 on the basis that they defend small territories around the nests, and the other two as group-living on 144the basis that male access to reproduction depended on lek attendance, and the data documented male 145 LRS (Appendix S1). With these decisions, all the populations that I categorized as solitary were also 146 territorial during the breeding season. Most of the populations that I categorized as group-living are 147 territorial too. However, group-living species will correspond to the control group. This is because, 148under my working hypothesis, their reproductive skews mostly come from within-territory social 149 dynamics rather than between-territory differences.

150 Quantifying landscape configuration in the study areas where the LRS datasets were collected

151 The enhanced vegetation index (EVI) is a remote-sensed spatially-explicit measure of the absorbance of

152 infrared light by green vegetation, available at a 250m resolution, and rescaled to take integer values

153 between 1 (no vegetation) and 100 (greenest vegetation).

I used the homogeneity of the EVI across adjacent pixels, denoted EVIHOM hereafter, to quantify landscape configuration (Tuanmu and Jetz 2015). Compared to metrics that use only the greenest time of the year, or the least green, or the dynamics of the seasonal change in greenness, this choice was expected to capture information of the same level of relevance for all the species and all of the worldwide study locations (Tuanmu and Jetz 2015, Tucker et al. 2019). In addition, variation in EVIHOM is largely driven by heterogeneity in landcover, which does not change seasonally as much as the greenness itself does.

161 The formula is EVIHOM(i) = $\sum_{A,B=1}^{100} \frac{P_i(A,B)}{1+(A-B)^2}$ where *A* and *B* represent possible EVI values between 1 and 162 100, and $P_i(A, B)$ is the proportion, among the pairs of pixels that are in the neighborhood of the *i*th 163 pixel, of pairs that take EVI values *A* and *B*. If all the pixels in the neighborhood of the focal pixel have 164 the same EVI value, then EVIHOM=1. Large differences in EVI values within the neighborhood of a 165 pixel cause the EVIHOM to decrease towards 0, because of the $(A - B)^2$ term in the denominator.

The EVIHOM was recently demonstrated to have the best power out of a series of 14 metrics of the same type to predict macroecological patterns such as the number of American passerines in a grid cell (Tuanmu and Jetz 2015) and the travel speed of large birds (Tucker et al. 2019).

169 Because the study animals were sampled over study regions that varied from a few hectares to a full 170 country, I retrieved the EVIHOM value within a radius of 1 to 100km (depending on the quoted study 171 area). I used the median EVIHOM in that circle, removing cities and open water as in the original 172 dataset. The results did not qualitatively change if setting all circle radii to 5km. Next, because large 173 animals range more widely than small animals, I rescaled the EVIHOM metric by dividing it by the log-174 transformed body mass, yielding the metric h = EVIHOM/log(mass). Most of the regressions became statistically non-significant if I removed the allometric scaling (i.e., h = EVIHOM) but they hold if I 175 176 removed the log-transformation of body mass.

177 *Comparative analysis*

Each of the populations contributed a control (group-living) or a treatment (solitary) sample. Across populations, I regressed *h* against the skewness, the log-transformed Hill's tail index, and the logittransformed Gini coefficient, separately for control and treatment samples.

I weighted the regressions by the inverse of the sampling variance of the dependent variables. I incorporated the fixed effects of the sex, the mating system ('mostly monogamous' vs. 'polygynous or promiscuous'), and their interaction. I also tentatively added the fixed effect of the mean LRS of the populations to represent any dependency on the mean in the skew metrics. Lastly, I added the fixed effect of the taxonomic class (birds vs. mammals + one reptile). These fixed effects captured most of the between-species variance. This means that I failed to fit a mixed model with non-null phylogenetic inertia or with a species random effect, as long as the aforementioned fixed effects were already in the model. This suggests that the included species were sufficiently diverse to overcome the effect of phylogenetic inertia in the dependent variables, or that phylogenetic inertia was weak. There were yet only four mammalian solitary species. To quantify the maximum extent to which this taxonomic bias could be confounding, I performed a likelihood ratio test comparing the above model and the model in which I added the interaction between *h* and the taxonomic class. If the test was negative (P>0.05), I concluded that it was possible that the differential effect of *h* in the treatment sample was caused by an excess of birds in that sample.

195 General model for the simulations

196 I considered a grid of 2500 potential territories of which the quality varied randomly with a known 197 spatial autocorrelation range (Appendix S2, part A). At the first time step, 2500 individuals were 198 distributed in the grid cells. Their individual quality was drawn at random from a normal distribution. 199 At each time step, I went through all the pairs of neighbors in the grid and switched their positions whenever one of the neighbors was of lower individual quality and but hold a better territory (Fig. 2a; 200 Appendix S2, part A). Next, the individuals reproduced following a Poisson model and died following 201 202 a binomial model, with expected fecundity and survival rates that depended on individual quality and 203 the quality of the current territory, according to sigmoid functions. I recorded the individual lifetime 204 reproductive success after 30 time steps (only counting individuals that had completed their lifetime).

205 Offspring always emigrated out of the study area. Vacant territories were settled by random 206 individuals. These simplifying assumptions allowed the model to ignore the effect of selection on 207 individual quality, as a first approach.

208 The main unrealistic aspect of the model is that in reality, territorial individuals are reluctant to change 209 location once they have established precedence on a territory (Komdeur 1992, Eason and Hannon 1994, 210 McGinn et al. 2022). However, the model applicability is not seriously challenged for two reasons. First, spatial switches similar to those considered in the model occur during the immature period (Delgado 211 212 et al. 2014, Ducros et al. 2019). Second, the spatial switches of the model may adequately represent any displacement of the boundary between adjacent territories following a conflict. Boundary 213 214 displacements are empirically more common than changes in territory location (Calsbeek and Sinervo 215 2002, Vanpé et al. 2009, Mosser and Packer 2009, Hartmann et al. 2017).

216 Lastly, I devised two null models. The first null model corresponded to the ideal despotic distribution.

217 Each time an individual died and was replaced, I shuffled the individuals so that the match between

- 218 individual quality and territory quality was always perfect. The second null model did not feature any
- 219 territory switch. The individuals remained in their initial territory for their whole life.
- 220 Model parameterization and sensitivity analysis

- 221 The survival and fecundity functions were chosen to represent three paces of life: fast-paced, medium,
- and slow-paced life histories (Appendix S2, part B). In the fast-paced species, the breeding effort was
- 223 maximized and its dependency on territory and individual quality was lower than in the other two
- 224 species. By contrast, in the slow-paced species, the survival probability was maximized to represent
- 225 known patterns in life history variation across species (Péron et al. 2016).
- 226 Next I made the range of the spatial autocorrelation in territory quality to vary between 0 (each territory
- 227 was an independent and identically distributed random variable) and 1000 (very gradual and clinal
- 228 change in territory quality over the grid). I ran 10 simulations per value of the range and per species. I
- 229 recorded the distribution of LRS across individuals for each simulation.
- 230 Results
- 231 *Comparative analysis*
- 232 In solitary species, there was evidence that the skewness increased with the h metric of landscape
- homogeneity (McFadden's $r^2 = 0.32$, Wald's Z statistic = 2.2; ANOVA P-value = 0.03), the Gini coefficient decreased ($r^2 = 0.22$; Z = -2.4; P = 0.02) and weak evidence that the Hill's tail index decreased ($r^2 = 0.12$; Z = -1.2; P = 0.2) (Fig. 3).
- 236 In group-living species, these correlations were in the opposite direction, the support was weak, or both
- 237 (Fig. 3; skewness $r^2 = 0.15$, Z = -0.5, P = 0.7; Gini $r^2 = 0.56$, Z = 1.94, P = 0.001; Hill $r^2 = 0.17$, Z = 0.75, P = 0.75, P
- 238 0.1).
- For the skewness and Hill's index, but not for the Gini coefficient, it was possible for these differences
 to be explained by the taxonomic bias, i.e., the lack of mammals among solitary species (LRT P-values:
 skewness 0.26, Gini 0.009, Hill 0.49).
- 242

- 243 Fig. 3: Left panel: Covariation between the landscape configuration (x-axis) and three metrics of the reproductive
- skew (y-axis) in the simulations. The shaded areas represent the 80% confidence interval of the simulation outcome
- 245 (excluding the two extreme results). Right panel: Same covariation observed in the comparative analysis.



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249 In the three model species (fast-paced, medium, and slow-paced), the reproductive skew changed when 250 the range of the spatial autocorrelation in territory quality changed (Fig. 3). As the range of the spatial 251 autocorrelation in territory quality increased, both the skewness and the Gini coefficient increased (Fig. 252 3). In other words, coarse-grained landscapes with a large autocorrelation range generated more skewed 253 distributions of lifetime reproductive success than fine-grained landscapes, but the distributions were yet more egalitarian, as also observed in the comparative analysis (Appendix S2, part C). By contrast, 254 under the ideal despotic distribution and under the null model with no territory switch, neither the Gini 255 256 coefficient nor the skewness responded to a change in the autocorrelation range (Fig. 3).

Regarding Hill's tail index, when the autocorrelation range increased, the index exhibited a dip then an increase (Fig. 3). This mostly happened for the medium species, but the pattern was still detectible in the other two species. In other words, the extreme performers were most frequent for intermediate values of the autocorrelation range. This makes this prediction hard to test because what constitutes an intermediate value expectedly changes across species and is not typically known.

262 Discussion

263 Studies into reproductive skews have been dominated by group-living species, especially those with a 264 steep effect of the social rank on the breeding output (Johnstone 2000). Here, I adopted a relatively basic, demographic definition of "reproductive skew", and I used three different metrics to quantify it, making 265 it possible to focus on the reproductive skews of solitary, territorial species. In solitary, territorial 266 species, I predicted that the socio-spatial structure would depend on the landscape configuration, 267 268 yielding a correlation between the landscape configuration and the reproductive skew. In a comparative 269 analysis of 46 species, the distribution of lifetime reproductive success was indeed more skewed, but 270 also more egalitarian, in homogeneous than heterogeneous landscapes. My explanation for the increase 271 in skewness is that homogeneous landscapes facilitate the sorting of individual and territory quality. 272 My explanation for the increase in egalitarian properties, i.e., decrease in Gini coefficient, is that 273 homogeneous landscapes feature blocks of good territories separated by blocks of bad territories, and 274 thereby the shielding effect depicted in Figs. 2b and 2c affects more individuals than in heterogeneous 275 landscapes. This is supported by the fact that the theoretical model depicted in Fig. 2 reproduced the 276 observed correlations. By contrast, the ideal despotic model cannot explain the observed correlations 277 (Fig. 3). The proposed model is clearly too simple for me to claim that the congruence of patterns 278 represents strong inference. Nevertheless, the exercise further brought to the fore the interest of 279 analyzing the shape of the distribution of fitness components beyond the mean and the variance 280 (Tuljapurkar et al. 2020). I also highlighted an intriguing aspect of the socio-spatial organization that 281 may be general to many species of territorial animals or any situation where individuals can secure 282 exclusive access to some resource item (Figs. 2b and 2c).

283 On the use of econometrics in biodemography

While the skewness is familiar to ecologists, I also used in this paper two statistics that come from the field of economy: the Gini coefficient and Hill's tail index. In economy, they are used to describe and analyze the accumulation of wealth and influence, e.g., pyramid schemes, Pareto laws, and income inequalities (Wegrzycki et al. 2017, Pluchino et al. 2018).

- There are many examples of accumulation processes in vertebrate biodemography: alpha individuals that monopolize the group reproductive output (Johnstone 2000), dominant territory owners that combine their intrinsic advantage to the advantage associated with a good territory over multiple breeding attempts (Hochachka 2006). Tail indexes appear especially suited to document the fitness consequences of these processes. Overall, in this study, 18% of the datasets exhibited a very heavy tail ($\alpha < 2$). $\alpha < 2$ means that the density function decreased slower than $1/LRS^2$ for very large *LRS* values. In other words, the situation in which a few individuals monopolize reproduction was not rare, but it
- is not the general case either.

296 Hill's tail index appeared somewhat less informative than the skewness and Gini coefficient in this 297 study (Fig. 3). An important caveat regarding tail indices is that they are, by construction, computed from a small sample, typically <10% of the total sample. They can be instable for this reason, which is 298 299 maybe why in the simulation, it was difficult to draw a clear prediction based on Hill's tail index (Fig. 300 3). Hill's tail index nevertheless did capture information not conveyed by the either the Gini coefficient 301 or the skewness (both r² < 20%). For example, male Verreaux's sifakas Propithecus verreauxi exhibited 302 one of the heaviest tail indexes ($\alpha = 1.8$) but one of the most egalitarian Gini coefficients (G = 0.33) (data: 303 Lawler 2007). Hill's tail index seemed to capture the occurrence of a few dominant males that sired most 304 of the offspring, whereas the Gini coefficient seemed to capture the fact that the rest of the group was 305 egalitarian in terms of access to reproduction. These are two major aspects of the "lemur syndrome" (Kappeler and Schäffler 2008). In the typical group-living vertebrate, the social hierarchy is more linear 306 307 (Appleby 1983, McDonald and Shizuka 2013), which would have generated a larger Gini coefficient. 308 Therefore, the Gini coefficient and Hill's tail index appeared complementary in this instance.

309 On the other hand, when the three metrics "light up" at the same time, they may indicate a strong 310 cumulative effect of fixed individual or environmental variation. For example, female Northern 311 elephant-seals Mirounga angustirostris (not incuded in the present study) tested consistently skewed for 312 all three statistics (S = 2.9; $\alpha = 2.2$; G = 0.45; Le Boeuf et al. 2019). This group-living species is very 313 iteroparous, with a strong cumulative effect of individual quality (Oosthuizen et al. 2021). Elephant-314 seals do not experience a major late-life cost if their start to breed early (Oosthuizen et al. 2021). In a faster-living species than elephant-seals, trade-offs between the first and subsequent breeding attempts 315 316 (functional or allocation) could theoretically influence the shape of the distribution of LRS more than 317 any fixed individual trait. The outcome of the first breeding attempt is indeed expected to be stochastic, 318 making it possible for reproductive skews to emerge by chance only (Tuljapurkar et al. 2020). For 319 example, common kestrels (*Falco tinnunculus*) exhibit a moderate skew (S = 1.6; $\alpha = 4.0$; G = 0.36) but it 320 is reportedly driven by stochasticity, rather than by fixed variation in individual or territory quality 321 (Broekman et al. 2020). This maybe suggests that combining the three skew metrics, instead of using 322 just the skewness, can help explore and characterize the relative importance of late-life breeding 323 attempts and in particular the influence of the stochastic outcome of the first breeding attempt.

324 Interpretation in graph theory terms

In Figs. 2b and 2c, the neighbors of an individual protect it from challenges by third parties. In graph theory terms, one would term that an indirect connection between the focal individual and its potential competitors. The number of indirect connections, termed the social reach, and the eigenvector centrality which is computed from the adjacency matrix, both measure the influence that a focal individual garners through its direct and indirect connections (Newman 2008). Their computation could be weighted according to the individual and territory qualities. The social reach and eigenvector centrality would then measure how many competitors are blocked from challenging a given individual, how strong they are, and how incentivized they are, i.e., the advantage that the individual gains compared to if there was no spatial constraint on who can interact with whom.

334 Elsewhere, in more classical types of animal social networks, the social reach and the eigenvector 335 centrality score have been correlated to aspects of individual fitness. For example, among male manakin 336 birds that collaborate to display for the females, the centrality of an individual in the collaboration 337 network predicted its eventual accession to alpha status (McDonald 2007, Ryder et al. 2008). In 338 hierarchized groups, the fitness benefits associated with the social rank, combined with the transitivity 339 of the social rank (Appleby 1983, McDonald and Shizuka 2013), suggest that top individuals rely on intermediate rankers to control the individuals down the line (Von Holst et al. 2002, Addessi et al. 2008). 340 341 Lastly, the position of an individual in contact networks predicted the odds or the speed at which it 342 picked up new information (Aplin et al. 2012, Allen et al. 2013, Claidière et al. 2013, Kulahci et al. 2016).

343

In conclusion, nontrivial patterns may emerge from simple decision rules, because of indirect effects 344 345 that propagate in the socio-spatial structure of the population. These effects would be challenging to document directly in the field because of the exponential number of indirect connections each 346 347 individual has in a grid network and because any missing observation could disproportionately 348 influence the inference. On the other hand, the LRS expectedly integrates the influence of all these social interactions, which was confirmed here by the fact that the reproductive skew responded to the 349 350 landscape configuration. For this reason, and following the lemur example outlined above, computing 351 the different aspects of the reproductive skew appears promising in order to help quantify the between-352 species variance in the social organization. Following the kestrel and elephant seal examples, the 353 reproductive skew may also correlate with the relative contribution of late-life breeding attempts to 354 LRS, and in particular the magnitude of the effect of the stochastic outcome of the first breeding attempt. 355 The fact that the three skew metrics (skewness, Gini coefficient, and Hill's tail index) appeared 356 complementary to each other in this study is especially promising regarding their ability to help 357 discriminate between the numerous drivers of variation in LRS across populations. I recommend that 358 researchers interested in individual heterogeneity use not only the variance and skewness, but also the 359 Gini coefficient and Hill's tail index.

360

Supplementary Materials: Appendix S1: Dataset for the comparative analysis. Appendix S2: (A) R script (B) Parameterization (C) Agreement test.

Funding: This research received no external funding.

Data Availability Statement: This manuscript does not use new data. All data sources are listed in Appendix S1.

Acknowledgments: I thank all the people who contributed to the collection and curation of the datasets of lifetime reproductive success over the years.

Conflicts of Interest: The author declares no conflict of interest

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