



HAL
open science

Reproductive skews of territorial species in heterogeneous landscapes

Guillaume Péron

► **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-03824494v1>

Submitted on 5 Dec 2023

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

Reproductive skews of territorial species in heterogeneous landscapes

Guillaume Péron

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

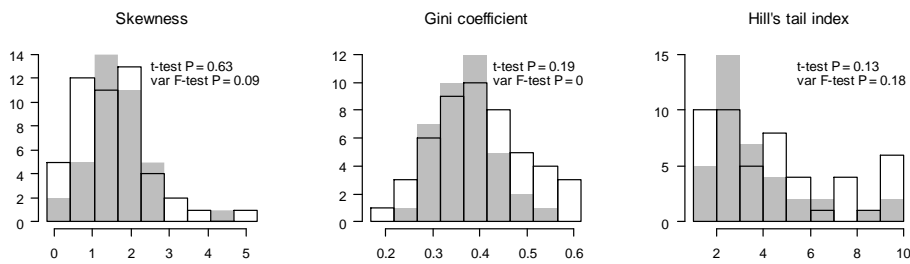
1 **Introduction**

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
5 and Ferrer 2008, Sergio et al. 2009). Such patterns if they are perfect are termed ideal despotic
6 distributions (Fretwell 1972). Under an ideal despotic distribution, the best individuals cumulate their
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
13 et al. 2020, Broekman et al. 2020). In addition, the ideal despotic model is well-known for lacking realism.
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
18 skews. Indeed, group-living species provide many examples where the main skew-generating
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
26 very similar to the reproductive skews of solitary, territorial species (Fig. 1). This suggests that a
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.

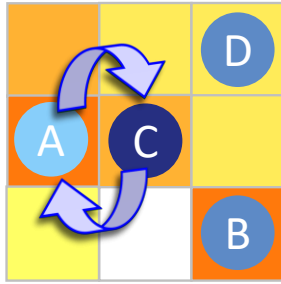


32
33 To further explore how spatial constraints influence the reproductive skew of territorial species,
34 I performed a comparative analysis across terrestrial vertebrates of the relationship between landscape
35 configuration and three measures of the shape of the distribution of lifetime reproductive success: the
36 skewness, the Gini coefficient of inequality, and Hill's tail index (see methods). Next, I devised a
37 theoretical scenario designed to explain the patterns that I found in the comparative analysis.
38 Individuals had a fixed individual quality, representing the effect of the genotype and the conditions
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.
41 At each time step, neighbors switched positions whenever their territory and individual qualities did
42 not match (Fig. 2a). This simple model corresponds to observations in many species, such as owls
43 (McGinn et al. 2022), gamebirds (Eason and Hannon 1994) and songbirds (Naguib et al. 2004), and also
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
46 movement heuristic is that some territories become effectively invisible to potential challengers, or at
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-

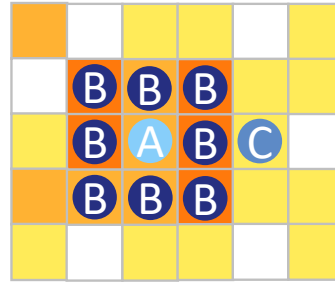
58 tailed distributions of lifetime reproductive success than heterogeneous landscapes, but also more
 59 egalitarian properties, as more individuals benefit from the shielding effect, and as the socio-spatial
 60 structure is increasingly modular.

61 **Fig. 2:** Theoretical model. (a) Neighbors switch position whenever the difference in individual quality (shades of blue)
 62 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.

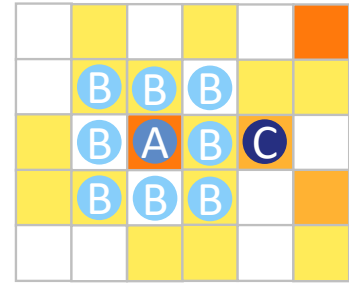
(a) Basic principle



(b) Situation 1



(c) Situation 2



65

66 Material and methods

67 *Econometrics to quantify the reproductive skew*

68 The *Gini coefficient* sums all the pairwise differences between individual LRS values. Denoting n the total
 69 number of records, x_i and x_j the LRS (or other aspect of performance) of individuals i and j , and \bar{x} the
 70 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
 71 same, and value 1 if only one individual has a positive reproductive output. I used Davidson's (2009)
 72 formula for the standard error of G . The main issue with the Gini coefficient is the presence of \bar{x} at the
 73 denominator. In practice, the computation is more stable if the data are manipulated so that the
 74 minimum performance value is set to 1 instead of 0.

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

82 To focus on the very best performers only, and quantify how far from the rest of the population they sat
 83 and how frequent they were, I selected *Hill's tail index* (Hill 1975). Based on the theoretical distribution
 84 $L(x)x^{-\alpha}$ where $L(x)$ is any slowly varying function, and α is Hill's index, the estimator is $\hat{\alpha}^{(k)} =$
 85 $k / \sum_{i=1}^k \log\left(\frac{x_{n-i+1}}{x_{n-k}}\right)$, where the records x_1, \dots, 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
106 mammals, and 1 reptile. The relatively large number of species (46), their large taxonomic diversity, the
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
114 the above criteria. In order to also sample datasets published between 1989 and 2012, I used
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:

120 “kestrel”, “tit or titmice”, “flycatcher”, “owl”, “bat”, “deer”, “macaque”, “chimpanzee”, “mouse”, and
121 “meerkat”. For each of the taxa names, I considered the first 20 results as sorted by the search engines
122 with default sorting criterion, as well as the cited and citing literature (first 20 citing articles). I then used
123 the title, abstract, and supplementary material titles of the articles to determine whether the articles
124 contained publicly available LRS data. This yielded 33 studies that also met the above criteria. I
125 acknowledge the possibility of observer and popularity biases in this procedure, but the final result
126 suggests a representative sample nonetheless.

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

133 Lastly, I defined two broad categories of social organization: “solitary” or “group-living”. I considered
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,
136 mostly forage alone, and only associate with their current mate and recent dependent offspring. Typical
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
139 proved hard to categorize. I categorized polar bear (*Ursus maritimus*) as group-living because of routine
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
142 colonies or alone, and may forage in groups or alone when breeding. I classified two of these as solitary
143 on the basis that they defend small territories around the nests, and the other two as group-living on
144 the 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,
148 under 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).

154 I used the homogeneity of the EVI across adjacent pixels, denoted EVIHOM hereafter, to quantify
155 landscape configuration (Tuanmu and Jetz 2015). Compared to metrics that use only the greenest time
156 of the year, or the least green, or the dynamics of the seasonal change in greenness, this choice was
157 expected to capture information of the same level of relevance for all the species and all of the
158 worldwide study locations (Tuanmu and Jetz 2015, Tucker et al. 2019). In addition, variation in
159 EVIHOM is largely driven by heterogeneity in landcover, which does not change seasonally as much as
160 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.

166 The EVIHOM was recently demonstrated to have the best power out of a series of 14 metrics of the same
167 type to predict macroecological patterns such as the number of American passerines in a grid cell
168 (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 $h = EVIHOM/\log(\text{mass})$. Most of the regressions became
175 statistically non-significant if I removed the allometric scaling (i.e., $h = EVIHOM$) but they hold if I
176 removed the log-transformation of body mass.

177 *Comparative analysis*

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

181 I weighted the regressions by the inverse of the sampling variance of the dependent variables. I
182 incorporated the fixed effects of the sex, the mating system ('mostly monogamous' vs. 'polygynous or
183 promiscuous'), and their interaction. I also tentatively added the fixed effect of the mean LRS of the
184 populations to represent any dependency on the mean in the skew metrics. Lastly, I added the fixed
185 effect of the taxonomic class (birds vs. mammals + one reptile). These fixed effects captured most of the
186 between-species variance. This means that I failed to fit a mixed model with non-null phylogenetic
187 inertia or with a species random effect, as long as the aforementioned fixed effects were already in the

188 model. This suggests that the included species were sufficiently diverse to overcome the effect of
189 phylogenetic inertia in the dependent variables, or that phylogenetic inertia was weak. There were yet
190 only four mammalian solitary species. To quantify the maximum extent to which this taxonomic bias
191 could be confounding, I performed a likelihood ratio test comparing the above model and the model in
192 which I added the interaction between h and the taxonomic class. If the test was negative ($P > 0.05$), I
193 concluded that it was possible that the differential effect of h in the treatment sample was caused by an
194 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
200 whenever one of the neighbors was of lower individual quality and but hold a better territory (Fig. 2a;
201 Appendix S2, part A). Next, the individuals reproduced following a Poisson model and died following
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,
211 spatial switches similar to those considered in the model occur during the immature period (Delgado
212 et al. 2014, Ducros et al. 2019). Second, the spatial switches of the model may adequately represent any
213 displacement of the boundary between adjacent territories following a conflict. Boundary
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,
222 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*

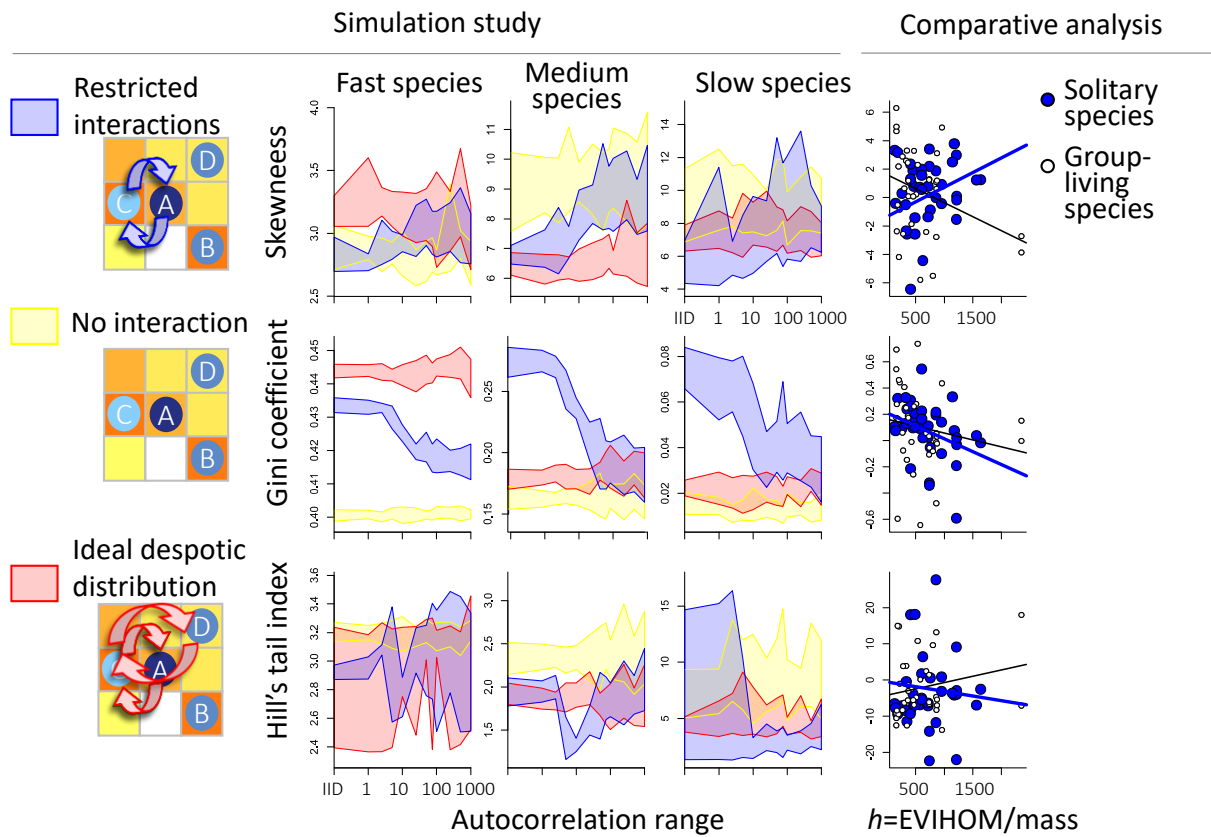
232 In solitary species, there was evidence that the skewness increased with the h metric of landscape
233 homogeneity (McFadden's $r^2 = 0.32$, Wald's Z statistic = 2.2; ANOVA P-value = 0.03), the Gini coefficient
234 decreased ($r^2 = 0.22$; $Z = -2.4$; $P = 0.02$) and weak evidence that the Hill's tail index decreased ($r^2 = 0.12$;
235 $Z = -1.2$; $P = 0.2$) (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 $r^2 = 0.17$, $Z = 0.75$, $P =$
238 0.1).

239 For the skewness and Hill's index, but not for the Gini coefficient, it was possible for these differences
240 to be explained by the taxonomic bias, i.e., the lack of mammals among solitary species (LRT P-values:
241 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
 244 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.



246

247

248 *Simulation study*

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
 254 yet more egalitarian, as also observed in the comparative analysis (Appendix S2, part C). By contrast,
 255 under the ideal despotic distribution and under the null model with no territory switch, neither the Gini
 256 coefficient nor the skewness responded to a change in the autocorrelation range (Fig. 3).

257 Regarding Hill's tail index, when the autocorrelation range increased, the index exhibited a dip then an
 258 increase (Fig. 3). This mostly happened for the medium species, but the pattern was still detectible in
 259 the other two species. In other words, the extreme performers were most frequent for intermediate
 260 values of the autocorrelation range. This makes this prediction hard to test because what constitutes an
 261 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,
265 demographic definition of “reproductive skew”, and I used three different metrics to quantify it, making
266 it possible to focus on the reproductive skews of solitary, territorial species. In solitary, territorial
267 species, I predicted that the socio-spatial structure would depend on the landscape configuration,
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*

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

288 There are many examples of accumulation processes in vertebrate biodemography: alpha individuals
289 that monopolize the group reproductive output (Johnstone 2000), dominant territory owners that
290 combine their intrinsic advantage to the advantage associated with a good territory over multiple
291 breeding attempts (Hochachka 2006). Tail indexes appear especially suited to document the fitness
292 consequences of these processes. Overall, in this study, 18% of the datasets exhibited a very heavy tail
293 ($\alpha < 2$). $\alpha < 2$ means that the density function decreased slower than $1/LRS^2$ for very large LRS values.
294 In other words, the situation in which a few individuals monopolize reproduction was not rare, but it
295 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
298 from a small sample, typically <10% of the total sample. They can be instable for this reason, which is
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 either the Gini coefficient
301 or the skewness (both $r^2 < 20\%$). 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"
306 (Kappeler and Schaffler 2008). In the typical group-living vertebrate, the social hierarchy is more linear
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 included 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
315 faster-living species than elephant-seals, trade-offs between the first and subsequent breeding attempts
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*

325 In Figs. 2b and 2c, the neighbors of an individual protect it from challenges by third parties. In graph
326 theory terms, one would term that an indirect connection between the focal individual and its potential
327 competitors. The number of indirect connections, termed the social reach, and the eigenvector centrality
328 which is computed from the adjacency matrix, both measure the influence that a focal individual
329 garners through its direct and indirect connections (Newman 2008). Their computation could be

330 weighted according to the individual and territory qualities. The social reach and eigenvector centrality
331 would then measure how many competitors are blocked from challenging a given individual, how
332 strong they are, and how incentivized they are, i.e., the advantage that the individual gains compared
333 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
340 intermediate rankers to control the individuals down the line (Von Holst et al. 2002, Addessi et al. 2008).
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

344 In conclusion, nontrivial patterns may emerge from simple decision rules, because of indirect effects
345 that propagate in the socio-spatial structure of the population. These effects would be challenging to
346 document directly in the field because of the exponential number of indirect connections each
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
349 interactions, which was confirmed here by the fact that the reproductive skew responded to the
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

References

- Addessi, E. et al. 2008. Preference transitivity and symbolic representation in capuchin monkeys (*Cebus apella*). - *PLoS One* 3: e2414.
- Albon, S. D. et al. 1987. Early development and population-dynamics in red deer .2. Density-independent effects and cohort variation. - *J. Anim. Ecol.* 56: 69–81.
- Allen, J. et al. 2013. Network-based diffusion analysis reveals cultural transmission of lobtail feeding in humpback whales. - *Science* 340: 485–488.
- Aplin, L. M. et al. 2012. Social networks predict patch discovery in a wild population of songbirds. - *Proc. R. Soc. B-Biological Sci.* 279: 4199–4205.
- Appleby, M. C. 1983. The probability of linearity in hierarchies. - *Anim. Behav.* 31: 600–608.
- Balbontin, J. and Ferrer, M. 2008. Density-dependence by habitat heterogeneity: individual quality versus territory quality. - *Oikos* 117: 1111–1114.
- Broekman, M. J. E. et al. 2020. Relative contributions of fixed and dynamic heterogeneity to variation in lifetime reproductive success in kestrels (*Falco tinnunculus*). - *Popul. Ecol.* 62: 408–424.
- Buston, P. M. and Zink, A. G. 2009. Reproductive skew and the evolution of conflict resolution: A synthesis of transactional and tug-of-war models. - *Behav. Ecol.* 20: 672–684.
- Caeiro, F. and Gomes, I. M. 2016. Threshold selection in extreme value analysis. - In: *Extreme Value Modeling and Risk Analysis: Methods and Applications*. pp. 69–86.
- Calsbeek, R. and Sinervo, B. 2002. An experimental test of the ideal despotic distribution. - *J. Anim. Ecol.* 71: 513–523.
- Candolin, U. and Voigt, H.-R. 2001. Correlation between male size and territory quality: consequence of male competition or predation susceptibility? - *Oikos* 95: 225–230.
- Claidière, N. et al. 2013. Diffusion dynamics of socially learned foraging techniques in squirrel monkeys. - *Curr. Biol.* 23: 1251–1255.
- Clutton-Brock, T. H. 1988. *Reproductive Success Studies of Individual Variation in Contrasting Breeding Systems* (T Clutton-Brock, Ed.). - University of Chicago Press.
- Datta, S. 1988. The acquisition of dominance among free-ranging rhesus monkey siblings. - *Anim. Behav.* 36: 754–772.
- Davidson, R. 2009. Reliable inference for the Gini index. - *J. Econom.* 150: 30–40.
- Delgado, M. del M. et al. 2014. A statistical framework for inferring the influence of conspecifics on movement behaviour. - *Methods Ecol. Evol.* in press.
- Ducros, D. et al. 2019. Beyond dispersal versus philopatry? Alternative behavioural tactics of juvenile roe deer in a heterogeneous landscape. - *Oikos* in press.
- Eason, P. and Hannon, S. J. 1994. New birds on the block: new neighbors increase defensive costs for territorial male willow ptarmigan. - *Behav. Ecol. Sociobiol.* 34: 419–426.
- Ens, B. J. and Goss-Custard, J. D. 1984. Interference Among Oystercatchers, *Haematopus ostralegus*, Feeding on Mussels, *Mytilus edulis*, on the Exe Estuary. - *J. Anim. Ecol.* 53: 217.
- Fisher, R. A. 1930. The moments of the distribution for normal samples of measures of departure from normality. - *Proc. R. Soc. London. Ser. A - Math. Phys. Sci.* 130: 16–28.
- Fretwell, S. D. 1972. *Populations in a Seasonal Environment*. - Princeton University Press.
- Hartmann, S. A. et al. 2017. Decline in territory size and fecundity as a response to carrying capacity in an endangered songbird. - *Oecologia* 183: 597–606.
- Hemelrijk, C. K. 1999. An individual-orientated model of the emergence of despotic and egalitarian societies. - *Proc. R. Soc. B Biol. Sci.* 266: 361–369.

- Hill, B. M. 1975. A Simple General Approach to Inference About the Tail of a Distribution. - *Ann. Stat.* 3: 1163–1174.
- Hochachka, W. M. 2006. Unequal lifetime reproductive success and its implication for small isolated populations. - In: Smith, J. N. M. et al. (eds), *Conservation and biology of small populations: the song sparrows of Mandarte Island*. Oxford University Press, pp. 155–173.
- Johnstone, R. A. 2000. Models of reproductive skew: A review and synthesis. - *Ethology* 106: 5–26.
- Josi, D. et al. 2021. Age- and sex-dependent variation in relatedness corresponds to reproductive skew, territory inheritance, and workload in cooperatively breeding cichlids. - *Evolution* 75: 2881–2897.
- Kappeler, P. M. and Schäffler, L. 2008. The lemur syndrome unresolved: Extreme male reproductive skew in sifakas (*Propithecus verreauxi*), a sexually monomorphic primate with female dominance. - *Behav. Ecol. Sociobiol.* 62: 1007–1015.
- Komdeur, J. 1992. Importance of habitat saturation and territory quality for evolution of cooperative breeding in the Seychelles warbler. - *Nature* 358: 493–495.
- Kulahci, I. G. et al. 2016. Social networks predict selective observation and information spread in ravens. - *R. Soc. Open Sci.* 3: 160256.
- Lawler, R. R. 2007. Fitness and extra-group reproduction in male Verreaux's sifaka: An analysis of reproductive success from 1989–1999. - *Am. J. Phys. Anthropol.* 132: 267–277.
- Le Boeuf, B. et al. 2019. Lifetime reproductive success of northern elephant seals (*Mirounga angustirostris*). - *Can. J. Zool.* 97: 1203–1217.
- Lindstrom, J. 1999. Early development and fitness in birds and mammals. - *Trends Ecol. Evol.* 14: 343–348.
- Maher, C. R. and Lott, D. F. 1995. Definitions of territoriality used in the study of variation in vertebrate spacing systems. - *Anim. Behav.* 49: 1581–1597.
- McDonald, D. B. 2007. Predicting fate from early connectivity in a social network. - *Proc. Natl. Acad. Sci. U. S. A.* 104: 10910–10914.
- McDonald, D. B. and Shizuka, D. 2013. Comparative transitive and temporal orderliness in dominance networks. - *Behav. Ecol.* 24: 511–520.
- McGinn, K. A. et al. 2022. Implications of non-ideal occupancy for the measurement of territory quality. - *Glob. Ecol. Conserv.* 35: e02097.
- Montana, L. et al. 2022. Large eastern grey kangaroo males are dominant but do not monopolize matings. - *Behav. Ecol. Sociobiol.* 2022 766 76: 1–16.
- Mosser, A. and Packer, C. 2009. Group territoriality and the benefits of sociality in the African lion, *Panthera leo*. - *Anim. Behav.* 78: 359–370.
- Murray, C. M. et al. 2007. Dominance rank influences female space use in wild chimpanzees, *Pan troglodytes*: towards an ideal despotic distribution. - *Anim. Behav.* 74: 1795–1804.
- Naguib, M. et al. 2004. Effects of territorial intrusions on eavesdropping neighbors: communication networks in nightingales. - *Behav. Ecol.* 15: 1011–1015.
- Newman, M. E. J. 2008. The mathematics of networks. - In: Blume, L. E. and Durlauf, S. N. (eds), *The New Palgrave Encyclopedia of Economics*. Palgrave Macmillan, pp. 312–334.
1989. Lifetime reproduction in birds (I Newton, Ed.). - Academic Press.
- Nystrom, K. G. K. 1997. Food density, song rate, and body condition in territory-establishing willow warblers (*Phylloscopus trochilus*). - *Can. J. Zool.* 75: 47–58.
- Oosthuizen, W. C. et al. 2021. Positive early-late life-history trait correlations in elephant seals. - *Ecology* 102: e03288.
- Ossberger, J. 2020. tea: Threshold Estimation Approaches, R package version 1.1. in press.
- Péron, G. et al. 2016. Evidence of reduced individual heterogeneity in adult survival of long-lived species. - *Evolution* 70: 2909–2914.
- Pluchino, A. et al. 2018. Talent versus luck: The role of randomness in success and failure. - *Adv. Complex Syst.* 21: 1850014.
- Pryke, S. R. et al. 2001. Agonistic carotenoid signalling in male red-collared widowbirds: Aggression related to the colour signal of both the territory owner and model intruder. - *Anim. Behav.* 62: 695–704.
- Ryder, T. B. et al. 2008. Social networks in the lek-mating wire-tailed manakin (*Pipra filicauda*). - *Proc. R. Soc. B Biol. Sci.* 275: 1367–1374.
- Saltzman, W. et al. 2009. Reproductive skew in female common marmosets: What can proximate mechanisms tell us about ultimate causes? - *Proc. R. Soc. B Biol. Sci.* 276: 389–399.
- Sergio, F. et al. 2009. Short- and long-term consequences of individual and territory quality in a long-lived bird. - *Oecologia* 160: 507–514.
- Spagopoulou, F. et al. 2019. Silver-spoon upbringing improves early-life fitness but promotes reproductive ageing in a wild bird. - *bioRxiv*: 535625.
- Spong, G. F. et al. 2008. Factors affecting the reproductive success of dominant male meerkats. - *Mol. Ecol.* 17: 2287–

2299.

- Tuanmu, M. N. and Jetz, W. 2015. A global, remote sensing-based characterization of terrestrial habitat heterogeneity for biodiversity and ecosystem modelling. - *Glob. Ecol. Biogeogr.* 24: 1329–1339.
- Tucker, M. A. et al. 2019. Large birds travel farther in homogeneous environments (V Boucher-Lalonde, Ed.). - *Glob. Ecol. Biogeogr.* 28: 576–587.
- Tuljapurkar, S. et al. 2020. Skewed distributions of lifetime reproductive success: beyond mean and variance (J Drake, Ed.). - *Ecol. Lett.* 23: 748–756.
- Vanpé, C. et al. 2009. Access to mates in a territorial ungulate is determined by the size of a male's territory, but not by its habitat quality. - *J. Anim. Ecol.* 78: 42–51.
- Von Holst, D. et al. 2002. Social rank, fecundity and lifetime reproductive success in wild European rabbits (*Oryctolagus cuniculus*). - *Behav. Ecol. Sociobiol.* 51: 245–254.
- Wegrzycki, K. et al. 2017. Why do cascade sizes follow a power-law? - 26th Int. World Wide Web Conf. WWW 2017: 569–576.