
Spatial Marked Point Patterns for Herd Dispersion in a Savanna Wildlife Herbivore Community in Kenya

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Summary. Quantitative descriptions of animal species' distributions at the ecosystem level are rare. In this study we used marked spatial point pattern analysis to characterize herd spatial distributions of several species comprising a savanna large herbivore community in Laikipia, central Kenya. Points are the herd centres, marks are the herd sizes. Previous research [15] identified possible discrepancies between prey and non-prey species on the basis of the nearest neighbour distance function. In this paper we make a similar distinction and analyse possible consequences. Analysis concentrated on Ripley's K -function on several data subsets. A digitised boundary of the area has been included. The herd patterns of Thomson gazelle and of the plains zebra were modelled with a Strauss marked point process. The pattern of the Thomson gazelle showed a single mode, whereas that of the plains zebra showed multiple modes. This can be well explained by the ecosystem behavior (habitat specialist versus habitat generalist) of the two species.

Key words: Herbivores, Laikipia, Nearest neighbour distances, Savanna, Spatial point pattern

1 Introduction

Herbivores living freely in nature tend to aggregate in groups or herds of various sizes. These herds usually do not randomly distribute and therefore display spatial distribution patterns [15]. An explanation for variation in animal grouping and distribution can be given on the basis of physiological grounds, invoking metabolic requirements, on ecological grounds, invoking habitat preference [8], feeding style, competition, facilitation [1, 11], and food distribution [17], and on climatic grounds [18]. In the past, both a statistical and an ecological study have been devoted to modelling herds of herbivores in space [14, 15]. None of these studies, however, employs a marked point pattern spatial statistics approach – herd size has not been taken into account so

far. A marked point pattern analysis explicitly uses the locations of herds and distances between the herds, whereas the size of a herd is likely to be related with ecological conditions.

Advances in Global Positioning System technology (GPS; see [19]), and spatial point pattern analysis [3, 13], permitted us to characterize spatial distributions of the nine most abundant large herbivore species in the Laikipia ecosystem of central Kenya. The data, representing marked point measurements of herds, were collected in 1996 during a total count of wildlife in an area of 7,100 km², using 10 aircraft equipped with GPS receivers [5]. Apart from the characterization, also herd size has been measured by counting the number of animals grouping together. We distinguish and further differentiate those that can be preyed upon by large carnivores (Plains zebra *Equus burchelli* (Gray)), impala *Aepyceros melampus*, Grant's gazelle *Gazella grantii*, eland *Taurotragus oryx* and hartebeest *Alcelaphus buselaphus*), those that are too large to be preyed upon (buffalo *Syncerus caffer*, elephant *Loxodonta africana* and giraffe *Giraffa, camelopardalis*) and those that are too small to be preyed upon (Thomson's gazelle *Gazelli thomsoni* (Gunther)).

Three methods of spatial point pattern analysis were used to characterize the distributions of wild herbivore herds for each species separately, and for all species combined: the marked K -function, the pair correlation function and fitting of the Strauss process to both the marked and the unmarked point process. Possible causes of observed patterns of dispersion within and among species are discussed.

The aim of this study has been to further explore the relations between herds of different animals species and combinations of species using marked points processes. We aimed to combine the sizes of the herds as additional information, having in mind that large herds of herbivores may show different behavior than herds of a smaller size. The study is illustrated with the unique point pattern data set from the Laikipia area.

2 Materials and Methods

2.1 Distribution Data

Data in this study were collected during a total count within Laikipia District over three days in September 1996 ([5]; the region is also described in [6]). The area of 7,100 km² was divided into daily counting blocks of approximately 200 to 300 km², and each block was allocated to one aircraft per day. Ten high winged aircraft were used simultaneously to systematically search each block. Each aircraft flew at heights between 70 and 130 m above ground level, following transects spaced 1 km apart. Whenever an animal or a group of animals was spotted, the aircraft deviated from its flight-line to circle the observed animals until their number was counted. Geographical co-ordinates of positions of the centers of the herds were recorded using a Trimble GPS

receiver. Overlaps and double counts at the boundaries of the blocks were identified and subtracted from the total wildlife numbers as a correction for count overlaps. This resulted in a data set of 1828 locations where at least one animal was observed (Fig. 1).

The observation of one or more animals at a given location is termed a herd. We make the basic assumption that each location is equally likely to host a herd. Deviations from randomness may occur due to external factors influencing the pattern. Such deviations are then of interest, both for the animals individually, and in their mutual relationships. Estimates of dispersion used here were affected by subjective variation among observers in their assignment of individuals to a her, but to the same degree.

In total, 55,201 animals of the 9 species were observed in this study, distributed over 3,025 herds. The maximum herd size equals 473 animals, whereas 322 solitary animals were observed, i.e. herds of size 1. Abundance varied widely among the nine species, largest herds occurring for plains zebra (Table 1). Also mean herd size varied widely, with plains zebra having the most herds (1,034) and a median herd size of (18 individuals herd⁻¹). The Thomson gazelle has less herds (211), and the animals tend to aggregate in herds of a smaller size (12 individuals herd⁻¹). Densities, i.e. number of herds per km², varies between the species in the area, the highest density occurring for Plains zebra (average intensity = 0.160 herds km²).

Table 1. Summary statistics of the two selected animal species, preyed and non-preyed species and all species

Process	Species	No.of herds	Total count	Group size			Average intensity
				mean	median	stdev	
X_1	Plains zebra	1,034	31,517	30.48	18	39.7	0.160
X_2	Thomson's gazelle	211	4,255	20.17	12	31.0	0.0326
\tilde{X}_1	Preyed Species	2,365	45,576	20.22	10	29.8	0.365
\tilde{X}_2	Non-preyed Species	660	9,445	15.30	8	23.1	0.102
X_\bullet	All Species	3,025	55,201	19.15	10	28.6	0.479

From a previous study [15] there was evidence that prey preference complementarity was an important factor in the distribution of herds. We found that herds of mid-sized prey species such as the plains zebra, which are more likely to be preferred by the dominant predators in this ecosystem (hyenas, lions and leopards), are expected to display less aggregated (even random) distributions. By contrast, herds of the smallest-sized species (Thomson's gazelle), as well as those of large-sized herbivores, are expected to experience lower predation pressure, and thus to be more aggregated. The Thomson gazelle, though, does not necessarily experience low predation pressure, as they are preyed upon by jackals.

To investigate prey preference, the dataset was split into two subsets: the combined data for large- and small-sized (habitat specialist or 'non-preferred'

prey) species, and on the combined data for the mid-sized (habitat generalist or 'preferred' prey) species. If habitat preference complementarity was operating, the result should be a tendency by both groups to shift towards a more regular dispersion pattern. If prey preference complementarity was operating, the result for the non-preferred prey group should be to remain aggregated, while the preferred prey group should become regularly spaced.

2.2 Measures of Dispersion

Spatial processes yielding herds of various sizes are characterised by a simple stochastic model applied to a region A , here the Laikipia area. Herds Y are represented by the coordinates of their centre of gravity and the animal species and are marked by the observed number of animals. Marks, contained in a set M . A marked point process is hence denoted by (Y, M) . As a result, A is summarised by a marked point pattern, consisting of the presence of at least one herbivore.

To describe the spatial point pattern generated by the distribution of the herbivores, we let (Y, M) be a nine-variate point process in A with jointly stationary components. The process consisting of all marked points regardless of type is denoted by $(X_{\bullet}, M) = \cup_{i=1}^9 (X_i, M_i)$, where (X_i, M_i) denotes the marked point process for the i^{th} herbivore. Similarly, the set (Y, M) can be decomposed as well into sets $X_{\bullet} = \cup_{i=1}^2 \tilde{X}_i$ with \tilde{X}_1 corresponding to the preyed species and \tilde{X}_2 to the non-preyed species, respectively. The density of the processes is denoted by λ , λ_i for each of the nine species and $\tilde{\lambda}$ for the preyed and nonpreyed species. In this paper, statistical inference for Y is based on distances. Although patterns may be non-stationary for several reasons, we take stationary processes as the starting point for our research. Non-homogeneity then appears as a result from the analysis, and could be analysed on the basis of [4].

The marked K -function

We consider the K -function to an arbitrary marked point pattern, in this study the centres of the herds. We consider here small herds and solitary species (herds of size up to 5), medium size herds (herds of sizes 6–25) and large sized herds (herds of sizes > 25 animals) and applied the multitype K -function.

We assume that X can be treated as a realisation of a stationary (spatially homogeneous) random spatial point process in the plane, observed through a bounded window W . The window W is in this study given by the edge of the Laikipia area. For edge correction we applied two correction procedures:

- the border method or *reduced sample* estimator [12]. This is the least efficient (statistically) and the fastest to compute.
- the translation correction method [9].



Fig. 1. Marked spatial point patterns of herds for the nine herbivores (*top*), the preyed and non-preyed species (center) and the Thomson gazelle and plains zebra (*bottom*) in the study area

For the analysis we have used the `spatstat` module in R ([2]). This displays the theoretical K -function for the Poisson type of model, under the assumption of isotropy, a border-corrected estimate of the K -function and a translation-corrected estimate of the K -function.

The pair correlation function

In this study we applied the pair correlation function of a stationary point process. First, the K -function is estimated and then a numerical derivative is taken. Irregularity of the window may be a drawback for this approach, but dealing with this requires specific software that is adjusted to this window, followed by numerical differentiation. At present, and in the frame of this study, our way is a clear direction to proceed. Commonly, smoothing splines approximate the derivative. Three numerical methods are available for the smoothing spline operations:

- apply smoothing to the K -function and estimate its derivative;
- apply smoothing to $Y(r) = \frac{K(r)}{2\pi \cdot r}$ constraining $Y(0) = 0$, and estimate the derivative of Y ;
- apply smoothing to $Y(r) = \frac{K(r)}{\pi \cdot r^2}$ constraining $Y(0) = 1$, and estimate its derivative.

The last option seems to be the best at suppressing variability for small values of r . However it effectively constrains $g(0) = 1$. If the point pattern seems to have inhibition at small distances, the second option effectively constrains $g(0) = 0$. The first option seems comparatively unreliable.

Fitting the Strauss process

For the different spatial patterns, a Strauss process has been fitted [7, 16]. The Strauss process on A with parameters $\beta > 0$ and $0 \leq \gamma \leq 1$ and interaction radius $\delta > 0$ can be described as a model with the conditional intensity

$$\lambda(u, y) = \beta \cdot \gamma^{t(u, y)} \quad (1)$$

where $t(u, y)$ is the number of points of Y that lie within a distance δ of the location u . If $\gamma = 1$ then the Strauss process reduces to the homogeneous Poisson process. Fitting was done by visual inspection of the observed intensities.

3 Results

3.1 Spatial Point Patterns

Spatial point patterns for the plains zebra and for the Thomson gazelle are displayed in Fig. 1, where the herd sizes are displayed as the size of the

circles. Clearly, the Thomson gazelle clusters in the South Western part of the area, the Plains zebra is more regularly distributed with both a high density and a highly aggregated spatial point pattern, showing evidence of clustering throughout the area. The Thomson gazelle shows clustering in the South-Western part. Both species appear to exhibit some aggregation. At a somewhat higher level, the preyed animals do not show any clustering, and the non-preyed species again show some clustering within the south-western sub-area. Finally, the plot of the combined spatial pattern is fairly dense with no apparent spatial pattern. A section with almost no herds occurs in the northern part of the area.

Figure 2 shows the three versions of the marked $K(r)$ functions, for the set of all herds (top), the preyed and the non-preyed species and for the individual Thomson gazelle and Plains zebra, respectively. The two corrected marked K -functions are relatively close together, but differ markedly from the theoretical one, as might be expected. In particular, the marked K -function for the Thomson gazelle shows a noisy behavior, but none of the latter two seems to deviate much from a quadratic behavior.

Pair correlation functions (fig. 3) were estimated for both the Thomson gazelle and the Plains zebra individually. Both pair correlation functions show an alternating sequence of values. None of the two pictures shows a hard core, therefore the two species have herds that may be close to each other. The maximum for both species occurs at approximately 2 km, showing that this distance is preferred for herds of both species. A peak at 1 km for the Thomson gazelle is probably caused by the relatively low number of data. A much higher peak occurs for the Thomson gazelle (up to 5) as compared to the Plains zebra (up to 2.2). Therefore, the distribution of Plain's zebra herds is somewhat closer to the Poisson process than that of the Thomson gazelle. Further, the tail of the pair correlation function is thinner for the Plains zebra than for the Thomson gazelle, at least for distances larger than 10 km. This indicates that randomness occurs for distances beyond 10 km for the Plains zebra, whereas that for the Thomson gazelle only appear for distances of 25 km and more. Herds of the Plains zebra do not show any regularity beyond distances of 10 km, whereas the Thomson gazelle shows regularity for distances up to 25 km.

A similar picture emerges when considering Strauss models. We first fitted those processes to the unmarked patterns (fig. 4) and applied distance parameters of 25 km for the Thomson gazelle and 15 km for the Plains zebra. These choices of parameters well represent the key factors for the distribution: a single mode distribution for the Thomson gazelle, with a peak somewhere in the South Western part of the Laikipia area, and a multi-modal distribution for the Plains zebra, representing their large abundance throughout the area.

We finally repeated fitting of the Strauss process to the marked process as well. Marked Strauss processes rarely occur in the literature [10]. We redistributed the marks according to herd size. Marks = 1 were assigned to herds of size up to 5, marks = 2 to herds of sizes 6–25, and marks = 3 to herds of sizes > 25 animals. As such, small, medium and large herds are distinguished

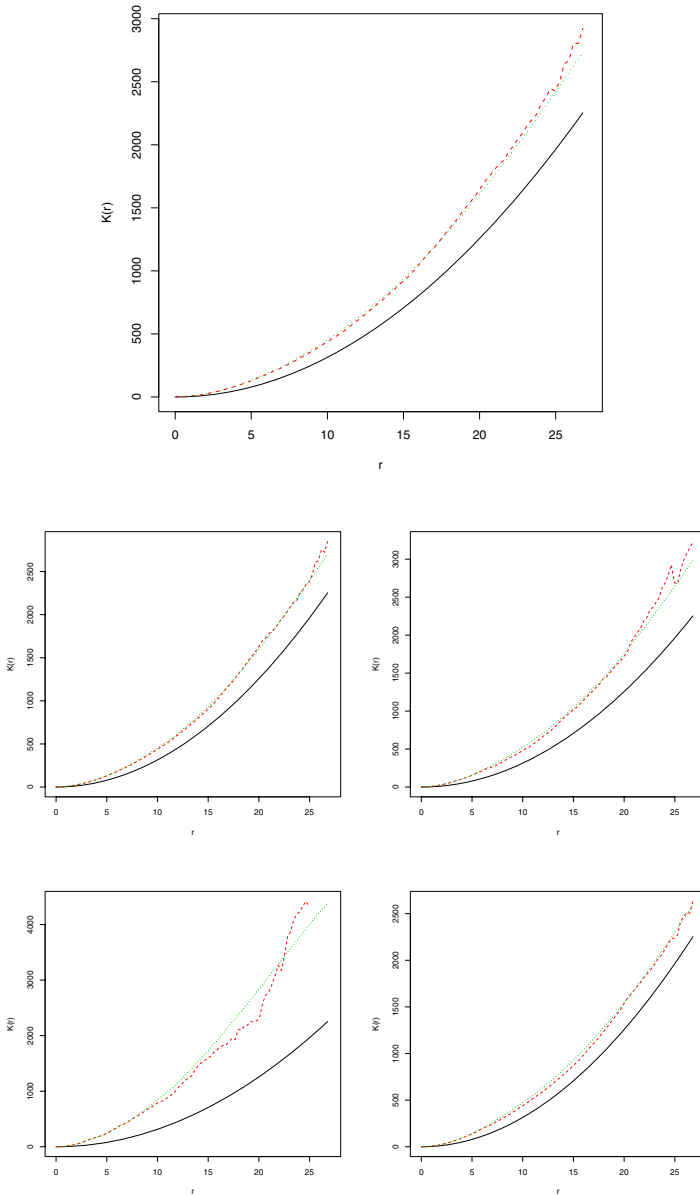


Fig. 2. Estimated marked $K(r)$ functions for herds of the nine herbivores (*top*), the preyed and non-preyed species (*center*) and the Thomson gazelle and plains zebra (*bottom*). The solid line is the theoretical $K(r)$, the dashed one is the $K(r)$ corrected for boundary of the area, the dotted one is the translation corrected $K(r)$

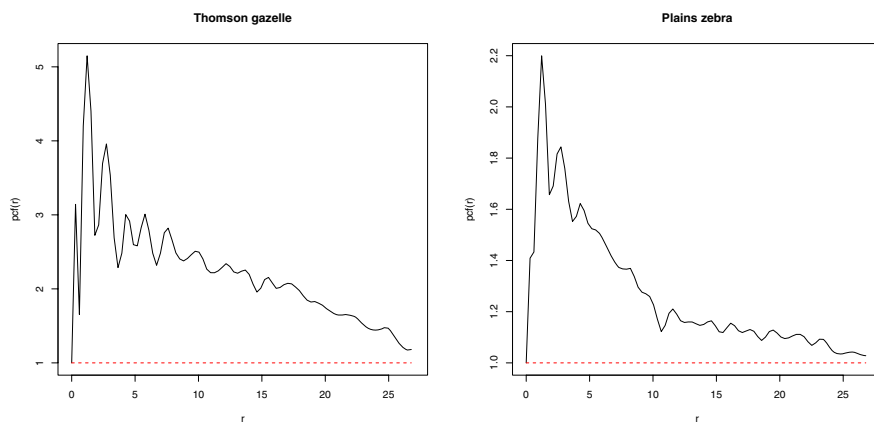


Fig. 3. Estimated pair correlation functions for the Thomson gazelle (*left*) and plains zebra (*right*)

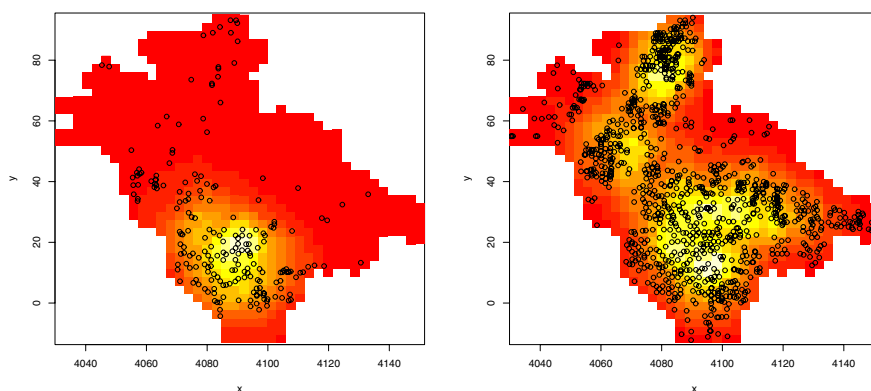


Fig. 4. Estimated unmarked Strauss process for the Thomson gazelle (*left*), using an $r = 25$ km parameter and the plains zebra (*right*), using an $r = 15$ km parameter.

for the two species (fig. 5). The results thus obtained do not violate earlier results.

4 Discussion

In this study we have used standard statistical software to analyse the data [2]. As a consequence, methods for stationary point patterns have been used, whereas some species, e.g. the Thomson gazelle, showed some clear non-stationarity. Currently, however, non-stationary analysis tools are not readily

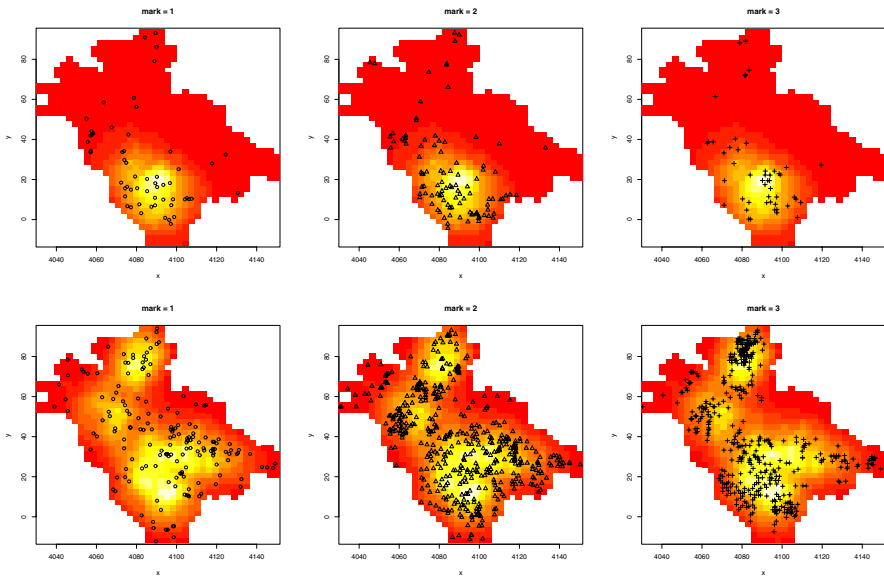


Fig. 5. Estimated marked Strauss process for the Thomson gazelle (*top*), using an $r = 25$ km parameter and the plains zebra (*bottom*), using an $r = 15$ km parameter. Marks are equal to 1 (*left*), 2 (*middle*) and 3 (*right*)

available. Non-standard software may serve as an extension in a future study. Also, a different method of estimating the pair correlation function, such as differentiating the $K(r)$ -function, might give different results. Our method is one possible method at hand, and it remains to be seen whether other methods might lead to different conclusions.

Spatial aggregation is a frequently encountered dispersion pattern in ecosystems, due to prevalence of potent aggregating forces such as habitat specificity, social structure and organization, philopatry, predator avoidance, and limited dispersal. Herbivore species in this study are subject to all these forces. Also the sizes of the herds in the study area are influenced not only by natural forces affecting herd dispersion, but also by 'unnatural' factors, such as displacement of wildlife by humans, cultivation, and livestock. In ecosystems such as this, where wildlife are displaced from some areas by humans and livestock, all species are likely to violate the assumption of random dispersion patterns typically made when sample counting. Factors that have a potentially organizing influence on herds within species, such as territoriality (Thomson's gazelle), or intra-specific competition, may have been operating. By contrast, plains zebra harems are known to associate and disassociate on a daily and seasonal basis (Rubenstein. *pers. comm.*), but this evidently does not result in significant aggregation at the landscape level. At least in this woodland-dominated habitat, 'exogenous' forces such as patchiness of pre-

ferred habitat are more likely account for aggregations of Thomson's gazelle herds, which prefer open, short grassland.

Factors causing herds of individual species to be aggregated or randomly dispersed in relation to their sizes either 1) complement each other when combined across space, or 2) are organised by factors that exert their influence on the entire community, or both. As an example of the former, which we refer to as 'habitat preference complementarity', we expect habitat generalists not only to be randomly dispersed, but also to be more abundant than habitat specialists. Also we expect specialists to be clustered in larger herds, than generalists. Plains zebra showed random distributions, but without overall association between rank of relative abundance and dispersion pattern ($P > 0.05$). By contrast, habitat specialists are expected to be aggregated within preferred patches, to display lower herd densities in transitional habitats, and to be absent from unsuitable habitats. When all species are pooled, the net effect is for herds to become regularly spaced across the landscape.

As an example of the latter, which we refer to as 'prey preference complementarity', predators are hypothesised to have a disaggregating effect on dispersion of preferred prey herds, which, when prey species are pooled, is manifested as an organizing effect by predators on the dispersion of preferred prey. Herds of preferred prey species, which could be aggregated in the absence of predation, react to predator functional responses by moving apart, becoming less aggregated, and alleviating pressure exerted by predator functional responses. Since predator functional responses are cued to multiple prey species, the net effect on combined prey herds is to cause a more regular pattern of dispersion.

We observe Thomson's gazelle as a small-sized species requiring open habitats with low biomass, and plains zebra as mid-sized species distributed across a variety of savanna habitats featuring grasslands associated with a range of tree densities. Because extreme habitat types, featuring either high or low vegetation biomass, are likely to be rarer and more patchy than intermediate habitat types, herbivore species preferring extreme habitat types are likely to display more aggregated distributions than are species preferring intermediate habitat types.

5 Conclusions

Combination of GPS technology with spatially explicit statistical techniques, in particular the marked K -function and the point correlation function, yield novel ways of characterizing dispersion patterns of wild herbivore herds and corresponding herd sizes. In particular, we found an interesting difference between the pair correlation function for the plains zebra with a correlation length of approximately 10 km and that of the Thomson gazelle with a correlation length of approximately 25 km.

Also, the herd patterns of Thomson gazelle was modelled with a Strauss marked point process, showing a single mode, whereas the herd pattern of the plains zebra showed multiple modes. This can be well explained by the ecosystem behavior (habitat specialist versus habitat generalist) of the two species.

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