

RESEARCH ARTICLE

Viability selection on coat spot patterns correlates with temperature anomalies in Masai giraffes

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Abstract

1. Phenotype-dependent demography may result from heterogeneous selection pressures, which can be altered by temperature anomalies. Understanding which phenotypes are best adapted to different temperatures could clarify how populations may adapt to climatic changes and guide effective conservation measures.
2. Animal markings are heritable phenotypic traits that show variation within populations, which suggest they may be adaptive. Variation in marking shape and size may influence thermoregulation and lead to differing individual responses to temperature anomalies. Therefore, markings may affect survival in variable and changing environments and be important for adapting to climate change.
3. Using resighting data from 810 wild giraffes over 8 years, we estimated viability selection on spot patterns and whether it was affected by temperature anomalies.
4. Calves with smaller lobate and adult males with smaller lobate or larger polygonal spots survived better. Additionally, calves and adult males with larger (vs. smaller) spots that experienced anomalously low (vs. high) temperatures survived better. Spot patterns had a smaller effect on adult females, with individuals of all spot types having lower survival in anomalously high temperatures.
5. *Synthesis and applications.* Spot patterns influenced giraffe survival and their effects were altered by temperature anomalies. In calves, spot size may help with thermoregulation while spot shape may conceal them from predators. In adults, sex-specific selection pressures suggest sex differences in heat tolerance and trade-off with different functions. Conservation management maintaining variation in spot patterns by facilitating genetic exchange (e.g. through habitat connectivity) may help giraffes to adapt to climate change. Markings may have fitness consequences in other mammalian species and be important for population adaptation.

KEYWORDS

capture–mark–recapture, climate change, colour patterns, heterogeneous selection, mammals, phenotypic variation, survival modelling, thermoregulation

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1 | INTRODUCTION

Selection pressures on phenotypes can be altered by climate change, which impacts the phenology, distribution or demography of many species (Paniw et al., 2021; Selwood et al., 2015). Gradual changes in average temperature may allow populations time to adapt to new conditions. In contrast, extreme weather events, such as heatwaves and cold spells, can have a strong impact on demographic parameters because they can push temperature anomalies beyond a species' tolerance limits (Gardner et al., 2016; Woodroffe et al., 2017). Optimal thermal phenotypes may shift in response to extreme temperature events, particularly when conditions fall outside a species' thermoneutral zone. To understand species adaptation to climatic changes and to implement effective conservation management, we need to understand which phenotypes are best adapted to which ecological conditions.

Animal markings, such as spots or stripes, are phenotypic traits that show variation in shape and size among individuals within populations. Markings are hypothesised to serve different functions, such as communication, predator avoidance or thermoregulation (Caro, 2005; Caro & Koneeru, 2021). Among-individual variation in markings may persist if variation in ecological factors related to these functions (population characteristics, predation pressure, temperature) causes heterogeneous selection on phenotypes. Markings may thus play a key role in population dynamics and persistence. Consequently, population management plans including markings as key phenotypic traits could help to maintain viable and resilient populations in variable and changing environments.

Animals maintain a stable body temperature through behavioural or morphological thermoregulation (Angilletta, 2009). Behavioural thermoregulation includes using cooler microclimates (e.g. shade, burrows), orienting the body or shifting activity timing (Giroux et al., 2023; Terrien et al., 2011). Morphological adaptations include optimising body shape and colour or marking patterns. Specifically, patterns may help with thermoregulation as darker or lighter colours may better absorb or dissipate heat (Hetem et al., 2009; Walsberg, 1983) and larger and uniform patterns may amplify heat absorption or dissipation. For example, dark spots on dragonfly wings increase body temperature and are smaller in hotter regions (Moore et al., 2019). Markings may thus play a key role in how populations adapt to temperature changes. Fitness consequences of markings are understudied, particularly in mammals (Lee et al., 2018). Key questions are whether markings affect fitness at different life stages, are under heterogeneous selection that could maintain their variation within populations, and whether temperature is a driver of selection.

Giraffes (*Giraffa* spp.) are large, long-lived, spotted animals with low evolutionary potential, putting them at high extinction risk (Fuller et al., 2016). Gene flow is low; thus, giraffes may be particularly vulnerable to rapid environmental changes (Brown et al., 2007; Lohay et al., 2023). Giraffes have individually unique coat spot patterns that do not change from birth to death (Foster, 1966) and which vary within populations (Dagg, 1968; Morandi et al., 2022). Spot traits

are heritable (h^2 from parent-offspring regressions = 0.08–1.06) (Lee et al., 2018), so they may have adaptive significance. In wild Masai giraffes (*G. tippelskirchi*), calves with larger and/or more lobate spots survived better during their first 4 months, and calves with smaller spots survived better during their first year (Lee et al., 2018). Spot characteristics may conceal calves from predators and contribute to differential survival rates at the earliest life stages. For adult giraffes, natural predation risk is low (Lee, Bond, et al., 2016). Thus, spot patterns in adults may have other functions. Spot patches of giraffes are underlain by a central artery and dense network of blood vessels that adjust blood flow to and from the patch, enabling control of heat exchange (Taylor et al., 2023). Spots may act as thermal windows whereby spot size affects heat exchange, which may affect thermoregulation in anomalously cold or hot temperatures. Spot traits may be under fluctuating selection driven by temperature anomalies if fitness outcomes are both pattern- and temperature-dependent.

We estimated viability selection on spot patterns—that is, the differential survival due to among-individual variation in spots—in a population of wild Masai giraffes to determine whether certain spot traits confer higher survival at different life stages. If coat spots help with thermoregulation, we also hypothesised that viability selection on spot patterns would correlate with land surface temperature anomalies. We quantified spot traits and survival rates using 8 years of photographic data from 810 individuals. We estimated apparent seasonal survival probabilities as a function of spot patterns and investigated whether this relationship, thus viability selection, was affected by temperature anomalies. Because a previous study found that temperature anomalies affected the survival of adult giraffes but not of calves (Bond et al., 2023), we predicted temperature anomalies to affect viability selection on spot patterns in adults only. Larger and more convex polygonal spots should facilitate heat exchange, that is, absorb more solar radiation enabling faster heating in colder temperatures or dump excess body heat in hotter temperatures. Alternatively, intermediate spot size and/or shape may better balance the risk of hypo- and hyperthermia.

2 | MATERIALS AND METHODS

2.1 | Study population

We monitored a population of Masai giraffes from January 2012 to February 2020 in the Tarangire Ecosystem in Tanzania (Latitude 2°S to 5°S, longitude 35°E to 37°E, elevation ranges from 950 to 1200m). The study area (822 km²) includes four protected areas and is entirely unfenced (Figure 1a; see area management details Text S1 in Supporting Information).

Following a robust design (Pollock, 1982), we collected photographic identification data during three primary sampling occasions per year, with two secondary survey events within each occasion. Sampling occasions were conducted at the end of each of the three precipitation seasons occurring in northern Tanzania: January (short rains), May (long rains) and September (dry season). The two

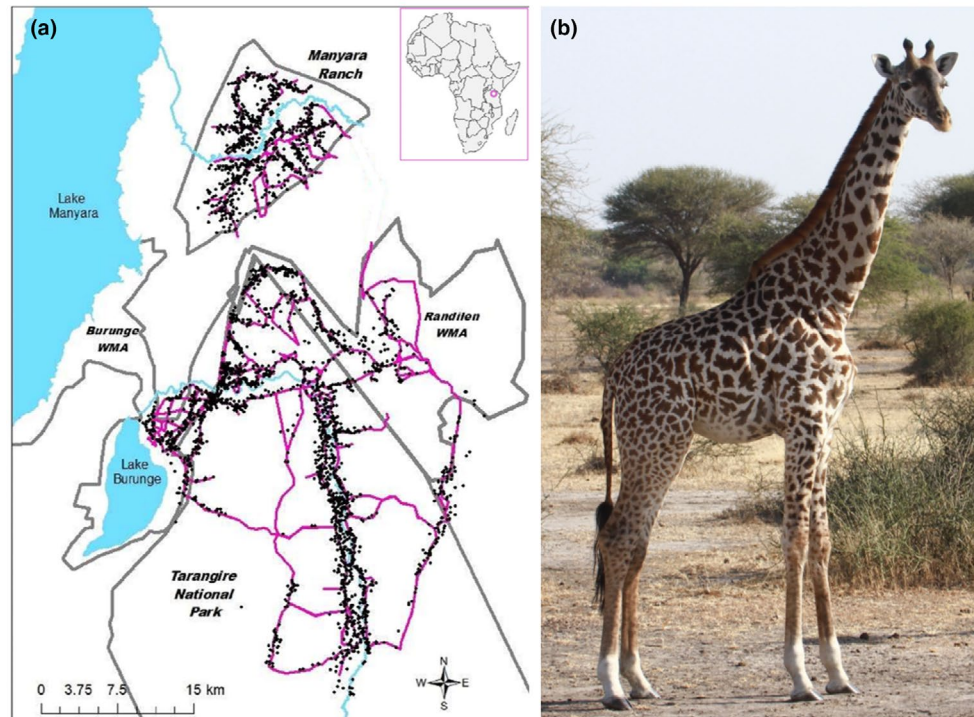


FIGURE 1 Study area and Masai giraffe photography (re)capture. (a) Map of the study area in the Tarangire Ecosystem with locations of encountered Masai giraffes (black dots) on road transects (purple lines) from 2012 to 2020. (b) Photography of the right side of an individual giraffe from about 100m for identification and to extract spot traits.

secondary surveys were conducted within a mean of 7 days. We drove all the same road transects covering our study area once during each survey (Figure 1a) (Lee & Bond, 2016). We photographed the right side of each giraffe encountered from about 100m to identify individuals based on their unique coat spot patterns (Figure 1b) with the software WildID (Bolger et al., 2012). We also recorded GPS location, sex and age class (calf 1 year, subadults 1 to 3 years, adult >3 years) based on visual characteristics (Lee, Bond, et al., 2016). The age class at first encounter determined the minimum age for each individual.

This research was conducted with permission from the Tanzania Wildlife Research Institute, the Tanzania Commission for Science and Technology, Tanzania National Parks, Manyara Ranch Conservancy, Tanzania Wildlife Authority and Burungu and Randilion Wildlife Management Areas. This study was observational, and disturbance was minimised by maintaining as much distance as possible from the giraffes during photographic data collection.

2.2 | Spot patterns

We quantified spot traits using ImageJ (Schneider et al., 2012) within a standardised rectangle fitted between the rear leg and the chest (Figure 2). Because the absolute size of the spots differs with the size of the individuals, measurements are in giraffe units (GU), where 1 GU corresponds to the height of the analysis rectangle, allowing for comparison among individuals of different body sizes. We excluded

incomplete spots and speckles ($<0.00001 \text{ GU}^2$) (Lee et al., 2018). We analysed seven spot traits as defined in Lee et al. (2018) spot number, mean area, perimeter, angle, circularity, roundness and solidity, as well as two coat background traits: background and convex background area, defined herein. Circularity indicates how circular the spot is and solidity how convex polygonal versus lobate the spot edge is. Background area corresponds to the total area between the spots (the lighter-coloured net between the spots seen in Figure 2) and convex background area is the area between the spots after a convex hull polygon is drawn over every spot. We extracted spot traits from 810 individuals (247 calves, 11 subadult males, 14 subadult females, 150 adult males and 388 adult females), representing 26% of the population, with others excluded due to poor photo quality (e.g. blur, obstructions, angle or distance >200m).

We summarised correlated spot traits into latent variables by performing a principal component analysis (PCA) with the nine spot traits mentioned above. In our statistical analyses, we used the first two principal component axes, PC1 and PC2, respectively referring to gradients of large to small size and convex polygonal to lobate shape (examples in Figure 2).

2.3 | Temperature anomalies

Temperature data were downloaded from the U.S. Geological Service's Famine Early Warning System NET data portal for the entire study area. We calculated seasonal temperature anomalies as



FIGURE 2 Variation in spot size (left to right = small to large) and shape (top to bottom = convex polygonal to lobate). Spot traits were extracted within an analysis rectangle fitted between the rear leg and the chest and from the back to the start of the posterior edge of the foreleg (yellow rectangle).

each season's deviation from the long-term seasonal means in units of standard deviations (SD). We subtracted the long-term seasonal mean (calculated from 2003 to 2019, with 2003 the earliest year data were available) from each seasonal temperature value and then divided by the seasonal standard deviation. Temperature anomalies ranged from -1.943 to 1.177 SD in the short rain season, -1.208 to 0.897 SD in the long rain season, and -1.648 to 1.402 SD in the dry season and were included in survival models as a primary survey-specific covariate to survival.

2.4 | Statistical analyses

To test for viability selection on spot patterns, we used Huggin's robust design capture-mark-recapture models to estimate stage-specific seasonal apparent survival rates as a function of individual covariates of spot traits (Amstrup et al., 2005). These models explicitly account for imperfect detection (p and c) and temporary emigration (γ' and γ''), thereby correcting for potential biases in survival estimates in open populations. We also accounted for individual heterogeneity in resighting and temporary emigration probabilities by including individual covariates as detailed below. We assumed similar detection rates within primary occasions ($p=c$) and random emigration ($\gamma'=\gamma''$). We estimated sex-specific survival rates for subadults and adults, and combined sexes for calves, thus

having estimates for five age-sex categories (calves, subadult males and females, adult males and females). Calf sex-specific survival rates are biased upward because many calves are only (re)captured before sex identification is possible. Previous analyses have shown that sex differences in survival are significant among adults only (Lee & Bond, 2022), thus combining sexes at the calf stage does not affect the results.

We used a multistep approach to determine which model best fits the data to ease model convergence. All models were run and ranked using RMark (Laake, 2013) in R v4.3.1 (R Core Team, 2023). Model selection was based on the difference in the small-sample corrected Akaike Information Criterion values ($\Delta AICc$) (Akaike, 1992; Burnham & Anderson, 2002). When the fit of two models was similar ($\Delta AICc < 2$), we considered the model with the greatest weight to be the most parsimonious model.

We first constructed a base model of detection probability, temporary emigration and survival based on previous findings, which we then kept constant while testing viability selection on spot patterns and effects of temperature anomalies. For the base model, we tested the known effects of individual covariates of age-sex classes, continuous minimum age, seasons, and individual spatial covariates of mean distance to the edge of the study or protected area (MeanDistSA and MeanDistPA, respectively) (Bond et al., 2023; Lee & Bond, 2022). We included continuous minimum age (in seasons) as a time-varying covariate to allow individuals to transition between

age classes (calves: 0–3; subadults: 3–9; adults > 9 seasons). We included spatial covariates to account for biases in detection and emigration due to individuals being closer to the limits of the study area and in survival rate due to expected positive effects of protected areas (Bond et al., 2023).

2.4.1 | Base model

The detection probability model included age-sex classes, seasons, and MeanDistSA. The temporary emigration model included age-sex classes, continuous minimum age, seasons, and MeanDistSA interactively with age-sex classes. The base survival model included age-sex classes, continuous minimum age, seasons, and MeanDistPA interactively with season. Thus, our base model to analyse the effects of spot patterns on survival was $\{S(\text{Age-Sex+Age+Season+MeanDistPA} + [\text{MeanDistPA} \times \text{Season}]), \gamma(\text{Age-Sex+Age+Season+MeanDistSA} + [\text{MeanDistSA} \times \text{Age-Sex}]), p(\text{Age-Sex+Season+MeanDistSA})\}$.

2.4.2 | Viability selection on spot traits

After determining the base model, we examined linear and nonlinear (quadratic) effects of coat patterns on survival by adding individual covariates of spot trait variables. We ranked models with each spot trait separately and as (quadratic) principal components (PC) to determine the most parsimonious survival model. We also included an interaction with age-sex classes to determine whether viability selection on spot patterns differed across life stages. To visualise the effect of spot patterns on survival, we plotted model predictions estimated using the mean values of all non-spot-trait variables.

2.4.3 | Effects of temperature anomalies on viability selection on spot traits

We then expanded the most parsimonious model of survival as a function of spot traits by adding the effect of temperature anomalies on survival in interaction with spot traits (as both linear and quadratic terms) and age-sex classes, as well as the three-way interaction PC1:Age-Sex:Temperature. This model tested our hypothesis that spot patterns help giraffes to thermoregulate and their effects may be nonlinear and may change with life stages.

3 | RESULTS

3.1 | Viability selection on spot traits

The first two components of the PCA explained about 40% and 28%, respectively, of the variation in spot traits. The first axis (PC1) summarised traits related to spot size (number, area, perimeter, convex background) representing a gradient from large to small

spots and the second axis (PC2) summarised traits related to spot shape (angle, roundness, circularity and solidity) representing a gradient from convex polygonal to more lobate spots (see Figure S1 and PCA loadings in Table S1).

The top-ranked spot trait survival model included an interactive effect of spot patterns (PC1 and PC2) that varied with life stage (age-sex classes; Table 1; see beta estimates in Table S2). Models with single spot traits all scored lower than PC models (see Table S3). Due to low sample size for individuals first detected as subadults, the model was unable to provide reliable estimates for this life stage, thus we only report and discuss results for calves and adults. Similarly, quadratic models were not reliable likely due to lack of statistical power or overparameterisation. We thus report results of the model selection on linear models.

The effect of spot patterns on survival was strongest in calves (Figure 3). Calves with smaller and more lobate spots had a higher survival rate. For calves with more convex polygonal spots, the size of the spots had less effect on survival. In adult males, viability selection on spot traits was disruptive: individuals with larger and more convex polygonal, or smaller and more lobate spots had higher survival compared to those with spots of intermediate size and circularity (Figure 3). In adult females, selection on spot traits was less but clearly directional: individuals with larger spots tended to have a slightly higher survival probability (Figure 3).

3.2 | Effect of temperature anomalies on viability selection on spot traits

Adding temperature anomalies to the most parsimonious spot trait survival model improved the model fit (Table 1). Quadratic models were again not reliable; thus, results are from the model selection on linear models. Four models were equivalent ($\Delta\text{AICc} < 2$), but the first model carried almost two times the weight of the second model. The top-ranked survival model included an interaction of temperature anomalies with PC1 (spot size) and age-sex classes (see beta estimates in Table S4). A survival model including a season \times temperature interaction was ranked far below the top model ($\Delta\text{AICc} = 13.83$), indicating effects were similar in all three seasons. Viability selection on spot patterns correlated with temperature anomalies more strongly in calves than in adults, and more strongly in adult males than in adult females (Figure 4). Adult females of all spot types experiencing the highest temperature anomalies had the lowest survival, but those with smaller spots had slightly lower survival than those with larger spots. Adult males with the smallest spots had the lowest survival ($S = 0.83$) when experiencing anomalously low temperatures compared to males with the largest spots ($S = 0.99$). This relationship was reversed when males experienced anomalously high temperatures, but weaker, as males with the largest spots had a survival probability of 0.92. At seasonal average temperature, the size of the spots of adult males was not important to survival, suggesting that all phenotypes are adapted to the average temperature conditions. Viability selection

TABLE 1 Model selection results for viability selection on spot patterns as principal components (PC1 and PC2) and temperature (Temp) effects. The first four models were equivalent ($\Delta AICc < 2$) but the top-ranked model carried more weight. MeanDistPA stands for the individual covariate of mean distance of the individual to edge of protected area.

Model	df	loglik	$\Delta AICc$	Weight
S (Age-Sex+Age+Season+MeanDistPA+PC1+PC2+Temp+MeanDistPA:Season+PC1:PC2+PC1:Temp+Age-Sex:Temp)	59	-18045.37	0	0.33
S (Age-Sex+Age+Season+MeanDistPA+PC1+PC2+Temp+MeanDistPA:Season+PC1:PC2+PC1:Temp+Age-Sex:Temp+PC1:Age-Sex:temp)	63	-18041.93	1.22	0.18
S (Age-Sex+Age+Season+MeanDistPA+PC1+PC2+Temp+MeanDistPA:Season+PC1:PC2+PC2:Temp+Age-Sex:Temp)	59	-18046.06	1.38	0.16
S (Age-Sex+Age+Season+MeanDistPA+PC1+PC2+Temp+MeanDistPA:Season+PC1:PC2+PC1:Temp+PC2:Temp+Age-Sex:Temp)	60	-18045.15	1.59	0.15
S (Age-Sex+Age+Season+MeanDistPA+PC1+PC2+Temp+MeanDistPA:Season+PC1:PC2+PC1:Temp+PC2:Temp+Age-Sex:Temp+PC1:Age-Sex:Temp)	64	-18041.61	2.61	0.09
S (Age-Sex+Age+Season+MeanDistPA+PC1+PC2+Temp+MeanDistPA:Season+PC1:PC2+PC1:Temp+PC2:Temp+Age-Sex:Temp+PC1:Age-Sex:Temp+PC2:Age-Sex:Temp)	68	-18037.75	3.01	0.07
S (Age-Sex+Age+Season+MeanDistPA+PC1+PC2+Temp+MeanDistPA:Season+PC1:PC2+Age-Sex:Temp+PC1:PC2:Age-Sex)	58	-18049.00	5.24	0.02
S (Age-Sex+Age+Season+MeanDistPA+PC1+PC2+MeanDistPA:Season+PC1:PC2+PC1:Age-Sex+PC2:Age-Sex +PC1:PC2:Age-Sex)	53	-18058.43	13.98	<0.001
S (Age-Sex+Age+Season+MeanDistPA+MeanDistPA:Season)	38	-18081.37	29.57	<0.001
S (Age-Sex+Age+Season+MeanDistPA+PC1+PC2+MeanDistPA:Season)	40	-18080.79	32.42	<0.001
S (Age-Sex+Age+Season+MeanDistPA+PC1+PC2+MeanDistPA:Season+PC1:PC2)	41	-18080.40	33.74	<0.001

on spot patterns was also disruptive in calves. However, calves were strongly adversely affected by anomalously high temperatures, with the survival probability of calves with the largest spots decreasing to 0.33. All calves survived better when temperatures were anomalously low compared to anomalously high, except calves with the smallest spots, which had a stable survival probability across the whole range of temperature anomalies.

4 | DISCUSSION

Our analyses of viability selection on giraffe spot patterns showed that spot size and shape affected survival probability, and the relationship differed among life stages and sexes. Viability selection on spot patterns in calves and adult males was disruptive, though in calves, as the spots became more convex polygonal, their size had less influence on survival. In adult females, viability selection on spot patterns was slightly negatively directional. Additionally, viability selection on spot size correlated with temperature anomalies in calves and adult males, and slightly in adult females, suggesting a role of spot patterns in thermoregulation.

Results for calves expand upon a previous study that examined calf survival correlates of spot traits during their first season, first year, and first 3 years (Lee et al., 2018). As observed here between calves and adults, this previous study found different results for the different juvenile life stages and specifically during their first year, calves with smaller spots had higher survival. Our analysis confirmed the importance of small spots on first year survival while additionally showing an interactive effect of spot shape and size. The interactive

effect suggests that the overall patterns rather than specific traits are under selection. The change in selection strength and/or direction across life stages suggests that the functions of spot patterns change throughout life.

Importantly, our analyses showed, for the first time to our knowledge, fitness effects of spot patterns in adult mammals, particularly in males. In long-lived species with late maturity and low reproductive output, adult survival generally contributes most to population growth rates (Saether et al., 2013), which is also the case in giraffes (Bond et al., 2025; Lee, Bond, et al., 2016). If fitness effects of spot patterns ultimately affect population growth, spots could be a key phenotypic trait for population persistence and conservation of the endangered giraffe. For example, as extreme spot sizes and shapes confer higher male survival probabilities, conservation plans should maintain variation in spot patterns by preserving connectivity among subpopulations to facilitate mate choice and genetic exchange.

Animal markings can have various adaptive functions such as camouflage or thermoregulation (Caro, 2005). Viability selection on spot size correlated with temperature anomalies, which suggests that spot patterns on giraffe coats may help with thermoregulation. Thermoregulation is energetically demanding and may trade off with other vital functions (Angilletta, 2009; Cunningham et al., 2021). Calves are likely to lose heat faster than adults because of their greater surface-to-volume ratio. Moreover, young calves spend time in the shade hidden in bushes away from predator sight (Mitchell & Skinner, 2004), which reduces exposure to the sun. Calves with larger spots may benefit from greater absorption capacity of solar radiation, allowing them to expose themselves to the sun for less time when they need to upregulate their temperature, or to absorb

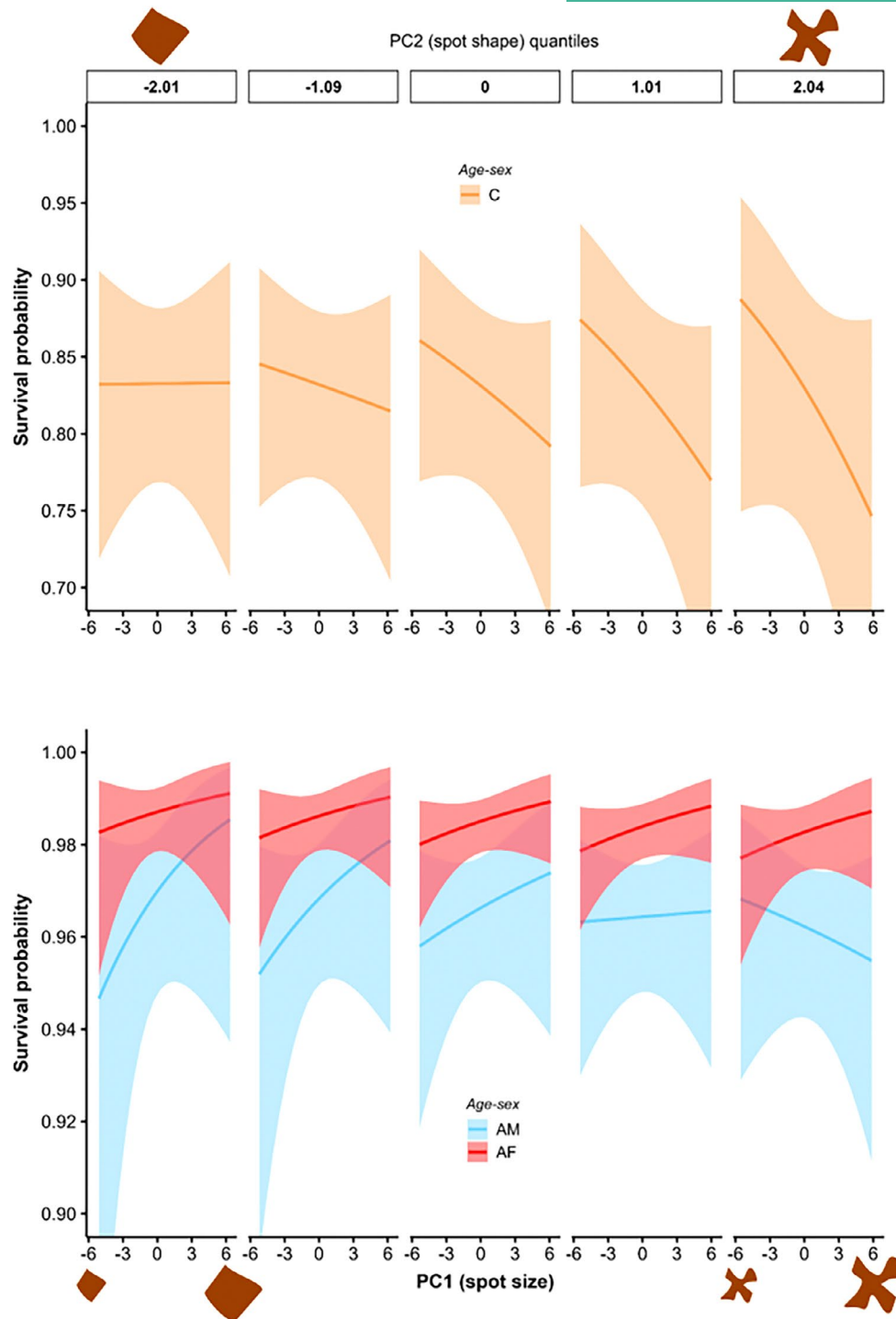


FIGURE 3 Viability selection on spot patterns for calves (C, orange, top panel), adult males (AM, blue, bottom panel) and females (AF, red, bottom panel). Survival probability is represented as a function of spot size (PC1; negative to positive values = smaller to larger spots, obtained after multiplying PC1 values by -1) for spot shape mean (PC2 = 0) and quantiles (PC2 = 0.1, 0.25, 0.75 and 0.9; negative to positive values = convex polygonal to lobate spots) to ease visualisation of PC1:PC2 interactive effect on survival. Note the scale difference on the y-axis. Calves with smaller and more lobate spots had a higher survival rate than calves with larger and more polygonal spots. Viability selection in adult males was disruptive while in females, selection tended to be slightly positively directional.

solar radiation more efficiently through vegetation cover. This could explain the higher survival probability of calves with larger spots that have experienced anomalously cold temperatures. Conversely, the lower survival of calves with larger spots that experienced

anomalously hot conditions may result from hyperthermia. Calves with smaller spots showed less variation in survival probability with temperature anomalies. However, though their survival probability was the highest when experiencing anomalously high temperatures,

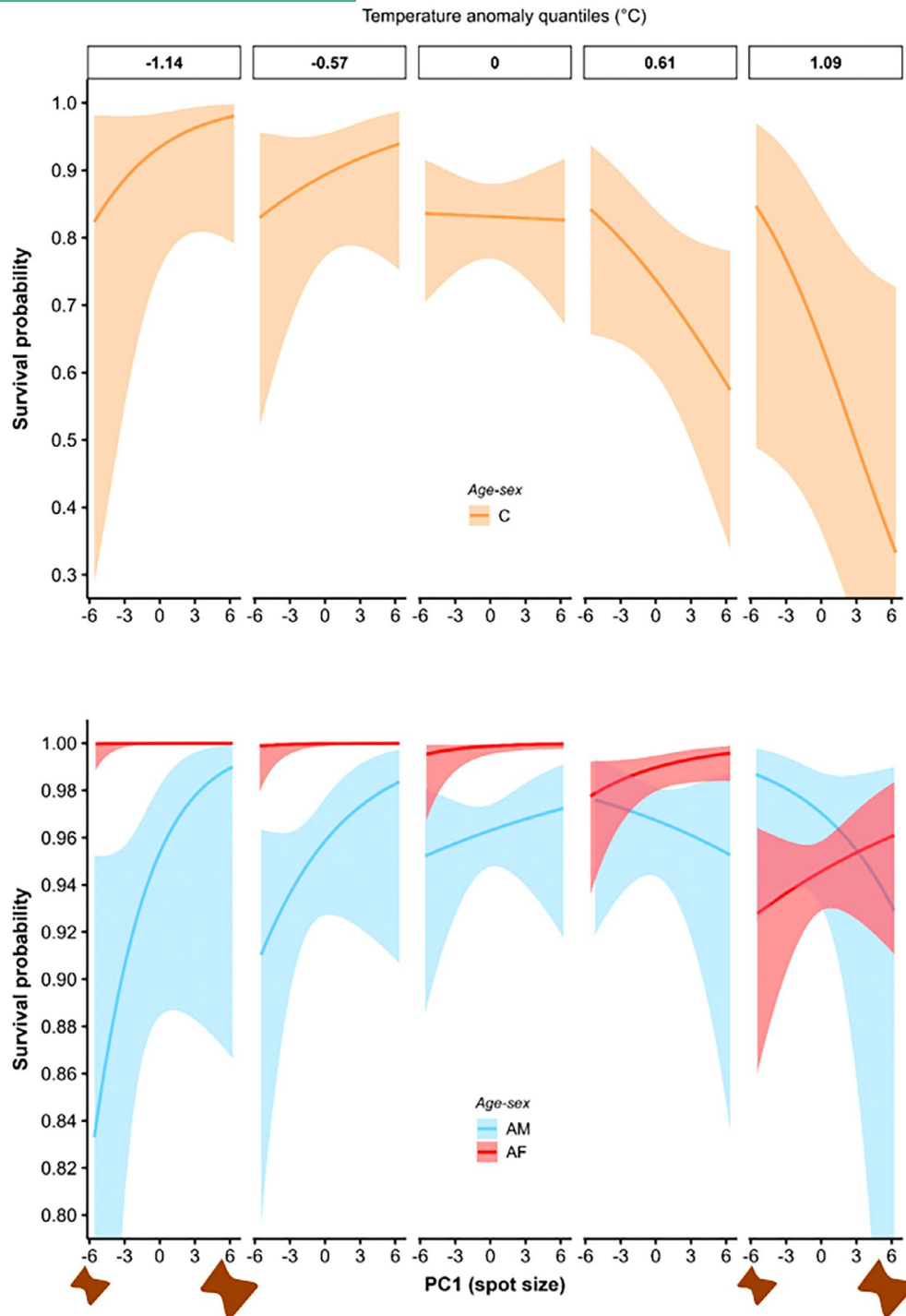


FIGURE 4 Viability selection on spot size in calves (C, orange, top panel), adult males (AM, blue, bottom panel) and females (AF, red, bottom panel) as a function of temperature anomalies. The effect of spot size (PC1; gradient from smaller to larger spots—values were multiplied by -1) on survival is shown at seasonal temperature average ($T^{\circ}\text{C}=0$) and temperature anomaly quantiles 0.1, 0.25, 0.75, 0.9 (gradient from anomalously low to anomalously high temperatures). Note the scale difference on the y-axis. Viability selection was disruptive in calves and adult males, with individuals with larger versus smaller spots surviving better when experiencing anomalously low versus high temperatures. Females had lowest survival when experiencing anomalously high temperatures.

it never reached the maximum survival probability of calves with larger spots that experienced anomalously cold temperatures. Small spots may thus confer an energetic trade-off minimising hypothermia in colder environments and hyperthermia in hotter

environments. Notably, at anomalously high temperatures, selection pressure on spot patterns was strong but the survival probability of calves with smaller spots was similar to that of all phenotypes at seasonal average temperature. Calves with smaller spots seem to be

the phenotypes with the greatest adaptive potential to face current temperature rise.

Temperature anomalies only altered the effect of spot size on survival, though overall spot size affected survival interactively with spot shape. Spot shape may thus play a role in another context than thermoregulation. Calves are subjected to high predation risk in their first year (Strauss & Packer, 2013). Specific spot shapes, rather than sizes, may best conceal calves from predators. Irregular edges may resemble leaf shadows and branches of bushes under which calves hide compared to solid shapes. Calves with more lobate spots may be less predated overall, which may explain the higher survival probability of calves with smaller lobate spots. However, calves with larger lobate spots had lower survival than calves with more convex polygonal spots, irrespective of spot size. Survival differences among phenotypes may vary with vegetation cover, whereby spot patterns could provide varying levels of camouflage depending on background complexity or structure. For example, predation on moths differing in their camouflage levels has been shown to be lower in higher complexity backgrounds (Rowe et al., 2021). A computer-based experiment found that survival was higher when the size of the spots and of the background elements were similar, but that survival did not differ between phenotypes in a habitat with two contrasting backgrounds (Toh & Todd, 2017). Alternatively, predator-prey interactions can change with temperature, notably through changes in both predator and prey biomass or behaviour (Bastille-Rousseau et al., 2018; Bretagnolle & Terraube, 2019; Creel et al., 2016). Survival of giraffe calves has been shown to be higher in the presence of other prey species, suggesting a dilution effect of lion predation on giraffe calves (Lee, Kissui, et al., 2016). Moreover, the density of lions, the main predator of giraffes, was higher in populations subjected to lower mean annual temperature (Celesia et al., 2010) and low temperature seasonality (Jones et al., 2021). Temperature fluctuations, especially temperature anomalies, may therefore affect predator population dynamics. Predation pressure and temperature anomalies may drive, additively or interactively, viability selection on spot patterns of giraffe calves. Overall, which spot patterns are advantaged seems to be context-dependent, with multiple ecological factors shaping the spot size and shape in giraffe calves.

In adults, viability selection on spot patterns correlated with temperature anomalies in males but little in females. Sexual differences in the role of spot patterns may relate to sexual differences in behaviour or energetic demands. Adult male giraffes are 30–40% heavier than females, which increases their energetic demands and makes thermoregulation more challenging, but also allows a higher heat load, thus a greater heat tolerance. The heat load may however be exceeded for individuals with larger spots when experiencing anomalously high temperatures. Stronger selection pressures in anomalously cold temperatures suggest that adult male giraffes are better adapted to hot environments and larger spots confer greater cold tolerance. Adult females have high energy requirements throughout most of their lifetime as gestation lasts about 15 months and suckling about 12 months, and they can be pregnant and nursing

at the same time (Deacon et al., 2015). These energy requirements may be greater than the benefit differential between larger and smaller spots and explain why spot patterns affected female survival less than other age-sex classes, and all females had lower survival when experiencing anomalously high temperatures. These results contrast with findings from a previous study (Bond et al., 2023), where adult female giraffes had the lowest survival when experiencing anomalously cold temperatures. This previous study did not examine spot traits and used a larger dataset that also included rainfall and NDVI (a vegetation index) alongside temperature, so differences in modelling structure may explain this inconsistency. Here, females with smaller spots experienced slightly higher mortality when experiencing anomalously hot conditions, which suggests that females with larger and smaller spots may differ in the physiological mechanisms allowing them to bear heat anomalies. Females with larger spots may have a greater amount of melanin pigments protecting against solar radiation or oxidative stress (Ducrest et al., 2008).

Male and female giraffes also differ in their behaviour. Adult females stay in groups with their calves (Langman, 1977), whereas adult males spend most of their time roaming between female groups in search of fertile females (Pratt & Anderson, 1985). To limit their energetic expenditure, females may use behavioural thermoregulation (Mitchell et al., 2017). Behavioural thermoregulation may be costlier for males as it would trade off with searching for and guarding potential mates. Males with different spot sizes may differ in their activity and aggressiveness behaviours. Indeed, colour polymorphism has been shown in several taxa to correlate with other traits, including behaviour (Ducrest et al., 2008). Melanin-based colouration generally correlates with greater energetic balance but also positively with activity and aggressiveness levels. If males with larger spots, thus with more melanin pigments, are more active, they likely produce more heat and are more exposed to solar radiation, which may be beneficial in anomalously low temperatures but detrimental in anomalously high temperatures. Dominant adult males also become darker coloured with age (Castles et al., 2019). If their aggressiveness and dominance give them better access to mates, nutritive food or water, this may offset their greater energy expenditure. However, a greater nutrient intake may not fully counterbalance heat production, or lower capacity of heat dissipation, when temperatures are anomalously high. Heterogeneous selection on spot patterns with temperature may thus be due to direct effects of the spots (e.g. through thermoregulation), or melanisation, or to their pleiotropic effects with other traits (e.g. metabolism, immune function, stress hormones). Further work on thermal physiology of giraffes would be required to identify the underlying mechanisms.

Heterogeneous selection on spot patterns with environmental conditions, here temperature anomalies, may explain the maintenance of variation in animal markings. Spot patterns in giraffes may help with thermoregulation, but further work is needed to demonstrate a causal effect of temperature and determine whether patterns within species have multiple functions. Thermoregulation by markings may be complicated by interactions with various other mechanisms such as skin insulation, behavioural thermoregulation,

hydroregulation capacities and ecological conditions (e.g. access to water, wind speed) (Hetem et al., 2009; Mitchell et al., 2018; Stuart-Fox et al., 2017). Subadult recruitment also contributes to population growth, thus estimating selection pressures at this life stage is warranted for a full understanding of spot pattern importance. Our work suggested disruptive viability selection on spot patterns, particularly in males. Though nonlinear models were not reliable here, future work would benefit from quantifying nonlinear effects of spot patterns on survival. This study highlights the importance of considering variation in spot patterns alongside the impact of climate change when developing giraffe conservation plans. Specifically, individuals with smaller spots may better endure the global temperature rise, but as the adult stage contributes most to population dynamics, conserving individuals with larger polygonal spots may also be important in other ecological contexts. Facilitating natural genetic exchange among subpopulations through increased habitat connectivity (e.g. by protecting and restoring habitat, lowering human disturbance) and augmenting wildlife law enforcement in areas vulnerable to poaching would enable the maintenance of variation and natural evolution in spot patterns. This may be a crucial conservation strategy to recover the endangered giraffe in an era of strong climatic variation. Markings may have fitness consequences in other mammalian species (e.g. spotted felids, striped felids and rodents, wild dogs with mottled patches) and be important for their adaptation and population management as well.

AUTHOR CONTRIBUTIONS

Conceptualisation: Alexia Mouchet, Derek E. Lee, Monica L. Bond, Douglas R. Cavener and Arpat Ozgul; Methodology: Alexia Mouchet and Arpat Ozgul; Supervision: Arpat Ozgul with Monica L. Bond; Funding acquisition: Derek E. Lee, Monica L. Bond, Alexia Mouchet and Arpat Ozgul; Data collection: Derek E. Lee, Monica L. Bond and James M. Madeli; Data processing: Derek E. Lee, Monica L. Bond and Douglas R. Cavener; Analyses and Visualisation: Alexia Mouchet with Arpat Ozgul; Writing–lead: Alexia Mouchet; All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no competing interests.

DATA AVAILABILITY STATEMENT

Data and code used in this study are available on the Figshare repository (Mouchet et al., 2026): dataset with encounter history and individual traits (DOI: [10.6084/m9.figshare.28450583](https://doi.org/10.6084/m9.figshare.28450583)), dataset with temperature anomalies (DOI: [10.6084/m9.figshare.28450547](https://doi.org/10.6084/m9.figshare.28450547)), and R script (DOI: [10.6084/m9.figshare.28450958](https://doi.org/10.6084/m9.figshare.28450958)).

STATEMENT OF INCLUSION

Our study brings together authors from different countries, including scientists based in the country where the study was carried out. Data collection also involved local field assistants. Whenever relevant, literature published by scientists based in Africa or involving co-authors from the region was cited.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Text S1. Study area protection management actions implemented in the different protected areas.

Figure S1. Loading plot of the principal component analysis (PCA) of giraffe spot traits (A) and percentage of variance explained by principal components (B).

Table S1. Loadings of the first three axes of the PCA of spot traits.

Table S2. Model estimates of the most parsimonious model of the effect of spot patterns on seasonal apparent survival.

Table S3. Model comparison for the effect of giraffe spot traits on apparent survival.

Table S4. Model estimates of the most parsimonious model of the effect of temperature anomalies on viability selection on giraffe spot patterns.

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