

**ORIGINAL RESEARCH PAPER**

# Populations are not continuous ecological units

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**Abstract:** Ecological populations are typically treated as continuous units, implicitly assumed to occupy homogeneous environments and to respond uniformly to ecological pressures. However, spatial analyses have shown that populations can be structured into discrete spatial units, raising the question of whether such units represent meaningful ecological entities. Here, we integrate spatial clustering, land-use and land-cover composition, and behavioural data to evaluate the ecological relevance of  $\alpha$ -populations within a widely distributed mammal population. We show that  $\alpha$ -populations are embedded in contrasting landscape contexts and exhibit consistent behavioural differentiation, despite behavioural measurements being obtained under standardized conditions. Multivariate analyses revealed congruent structuring of landscape and behaviour at the  $\alpha$ -population level, with limited overlap among units. Together, these results provide evidence that  $\alpha$ -p represent a useful operational frameworks for capturing internal population heterogeneity, suggesting that populations may not function as continuous ecological units. Recognising this hidden structure has implications for population ecology, spatial modelling and conservation assessments.

**Keywords:** fragmentation; landscape connectivity; spatial structure; alpha-hull; *Chrysocyon brachyurus*.

## 1. Introduction

Contemporary population ecology faces a fundamental dilemma of scale: the persistent application of global metrics to describe phenomena that are, by their very nature, local and heterogeneous (Wiens, 1989). Ecological populations are commonly treated as continuous entities, implicitly assumed to occupy relatively homogeneous environments and to respond uniformly to ecological pressures. This assumption underpins much of population ecology, conservation planning and spatial modelling, operating under the premise that individual variation dissolves into population means that adequately represent the adaptive response of the species (Hodapp *et al.*, 2018). However, in landscapes fragmented by the Anthropocene, such homogeneity constitutes a statistical fallacy. Growing empirical evidence shows that individuals within the same nominal population may experience markedly different ecological contexts, leading to regional variation in ecological and behavioural traits across multiple taxonomic lineages, from avian reproductive biology (Bloche *et al.*, 2023) to dietary plasticity and

activity budgets in mesocarnivores (Rodrigues *et al.*, 2007; Cruz *et al.*, 2022; Machado *et al.*, 2021).

These lines of evidence suggest that populations are structured into nuclei of distinct functionality, yet ecology has lacked an operational terminological and methodological framework capable of integrating spatial density with functional coherence. Recent work has demonstrated that spatial distributions within populations are often organised into discrete, recurrent spatial units that cannot be adequately described by traditional population or subpopulation concepts. In particular, the  $\alpha$ -population framework was proposed to identify population subunits emerging empirically from spatial clustering and spatial coherence, without relying on predefined habitat patches or administrative boundaries (Brito, 2026). Here, we propose the  $\alpha$ -population as an operational framework to identify sub-population structures emerging from these spatial processes. This approach revealed that population structure can arise from spatial processes alone, even in the absence of clear physical barriers.

However, spatial clustering by itself is insufficient to establish the ecological relevance of such units. For population subdivision to represent a meaningful level of biological organisation, spatial units must also exhibit consistent differentiation across other ecological dimensions, such as behaviour and environmental context. Without such evidence, spatial units risk being interpreted as analytical artefacts rather than functional ecological entities. The  $\alpha$ -population concept therefore provides a testable hypothesis: if  $\alpha$ -populations represent genuine ecological units, they should not only be spatially discrete, but also embedded in distinct environmental contexts and associated with coherent functional or behavioural patterns. Demonstrating convergence across these dimensions is critical to evaluate the ecological relevance  $\alpha$ -populations as spatially coherent units within populations.

Behaviour offers a particularly stringent test of this hypothesis. Behavioural responses integrate intrinsic traits and long-term environmental exposure, and may retain signatures of ecological conditions even when measured under standardised experimental settings. Persistent behavioural differentiation among  $\alpha$ -populations would suggest that spatial structuring may be associated with functional specialisation. Landscape structure represents a complementary dimension. Differences in land-use and land-cover among spatial units reflect variation in ecological constraints, disturbance regimes and anthropogenic pressure. If  $\alpha$ -populations occupy contrasting landscape contexts, population-level analyses based on averaged environmental descriptors may systematically obscure ecologically meaningful heterogeneity.

In the Brazilian context, the maned wolf (*Chrysocyon brachyurus*) emerges as a critical biological model to examine these dynamics. Although classified as a generalist, its persistence within agricultural matrices and fragmented Cerrado landscapes has revealed an unanticipated degree of niche specialisation (Rodrigues et al., 2007; Consorte-McCrea & Santos, 2013; Vynne et al., 2011). Recent studies on space use indicate that landscape structure defines functional units that transcend simple geographic occupancy (Magioli et al., 2021). Nevertheless, the delimitation of such units has often been subjective or anchored in administrative boundaries. Brito (2026) challenged this paradigm by proposing the  $\alpha$ -population as an empirically derived unit, identified through the integration of density-based clustering algorithms (Ester et al., 1996).

## 2. Material and Methods

### 2.1. Conceptual framework and study design

This study evaluates whether  $\alpha$ -populations constitute functionally coherent ecological units by integrating spatial structure, landscape composition and behavioural differentiation under a single analytical framework. All analyses were explicitly designed to test the ecological relevance of  $\alpha$ -populations as emergent population units. Behavioural data were not treated as an independent research focus, but as one of the functional dimensions used to assess whether spatially defined  $\alpha$ -populations exhibit consistent ecological differentiation beyond space alone.

The study combines three complementary components: (i) the spatial delimitation of  $\alpha$ -populations based on occurrence data, (ii) the characterisation of land-use and land-cover associated with each  $\alpha$ -population, and (iii) the reanalysis of behavioural, temperamental and physiological data, exclusively to test for functional differentiation among  $\alpha$ -populations.

### 2.2. Spatial delimitation of $\alpha$ -populations

Spatial population units were identified following the  $\alpha$ -population concept. Occurrence records were subjected to density-based spatial clustering using the DBSCAN algorithm (Density-Based Spatial Clustering of Applications with Noise). Clustering parameters were set to a maximum neighbourhood distance (eps) of 200 km and a minimum of three records per cluster, allowing the identification of recurrent spatial units while excluding isolated records as noise.

For each spatial cluster, the area of occurrence was delimited using the Alpha-Hull method ( $\alpha = 2$ ), generating polygons that represent the spatial extent of each  $\alpha$ -population. This approach allows population units to emerge empirically from spatial structure, without reliance on predefined habitat patches, political boundaries or dispersal assumptions.

The DBSCAN parameter (eps = 200 km) was based on conservative dispersal estimates for the species, ensuring that identified clusters reflect biologically connected nuclei (Brito, 2026). For the alpha-hull, we performed a sensitivity analysis testing  $\alpha$  values from 0.5 to 5.0;  $\alpha = 2$  was selected as the optimal balance to generate continuous and biologically plausible polygons (Brito, 2026). In the present study,  $\alpha$ -populations were not redefined or optimised, but treated as previously established spatial units, allowing an independent test of their ecological and functional relevance.

### 2.3. Landscape characterisation and land-use analysis

Land-use and land-cover (LULC) characterisation was conducted in a paired and

annualised manner. Each occurrence record was associated with the MapBiomass raster corresponding to its year of collection (1985–2024). MapBiomass Collection 10 was used for Brazilian territory, and compatible national datasets were used for Argentina, Bolivia, Paraguay and Uruguay, all with a spatial resolution of 30 m.

For each record, a circular buffer with a radius of 3 km (approximately 28 km<sup>2</sup>) was established to represent the average home range of the maned wolf (*Chrysocyon brachyurus*). LULC data extracted within each buffer were reclassified into six functional categories: Forest; Herbaceous and Shrub Vegetation; Agriculture and Pasture; Non-vegetated Areas; Water Bodies; and Non-observed areas. Landscape composition was quantified as the proportional coverage of each category and synthesised as mean values for each  $\alpha$ -population.

Environmental heterogeneity and ecological segregation among  $\alpha$ -populations were evaluated using Principal Component Analysis (PCA) based on individual-level LULC proportions. Ninety-five percent confidence ellipses were constructed to visualise landscape variation at both individual and  $\alpha$ -population levels.

#### 2.4. Behavioural and physiological data source and rationale

Behavioural, temperamental and physiological data were obtained from a previously published experimental study on captive maned wolves (Brito et al. 2024). The present study represents a secondary reanalysis of that dataset, guided by a distinct conceptual objective: to test whether  $\alpha$ -populations defined by spatial structure also exhibit functional differentiation.

The original dataset comprised 13 captive individuals housed at two Brazilian institutions. For the purposes of this study, each individual was assigned to an  $\alpha$ -population based on its locality of origin, defined by natal region. Locality of origin was treated as a proxy for population-level context, reflecting differences in biogeographic history, landscape structure and spatial isolation identified through the  $\alpha$ -population framework.

#### 2.5. Behavioural data collection and aggregation

Behavioural observations followed a focal sampling protocol with interval recording and were conducted across three experimental stages: Baseline I, Environmental Enrichment and Baseline II. Behavioural categories were classified using a predefined ethogram described in the original study.

For the present analysis, behavioural data were not analysed at the individual experimental level. Instead, behavioural metrics related to activity (locomotion, inactivity), social interaction (agonistic behaviour) and space use (time not visible) were standardised by observation effort and aggregated at the  $\alpha$ -population level. This aggregation allowed behavioural variation to be evaluated as a functional attribute of  $\alpha$ -populations rather than as an individual response to experimental treatments.

#### 2.6. Temperament and physiological metrics

Temperament was assessed using the Novel Object Test to quantify cautious and exploratory tendencies. A Caution Index was calculated based on the proportional expression of behavioural responses. Fecal glucocorticoid metabolites (GCM) were quantified as indicators of chronic physiological stress following established extraction and assay protocols.

Temperament and physiological metrics were retained as complementary functional descriptors but were analysed exclusively in relation to  $\alpha$ -population identity and associated biological variables.

#### 2.7. Statistical analysis of functional differentiation

Functional differentiation among  $\alpha$ -populations was evaluated using Generalized Linear Mixed Models (GLMMs). Behavioural, temperamental and physiological metrics were modelled as response variables, with  $\alpha$ -population included as the primary explanatory factor and individual identity included as a random intercept to control for repeated measures and individual-level non-independence. Interactions with sex and age were incorporated to account for demographic effects. Given the limited sample size, random slopes were not included.

Due to non-normal distributions, behavioural count data were modelled using a Poisson error structure within the lme4 package. We assessed overdispersion by calculating the ratio between the Pearson chi-square statistic and the residual degrees of freedom, ensuring that it remained close to unity. Model selection followed an iterative backward procedure based on the Akaike Information Criterion (AIC), and model fit was verified through the inspection of residual plots. Statistical significance was assessed at  $\alpha=0.05$ .

#### 2.8. Integration of landscape and functional dimensions

To assess whether spatially defined  $\alpha$ -populations represent coherent ecological units, behavioural metrics were analysed jointly with LULC composition. Multivariate ordination was used to evaluate whether  $\alpha$ -populations occupied distinct

positions in combined environmental–functional space. This integration allowed testing whether functional differentiation persisted after aggregation at the population-unit level and whether behavioural patterns covaried with landscape gradients.

All analytical steps were explicitly designed to test the ecological relevance of  $\alpha$ -populations and to ensure that identified patterns reflect genuine population-level organisation rather than analytical artefacts.

### 3. Results

Spatial clustering analysis identified multiple  $\alpha$ -populations distributed across the species' range, revealing clear spatial structuring rather than a continuous population pattern (Figure 1). These  $\alpha$ -populations occupied landscapes with markedly different land-use and land-cover (LULC) compositions, indicating substantial environmental heterogeneity among spatial units (Table 1; Figure 2). The proportion of agricultural areas varied widely across  $\alpha$ -populations, ranging from negligible values to strong dominance.  $\alpha$ -population 2 exhibited the highest agricultural cover (0.79), characterising a landscape almost entirely dominated by anthropogenic land use, whereas  $\alpha$ -populations 3 and 4 showed minimal to no agricultural influence. Intermediate levels of agricultural cover were observed in  $\alpha$ -populations 1, 5, 7, 8, 9 and 10, indicating mixed landscapes combining

natural and human-modified elements (Table 1; Figure 2).

Forest cover also varied substantially among  $\alpha$ -populations.  $\alpha$ -population 3 presented the highest proportion of forested areas (0.66), followed by  $\alpha$ -populations 9 (0.53) and 8 (0.45), indicating a strong association with more structurally complex and less modified environments. In contrast, forest cover was nearly absent in  $\alpha$ -population 2 and remained low in  $\alpha$ -populations 1 and 4, reflecting landscapes dominated by open or anthropogenic land-cover classes (Table 1; Figure 2). Herbaceous and shrub vegetation constituted the dominant land-cover class in some  $\alpha$ -populations, most notably in  $\alpha$ -population 4, which was almost entirely composed of herbaceous vegetation (0.90). High proportions of this class were also observed in  $\alpha$ -populations 1 and 3, whereas other  $\alpha$ -populations displayed lower and more variable herbaceous cover (Table 1; Figure 2).

Non-vegetated areas and water bodies consistently represented a small fraction of the landscape across most  $\alpha$ -populations, contributing little to overall land-cover composition. In contrast, the proportion of non-observed land-cover classes varied considerably among units, reaching high values in  $\alpha$ -populations 10 and 11 (both exceeding 0.55), while remaining negligible in several other  $\alpha$ -populations (Table 1). These patterns indicate marked differences not only in dominant land-cover classes but also in data availability and landscape observability among spatial units.

Table 1. Proportional land-use and land-cover (LULC) composition of each  $\alpha$ -population. Values represent mean proportional coverage of LULC classes within 3-km buffers aggregated by  $\alpha$ -population.

$\alpha$ -population	Agriculture	Forest	Herbaceous	Non Vegetated	Water	Not Observed
1	0.3169	0.219494	0.4047	2.34e-02	0.032453	0.00297
2	0.7881	0.000514	0.2108	6.21e-04	0.000000	0.00000
3	0.0000	0.660220	0.3384	1.40e-03	0.000000	0.00000
4	0.0743	0.021770	0.9039	3.56e-05	0.000000	0.00000
5	0.3698	0.261937	0.0919	2.14e-02	0.008246	0.24671
6	0.0551	0.424971	0.2155	1.51e-02	0.001684	0.28771
7	0.2218	0.317614	0.2461	5.68e-02	0.022341	0.13532
8	0.2342	0.445966	0.2603	1.38e-03	0.020875	0.03729
9	0.2409	0.525686	0.0171	1.38e-03	0.001520	0.21342
10	0.2527	0.121189	0.0613	2.44e-03	0.003558	0.55886

11

0.1321

0.164270

0.1406

2.45e-03

0.000442

0.56006

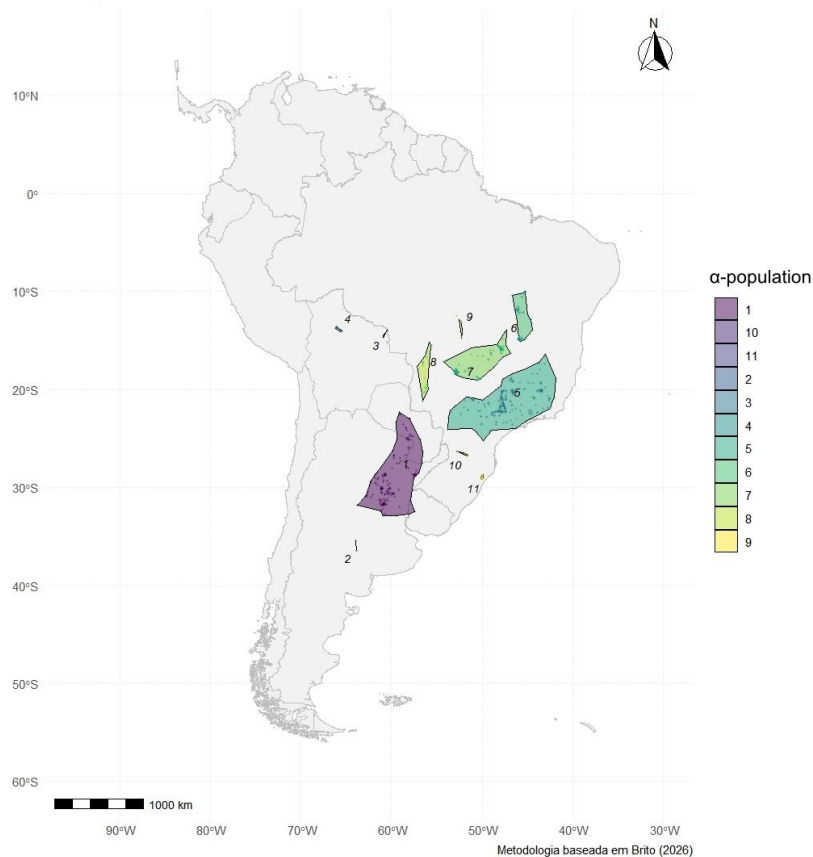


Figure 1. Spatial delimitation of  $\alpha$ -populations of the maned wolf (*Chrysocyon brachyurus*).  $\alpha$ -populations were identified using density-based clustering (DBSCAN) and delimited by alpha-hull polygons, revealing spatially discrete population units.

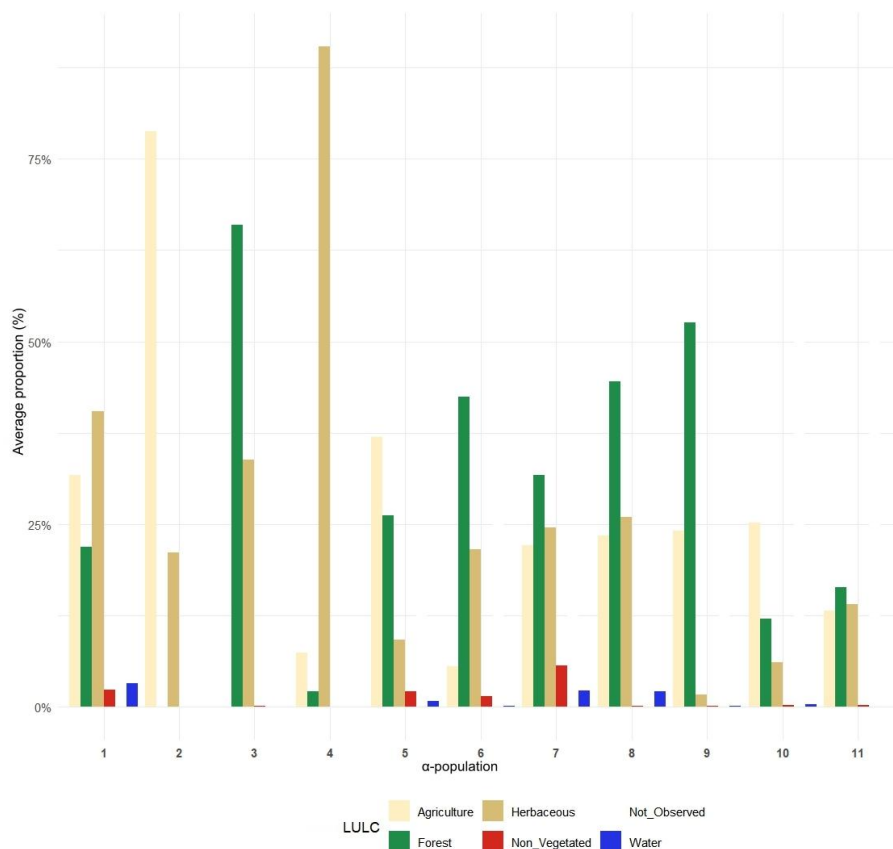


Figure 2. Mean proportion of land-use and land-cover (LULC) categories across  $\alpha$ -populations of the maned wolf (*Chrysocyon brachyurus*). Bars represent the relative contribution of each LULC category to the landscape composition of each  $\alpha$ -population, highlighting marked environmental heterogeneity among spatial population units.

Principal component analysis (PCA) based on proportional LULC composition revealed a clear segregation of  $\alpha$ -populations in multivariate environmental space (Figure 3). The first principal component was primarily associated with gradients of agricultural and herbaceous cover, whereas the second

principal component was strongly related to forest cover, as indicated by variable loadings (Table 2).  $\alpha$ -populations occupied distinct positions along these axes, with limited overlap among confidence ellipses, indicating that spatially defined units are embedded in contrasting landscape contexts (Figure 3).

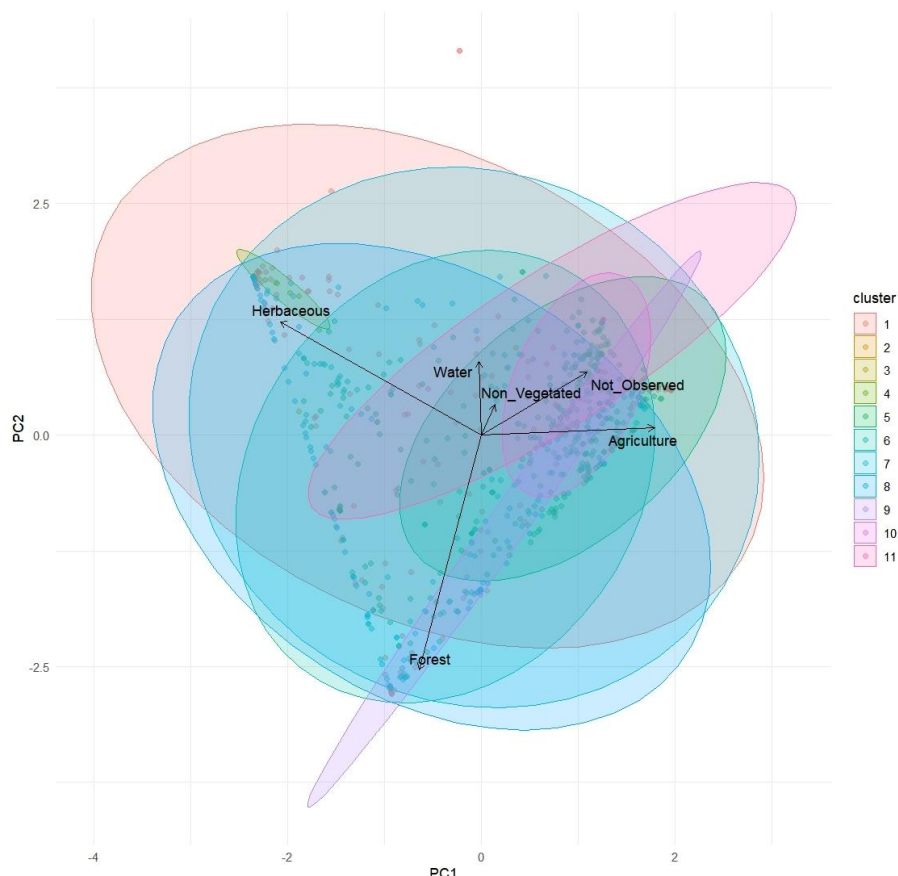


Figure 3. Principal component analysis (PCA) of  $\alpha$ -populations based on proportional land-use and land-cover composition. Points represent  $\alpha$ -populations positioned in multivariate environmental space, and ellipses indicate 95% confidence intervals. Separation along principal components reflects gradients of agricultural dominance, herbaceous cover and forest cover.

Table 2. Loadings of land-use and land-cover (LULC) variables on the principal components derived from PCA. Loadings indicate the contribution of each LULC category to the principal components used to describe environmental differentiation among  $\alpha$ -populations.

LULC Class	PC1	PC2	PC3	PC4	PC5	PC6
Agriculture	0.59198580	0.02643144	-0.49751479	0.3983062	-0.009600818	-0.4925375
Forest	-0.21190263	-0.83873812	0.03654271	-0.1551304	-0.122099605	-0.4596809
Herbaceous	-0.68643268	0.40527783	-0.05918405	0.2579282	0.081767039	-0.5365114
Non Vegetated	0.04792357	0.10946329	-0.32103281	-0.6863746	0.615950722	-0.1793143
Water	-0.00743775	0.26247794	-0.25956108	-0.4999141	-0.773895997	-0.1218562
Not Observed	0.36208878	0.22515050	0.75974133	-0.1724398	0.001831829	-0.4596229

Behavioural metrics also varied among  $\alpha$ -populations

and were structured according to landscape composition. Generalized linear mixed models revealed significant effects of  $\alpha$ -population identity on locomotion, agonistic behaviour, inactivity and non-visible behaviour (Table 3). Locomotion frequency increased significantly with  $\alpha$ -population, indicating differences in activity levels among spatial units (Figure 4). Agonistic behaviour was influenced by  $\alpha$ -

population, sex and their interaction, with sex-specific responses varying across  $\alpha$ -populations (Table 3; Figure 5a). Similarly, non-visible behaviour and inactivity showed significant effects of  $\alpha$ -population and sex, with interaction terms indicating that behavioural expression differed between males and females depending on the  $\alpha$ -population of origin (Table 3; Figure 5b–c).

Table 3. Results of generalized linear mixed models (GLMMs) evaluating the effects of  $\alpha$ -population identity and sex on behavioural variables of captive maned wolves (*Chrysocyon brachyurus*). Displayed are model estimates ( $\beta$ ), standard errors, z-values and p-values for significant predictors retained after iterative model selection. Individual identity was included as a random effect. Reference categories are indicated in the table footnotes.

Behaviour	Variable	Estimate (beta)	Standart Error	z-value	p-value ( $\alpha = 0.05$ )*
Locomotion	Intercept	2.193	1.218	1.801	0.071
	$\alpha$ -population <sup>1</sup>	0.340	0.151	2.239	0.025
Agonistic Behaviour	Intercept	-18.194	6.066	-2.999	0.002
	$\alpha$ -population	2.884	0.952	3.029	0.002
	Sex <sup>2</sup>	11.618	4.569	2.542	0.011
	$\alpha$ -population*Sex	-1.825	0.688	-2.652	0.008
Non visible	Intercept	2.815	2.022	1.393	0.163
	$\alpha$ -population	0.650	0.293	2.222	0.026
	Sex	2.790	1.265	2.206	0.027
	$\alpha$ -population*Sex	-0.432	0.196	-2.201	0.027
Inactive	Intercept	-7.705	3.427	-2.249	0.024
	$\alpha$ -population	1.250	0.493	2.534	0.011
	Sex	3.685	2.147	1.716	0.086

$\alpha$ -population\*Sex      -0.502      0.330      -1.518      0.129

\*Non-significant effects are not shown as they were removed from the model through the iterative selection process. <sup>1</sup> $\alpha$ -population; the reference variable was “ $\alpha$ -population 5”. <sup>2</sup>Sex (Male or Female); the reference variable was “Male”.

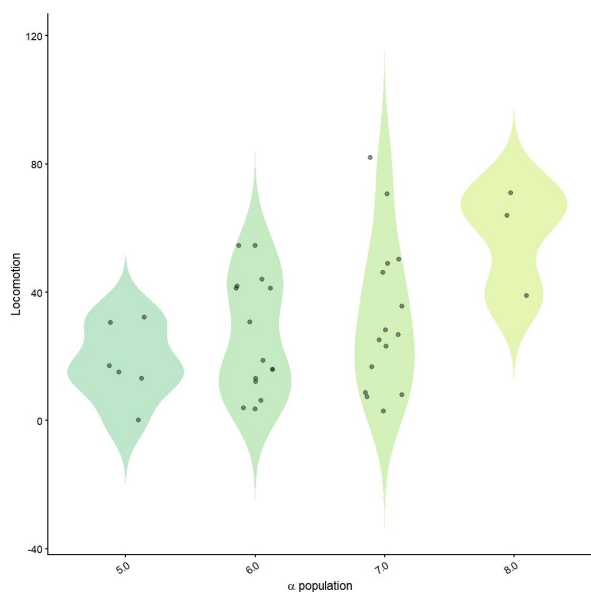


Figure 4. Frequency of locomotion behaviour in captive maned wolves (*Chrysocyon brachyurus*) according to  $\alpha$ -population of origin. Violin plots represent the probability density of locomotion records, and circles indicate individual observations. Behavioural data were collected under standardized experimental conditions in

Brazilian zoological institutions between December 2022 and March 2023.

When behavioural metrics were analysed jointly with land-use composition,  $\alpha$ -populations occupied distinct positions in combined environmental-behavioural space, reflecting consistent coupling between landscape structure and functional expression.  $\alpha$ -populations embedded in landscapes dominated by agricultural cover tended to exhibit higher locomotion frequencies and lower inactivity, whereas those associated with forested or herbaceous-dominated landscapes showed reduced locomotion and increased inactivity. Differences in visibility-related behaviours further reflected variation in landscape openness and structural complexity (Figures 4 and 5). Importantly, these patterns persisted despite behavioural data being collected under standardized captive conditions and remained evident after aggregation at the  $\alpha$ -population level, indicating that functional differentiation covaries with spatial and environmental structuring rather than arising solely from experimental context.

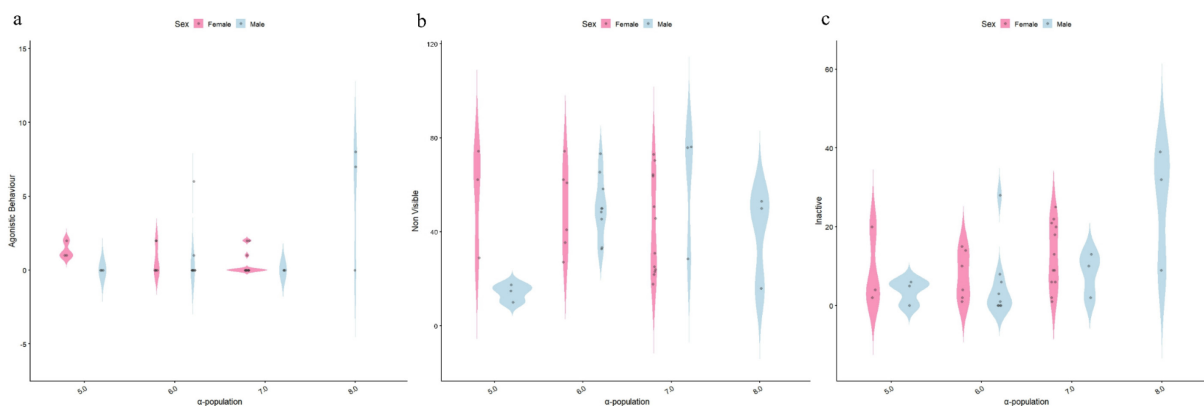


Figure 5. Frequency of (a) agonistic behaviour, (b) non-visible behaviour, and (c) inactivity in captive maned wolves (*Chrysocyon brachyurus*) as a function of  $\alpha$ -population and sex. Violin plots represent probability density distributions, and circles correspond to individual observations. Behavioural data were obtained under standardized experimental conditions, allowing comparison of functional differentiation among  $\alpha$ -populations.

## 4. Discussion

The results of this study provide evidence that ecological populations may exhibit spatially structured heterogeneity that is not captured when populations are treated as continuous and homogeneous units. The  $\alpha$ -

populations identified through spatial clustering were associated with contrasting landscape contexts and consistent patterns of variation in environmental composition, suggesting that spatial structure may correspond to management-relevant differentiation within populations.

The segregation observed in the principal component analysis (PCA) demonstrates that  $\alpha$ -populations occupy distinct regions of environmental space, primarily structured by gradients of agricultural dominance, forest cover and herbaceous vegetation. These patterns are consistent with previous evidence showing that landscape structure acts as a major ecological filter shaping species responses (Fletcher et al., 2019; Muñoz et al., 2023). Rather than constituting independent ecological entities, the  $\alpha$ -populations identified here represent spatial units embedded in contrasting land-use contexts that impose different ecological constraints. The discrete nature of  $\alpha$ -populations also has significant implications for ecoepidemiology. The occurrence and distribution of pathogens, such as *Sarcoptes scabiei*, represent a major threat to wild Neotropical canids (Brito and Garbino, 2026). In a landscape structured into isolated units, the dynamics of disease transmission may be altered, increasing the vulnerability of small  $\alpha$ -populations to local extinction due to health crises.

Behavioural variation among  $\alpha$ -populations was also detected, with differences in locomotion, inactivity and visibility associated with landscape composition. Although behavioural data were collected under standardized captive conditions, these patterns are consistent with the idea that long-term environmental exposure and biogeographic context may influence behavioural tendencies. Such tendencies are consistent with reported individual temperament traits (Brito et al., 2024) and reproductive physiological responses critical for the species' conservation (Brito et al., 2022). Similar associations between environmental heterogeneity and behavioural expression have been reported in a range of ecological contexts (Hertel et al., 2020; Richardson, 2024; Paula et al., 2023). However, given the limited sample size and captive origin of the data, these results should be interpreted as suggestive rather than demonstrative of functional differentiation.

The association between high agricultural cover and increased locomotion observed in some  $\alpha$ -populations may reflect altered energetic demands or risk perception in human-modified landscapes, consistent with the concept of a "landscape of fear" (Creel et al., 2022). In contrast,  $\alpha$ -populations embedded in more forested or structurally complex landscapes exhibited higher inactivity and lower visibility, potentially reflecting reduced disturbance or alternative spatial strategies. These patterns align with previous

studies on regional variation in diet, activity and space use in generalist carnivores (Silva et al., 2016; Arruda et al., 2021).

From a conceptual perspective, the  $\alpha$ -population framework differs from classical metapopulation models. While metapopulation theory emphasises predefined habitat patches and dynamics of colonisation and extinction (Hanski, 1998; Stover et al., 2022),  $\alpha$ -populations emerge empirically from spatial clustering and do not rely on a priori assumptions about habitat boundaries. Rather than representing a distinct level of ecological organisation,  $\alpha$ -populations constitute an operational spatial framework for exploring internal heterogeneity within populations.

From an applied standpoint, recognising spatially coherent units within populations has direct implications for wildlife management and conservation. Treating populations as homogeneous entities may mask localised responses to land-use change and lead to overly general management strategies (Smith et al., 2022; Thompson and Garcia, 2023). The  $\alpha$ -population framework provides a practical method for identifying population subunits that experience distinct ecological conditions and may therefore benefit from differentiated monitoring or management actions.

Several limitations should be acknowledged. Behavioural data were derived from a small number of captive individuals ( $n=13$ ), which limits broad generalizations. However, these standardized conditions allowed us to identify behavioral differences associated with the natal landscape, consistent with individual temperament traits (Brito et al., 2024). Furthermore, detailed observations of sub-adult females have shown how specific behavioral and physiological responses are critical for reproductive success (Brito et al., 2022). These results should thus be interpreted as suggestive evidence that functional differentiation covaries with spatial structuring.

Despite these limitations, the convergence of spatial, environmental and behavioural patterns indicates that  $\alpha$ -populations represent a useful operational framework for capturing spatially structured heterogeneity within ecological populations. Rather than proposing a new ontological level, this approach offers a practical tool for guiding empirical investigation and supporting conservation assessments in heterogeneous landscapes.

## 5. Conclusion

This study demonstrates that ecological populations cannot be adequately represented as continuous and homogeneous units. By integrating spatial clustering, land-use and land-cover composition, and behavioural data, we show that  $\alpha$ -populations

represent spatially coherent population units embedded in contrasting landscape contexts and associated with consistent functional differentiation. These results indicate that population-level averages mask substantial internal heterogeneity, which may lead to oversimplified interpretations of ecological processes and management needs.

The identification of  $\alpha$ -populations provides a practical and transferable framework for capturing spatially structured heterogeneity within populations, without relying on predefined habitat boundaries or administrative divisions. From a scientific perspective, this approach contributes to population ecology by offering an operational scale at which environmental variation and functional responses can be jointly examined. From an applied standpoint, recognising spatially distinct population units has direct implications for conservation planning, landscape management, and agricultural policies, as it allows management actions to be tailored to local ecological conditions rather than applied uniformly across broad regions.

Economically, this framework may support more efficient allocation of conservation resources and land-use planning by identifying areas where agricultural expansion, habitat modification, or mitigation measures are likely to have differential impacts on wildlife populations. By aligning ecological understanding with spatially explicit management,  $\alpha$ -populations can inform decision-making processes that balance biodiversity conservation with agricultural productivity.

Future research should expand this framework by incorporating larger sample sizes, in situ behavioural and movement data, and sensitivity analyses of clustering parameters. Applying the  $\alpha$ -population concept to other taxa and ecosystems will further clarify its generality and utility as a tool for ecological assessment in heterogeneous and human-modified landscapes.

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## Ethics

This study is based on secondary analyses of previously published datasets and does not involve new experimental procedures with animals. Behavioural and physiological data were obtained from studies conducted under controlled captive conditions and were originally collected in accordance with institutional ethical guidelines and applicable national regulations. All spatial and environmental analyses were performed using publicly available occurrence and land-use data. No ethical issues are expected to arise from the publication of this manuscript.