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

Alexia Mouchet[1], Derek E. Lee[2], Monica L. Bond[1,2], Douglas R. Cavener[3], James Madeli[2], Arpat Ozgul[1]

[1] Department of Evolutionary Biology and Environmental Studies, University of Zurich, Zurich, Switzerland

[2] Wild Nature Institute, Concord, NH, USA

[3] Department of Biology, Pennsylvania State University, University Park, Pennsylvania, USA

Corresponding authors: Alexia Mouchet (mouchet@bio.lmu.de) or Monica Bond (monica.bond@ieu.uzh.ch)

Abstract

Remarkable variation in animal colour patterns is often shaped by heterogeneous selection, reflecting adaptation to variable environmental conditions. However, the adaptive functions of patterns and drivers of selection remain poorly understood. Shape and size of colour patterns may help with thermoregulation and thus be altered by temperature anomalies, which are predicted to be more frequent with current climate change. Using resighting data from 810 individuals over eight years, we studied the effects of spot patterns on survival in a population of wild giraffes and whether this relationship was affected by temperature anomalies. Shape and size of spots interactively affected survival: calves with small lobate and adult males with small lobate or large polygonal spots survived better. Viability selection on spot size was altered by temperature anomalies: calves and adult males having larger spots survived better at anomalously low temperature whereas those with smaller spots survived better at anomalously high temperature. Spot patterns only weakly affected the survival of adult females, which all suffered from anomalously high temperature. In calves, spot size may help with thermoregulation while spot shape may conceal them from predators. In adults, sex-specific selection pressures suggest other functions to thermoregulation. Spot patterns at different life-stages can affect population dynamics and their evolution may be altered by climate change. This study highlights the importance of considering spot pattern variation in conservation plans of the endangered Masai giraffe, enabling populations to adapt to climate change and extreme weather events.

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

Introduction

Phenotypic variation within populations may result from phenotype-dependent demography caused by heterogeneous selection (Engen & Sæther, 2014; Lande, 2007). Heterogeneous selection may be driven by spatiotemporal variation in the environment, with spatial variation favouring different phenotypes in different environments and temporal variation favouring different phenotypes within the same environment (Siepielski et al., 2009, 2013). Knowing the environmental drivers of heterogeneous selection is thus paramount to understand the maintenance of phenotypic variation and how populations can adapt to environmental changes.

Climate is a potential driver of heterogeneous selection as it varies spatiotemporally and can affect population demography (Bonebrake & Mastrandrea, 2010; Paniw et al., 2021; Selwood et al., 2015; Siepielski et al., 2017). Notably, temperature is a climatic variable that influences reproduction and survival (Angilletta Jr., 2009; Woodroffe et al., 2017). These demographic parameters may be altered with temperature anomalies, such as heat and cold waves (Cunningham et al., 2021; Gardner et al., 2016; Tanner et al., 2017). To mitigate environmental temperature variation, animals maintain a relatively stable body temperature by thermoregulation, which may be enhanced through behavioural, physiological or morphological adaptations (Angilletta Jr., 2009). Morphological adaptations may include optimizing body shape and colour or marking patterns.

Marking patterns can show remarkable variation in shape and size among individuals within populations, which suggests they may be adaptive, and that their fitness costs and benefits vary with the environment. For example, giraffes (*Giraffa* spp.) have individually unique coat spot patterns that do not change from birth to death (Foster, 1966) and which vary among and within populations (Dagg, 1968; Morandi et al., 2022). Aspects of size and shape of the spots are heritable (Dagg, 1968; Lee et al., 2018), which suggest they may have adaptive significance. Patterns may help with thermoregulation as darker vs. lighter colours may absorb vs. dissipate the heat (Hetem et al., 2009; Walsberg, 1983) and larger and uniform patterns may amplify heat absorption or dissipation. Patterns may also serve other functions, such as communication or predator avoidance (Caro, 2005). In a population of wild Masai giraffes (*G. tippelskirchi*) in Tanzania, calves with larger and/or more lobate spots survived better during the first 4 months of life and calves with smaller spots survived better during the first year of life (Lee et al., 2018). Spot characteristics may conceal calves from predators or, through some other mechanism, contribute to differential survival rates at the earliest life stages. However, for adult giraffes, predation risk is not a major threat (Lee, Bond, et al., 2016; Strauss & Packer, 2013a). Thus, spot patterns in adult giraffes may have other functions, which may favour similar or different spot characteristics across life-stages. For example, survival of both adult male and female Masai giraffes–but not calves–was lower during colder seasonal temperature anomalies (Bond et al., 2023). Spot patches on the coats of giraffes are underlain by a central artery and dense network of blood vessels that adjust blood flow to and from the patch, enabling efficient heating and cooling (Taylor et al., 2023). Spots may act as thermal windows whereby smaller spots may reduce and larger spots increase heat loss, which may help giraffes to thermoregulate faster in anomalously cold or hot temperatures, respectively. Thus, the size and shape of an adult's spots may directly influence its fitness by affecting its thermoregulatory performance. If so, adult giraffes having specific spot patterns may cope with anomalously cold or hot seasons better than individuals with other spot patterns. If spot patterns have different functions across life-stages or biological classes that favour different spot characteristics, variation in spot patterns may be maintained.

We studied fitness effects of spot patterns in a population of wild Masai giraffes in Tanzania to determine whether certain spot traits confer higher survival at different life-stages. Moreover, if coat spots help with thermoregulation, we expected viability selection on spot patterns to correlate with land surface temperature. To test these hypotheses, we quantified spot traits and survival rates using eight years of photographic data collected between 2012 and 2020. We extracted spot traits from the photographs of 810 individuals and summarised them using principal component analysis (PCA) into gradients of size (PC1) and shape (PC2). Using capture-mark-recapture models (CMR), we estimated apparent seasonal survival probabilities of giraffes as a function of their spot patterns and investigated whether this relationship was affected by temperature anomalies (deviations from seasonal averages). Because only adults suffered from temperature anomalies (Bond et al., 2023), we predicted temperature to affect viability selection on spot patterns in adults only. Larger and more convex polygonal spots should absorb more solar radiations enabling faster heating in colder temperatures. Males may suffer more from temperature anomalies due to their 30-40% larger body mass compared to females (Hall-Martin, 1977), which increases their energetic demands and makes thermoregulation more challenging. Additionally, the wide-ranging behaviour by males in search of mates throughout the year further amplifies their energy expenditure, potentially leading to stronger selection on spot patterns that aid in coping with extreme temperatures (Bercovitch et al., 2006; Pratt & Anderson, 1985a). Therefore, we also predicted selection on spot patterns may be stronger in males than in females.

Materials and Methods

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 1200 m). The study area (822 km²) includes four protected areas and is entirely unfenced (Fig. 1A). 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). Secondary surveys were conducted at 7-day intervals. During each survey, we drove on the same road transects following a fixed route covering our study area (Fig. 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 (Fig. 1B). Individual identification was achieved with the software WildID (Bolger et al., 2012). We also recorded GPS location, sex and age class (calf 0-3 months, subadults 4 months to 3 years, adult > 3 years) based on visual characteristics (Strauss & Packer, 2013b).

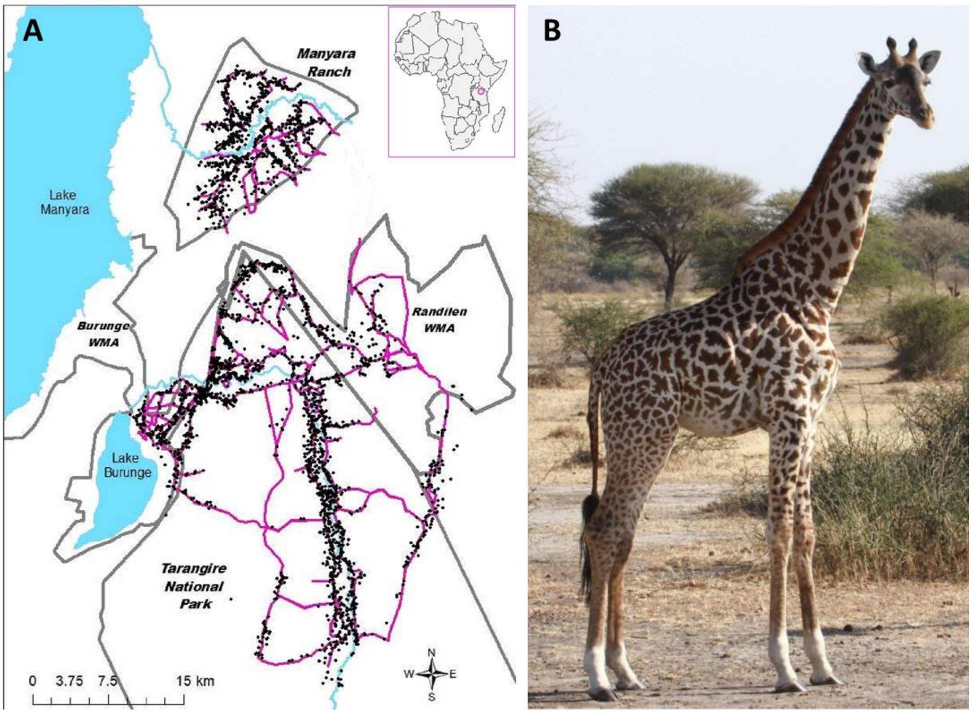

Figure 1. Study area and Masai giraffe photography (re)capture. A) Map of the study area in the Tarangire Ecosystem with locations of encountered Masai giraffes (black dots) on road transects (purple lines) from 2012-2020. B) Photography of the right side of an individual giraffe from about 100m for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

Spot patterns

We quantified spot traits within a standardised rectangle fitted between the rear leg and the chest (Figure 2)^{17} using ImageJ (Schneider et al., 2012). Because the size of the spots may differ with the size of the individuals, measurements are in giraffe units (GU), where 1GU corresponds to the height of the analysis rectangle, allowing for comparison among individuals. We excluded incomplete and too small (<0.00001 GU^2) spots. For more details, see (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 vs. lobate the spot edge is. Background area corresponds to the total area between the spots (the lighter-colored net between the spots seen in Fig. 2) and convex background area is the area between the spots after a convex hull polygon is drawn over every spot. We obtained high quality photographs of spot traits from 810 individuals (247 calves, 11 subadult males, 14 subadult females, 150 adult males and 388 adult females).

Figure 2. Variation in spot size (small to large) and shape (convex polygonal to lobate): smaller size in the left and third from left, larger size in the second from left and last images; more convex polygonal shape in the first two on the left and more lobate shaped in the last two images on the right. 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 on the image on the right).

Statistical analyses

To determine whether spot patterns affect individual survival, we used Huggin's robust design model to estimate stage-specific seasonal apparent survival rates (Amstrup et al., 2005). We additionally estimated detection probabilities (p and c) and temporary emigration (γ' and γ''), assuming similar detection rates within primary occasions (p=c) and random emigration (γ'=γ''). Life-stage categories were a combination of age classes and sexes (age-sex) because many calves are only (re)captured before sex identification is possible and not detected again. Sex-specific survival rates would thus be highly biased by the unknown-sex class with low survival rate. We therefore had five age-sex categories (calves, subadult males and females, adult males and females). Previous analyses have shown that sex differences in survival are not present among calves, begin to appear among subadults, and are significant among adults (Lee & Bond, 2022).

We used a multistep approach to determine which model fits best the data to ease model convergence. Model selection was based on the difference in the small-sample corrected Akaike Information Criterion values (ΔAICc) (Akaike, 1992; Burnham & Anderson, 2002). When the fit of two models was similar (ΔAICc<2), we considered the model with the greatest weight to be the most parsimonious model. We first determined the most parsimonious temporary emigration and detection probability models. Temporary emigration rate changed with age-sex classes, continuous age, and across seasons. Detection probability varied additively among age-sex classes and seasons. The model with an interactive effect scored similarly but we selected the simplest model. Additionally, temporary emigration decreased, and detection increased with the mean distance an individual was from the edge of the study area, both interactively with life-stages and with seasons for detection only. We included spatial covariates to account for biases in detection and emigration due to individuals being closer to the limits of the study area (i.e., each individual's mean distance to the edge of the study area) and in survival rate due to expected positive effects of protected areas (i.e., distance to edge of protected area) (for further details on distance measures, see (Bond et al., 2023). We then determined the most parsimonious survival model, which included age-sex classes, continuous age and seasons, as well as the distance from the edge of the protected area, in interaction with seasons. This survival model served as a base model to analyse the effects of spot patterns on survival.

To test the effect of coat traits on survival, we performed a principal component analysis (PCA) with the nine coat metrics mentioned above to identify correlated traits and summarise them in a few dimensions. We analysed whether the first two principal component axes (PC1 and PC2, respectively referring to gradients of large to small size and convex polygonal to lobate shape; see Figure 2 for examples) independently and interactively affected survival. We also analysed each spot trait independently to identify whether specific traits had effects on survival. We included an interaction with age-sex classes to determine whether viability selection on spot patterns differed across life-stages.

Finally, to test our hypothesis that spot patterns may help giraffes to thermoregulate, we expanded the most parsimonious model from the previous step by fitting the effect of temperature anomalies on survival in interaction with spot patterns (PC1, PC2) and age-sex classes. We expected temperature anomalies rather than natural variation in temperature in the different seasons to affect survival because giraffes are long-lived animals. We calculated temperature anomalies as deviations from seasonal averages in standard deviation units (sd) by subtracting the seasonal average from each temperature value and then dividing 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.

All models were run using RMark (Laake, 2013) in R v4.3.1 (R Core Team, 2023). To visualise the effect of spot patterns on survival, we plotted model predictions, which were estimated at the mean of all individual’s mean distance from the edge of the protected area.

Results

Effect of spot traits on survival

The first two components of the PCA analysis on the nine spot traits we extracted explained about 40% and 28%, respectively, of the variation in spot traits. The first axis (PC1) gathers traits related to spot size (number, area, perimeter, convex background) representing a gradient from large to small spots and the second axis (PC2), traits related to spot shape (angle, roundness, circularity and solidity) representing a gradient from convex polygonal to more lobate spots (Fig. S1).

The top-ranked seasonal apparent survival model included an interactive effect of spot patterns (PCA axes) that varied with life stage (age-sex classes; Table 1 and model estimates in Table S1). Models with single spot traits all scored lower (Table S2). Model predictions showed that the effect of spot patterns on survival was strongest in calves (Fig. 3). Calves with small and lobate spots had the highest survival rate. For calves with more convex polygonal spots, the size of the spots had less effect on survival. In adult males, predictions suggested disruptive viability selection on spot traits: adult males having larger and more convex polygonal, or smaller and more lobate spots had higher survival compared to adult males with spots of intermediate size and circularity (Fig. 3). In adult females, selection on spot traits was weak and directional: adult females with larger spots tended to have a slightly higher survival probability (Fig. 3).

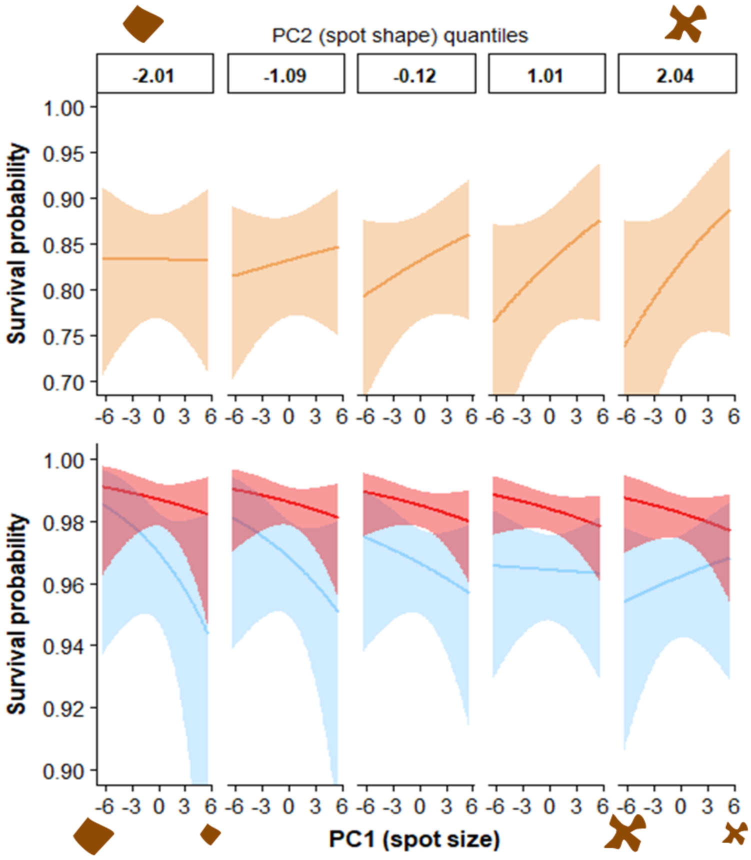

Figure 3: Effect of spot patterns on survival probability for calves (orange, top panel), adult males (blue, bottom panel) and adult females (red, bottom panel). Survival probability is represented as a function of spot size (PC1; negative to positive values denote a gradient of larger to smaller spots) for quantiles (0.1, 0.25, 0.5, 0.75 and 0.9) of spot shape (PC2; negative to positive values denote a gradient of convex polygonal to lobate spots) to ease visualisation of PC1:PC2 interactive effect on survival. Note the scale difference on the y-axis between the bottom and top panels. 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 tended to be disruptive while in females, selection was weakly negatively directional.

Effect of temperature on viability selection on spot traits

Adding temperature anomalies to the most parsimonious survival model described above improved the model fit (Table 1). Four models were equivalent based on their small-sample corrected Akaike Information Criterion (AICc) values (ΔAICc<2), but the first model carried almost two times the weight of the second model. The top-ranked model included an interaction of temperature anomalies with PC1 (i.e., spot size) and age-sex classes (model estimates in Table S3). Model predictions show that viability selection on spot patterns correlated with temperature anomalies more strongly in calves than in adults, and more strongly in males than in females (Fig. 4). Adult females of all spot types generally suffered from the highest temperature anomalies, but those having smaller spots suffered slightly more. This contrasts with findings from a previous study, where females suffered from anomalously cold temperature (Bond et al., 2023). This previous study did not examine spot traits, but used a larger dataset and incorporated additional variables, such as rainfall and NDVI, alongside temperature. Differences in dataset size, composition, and the inclusion of multiple environmental variables in the earlier analysis may explain this inconsistency. Adult males having smaller spots had lower seasonal survival than males having larger spots at anomalously low temperature, with a survival probability of about 0.83 for males having the smallest spots compared to a probability close to 1 for males having the largest spots. This relationship was reversed at anomalously high temperature but weaker, as males having the largest spots had a survival probability of about 0.92. At temperature close to seasonal average, 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 on spot patterns was also disruptive in calves. However, calves strongly suffered from anomalously high temperature, with the survival probability of calves having the largest spots decreasing down to 0.33. We note that all calves survived better when temperature was anomalously low compared to anomalously high, except calves with extremely small spots that had a stable survival probability across the whole range of temperature anomalies.

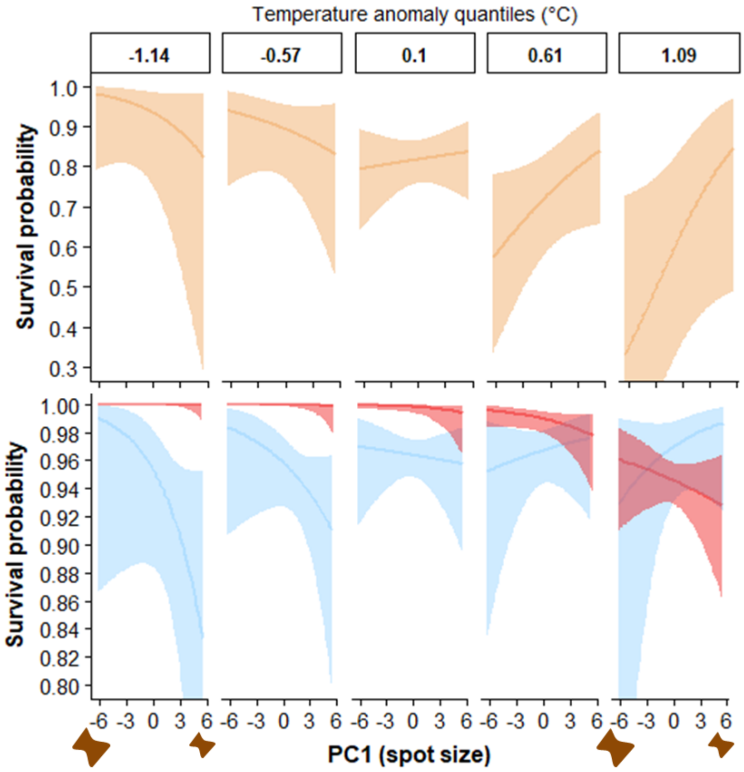

Figure 4. Viability selection on spot size in calves (orange, top panel), adult males (blue, bottom panel) and adult females (red, bottom panel) as a function of temperature anomalies. The effect of spot size (PC1; gradient from large to small spots) on survival is shown for temperature anomaly quantiles 0.1, 0.25, 0.5, 0.75, 0.9, which represent a gradient from anomalously low to high temperature. Note the scale difference on the y-axis between the

bottom and top panels. Viability selection was disruptive in calves and adult males, with individuals having larger vs. smaller spots surviving better at anomalously low vs. high temperature. Females generally suffered from anomalously high temperature.

Discussion

Colour and shape of animal coat patterns may have various adaptive functions such as camouflage or thermoregulation (Caro, 2005). Our analyses on giraffe spot patterns showed that the size and shape of the spots affected individual apparent survival probability and this relationship differed among life-stages and sex. Among adult males, those with larger and more convex polygonal or smaller and more lobate spots had the highest survival, whereas spot patterns only weakly affected the survival of adult females, with those having larger and more polygonal spots surviving slightly better. Among calves, those with smaller and more lobate spots had the highest survival probability and as the spots became more convex polygonal, their size had less influence on survival. These results expand upon a previous study that examined calf survival correlates of spot traits and principal components of spot traits during three age periods: first season, first year, and first 3 years (Lee et al., 2018). As found here, this previous study found different results for different life stages: during the first season of life, calves with larger and/or more lobate spots had higher survival; during their first year, calves with smaller spots had higher survival; and during their first three years, calves with rounder spots had higher survival. Our analysis confirmed the importance of small spots on first year survival while adding detail about the differential effects of spot shape as well as sex-specific adult effects. We were unable to estimate viability selection on spot patterns in sub-adults because of low sample size but the importance of roundness (which covaries with solidity and circularity in PC2, describing a more convex polygonal shape) in three-year survival in (Lee et al., 2018) echoes our results for polygonal shape effects in adult males and females.

In calves, viability selection on spot size correlated with temperature anomalies, which suggest that spot patterns may help with thermoregulation. Thermoregulation is energetically demanding because it increases metabolic rate and energy cannot be allocated to growth, reproduction or maintenance (Angilletta Jr., 2009; Rezende & Bacigalupe, 2015). Calves are likely to lose heat faster than adults because their small size increases their surface-to-volume ratio. Moreover, calves in their first months spend most of their time in the shade hidden in bushes away from predator sight (G. Mitchell & Skinner, 2004), which reduces exposure to the sun. Calves having larger spots may therefore benefit from their greater absorption capacity of solar radiation, providing a greater heat load and allowing them to either expose themselves more shortly to the sun when they need to upregulate their temperature, or to absorb more efficiently solar radiation through dense vegetation cover. Consequently, calves with larger spots could have a higher survival rate than calves with smaller spots in anomalously cold environments. However, the survival difference between phenotypes may vary with the degree of vegetation cover. In anomalously hot environments, calves having larger spots may instead suffer from hyperthermia, which could drastically lower their survival probability. Calves with smaller spots showed less variation in survival probability with temperature anomalies. However, though their survival probability was higher in anomalously high temperatures than calves having larger spots, it never reached the maximum survival probability of calves having larger spots in anomalously cold temperatures. Small spots may confer an energetic trade-off minimizing hypothermia in colder environments and hyperthermia in hotter environments.

Temperature anomalies only altered the effect of spot size on survival, though overall spot size (PC1) affected survival interactively with spot shape (PC2). These findings suggest that spot shape may play a role in another context than thermoregulation. Calves are subjected to high predation risk in their first year (Strauss & Packer, 2013b). 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 compare to solid shapes. Calves with more lobate spots may thus 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. 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; Selwood et al., 2015). Survival of giraffe calves has previously been shown to be higher in presence of other prey species, suggesting a dilution effect of lion predation on calves (Lee, Kissui, et al., 2016). Moreover, the density of lions, the main predator of giraffes, has been found to be higher in populations subjected to lower mean annual temperature (Celesia et al., 2010) and low temperature seasonality (Jones et al., 2021). It is therefore possible that temperature fluctuations, especially temperature anomalies, affect predator population dynamics. Consequently, predation pressure and temperature anomalies may drive, additively or interactively, viability selection on spot patterns of giraffe calves. Overall, which spot patterns are advantaged seem to be context-dependent, with multiple ecological factors shaping the spot size and shape of giraffe calves.

In adults, viability selection on spot patterns correlated with temperature anomalies in males but only weakly in females. This finding suggests that potential differences in thermoregulation capacities related to spot patterns in calves may be compensated through other mechanisms in adults. For example, adults may use behavioural thermoregulation such as seeking shade or facing the sun to downregulate their temperature, or conversely, expose their body to the sun to upregulate their temperature (G. Mitchell et al., 2017). Sexual differences in the role of spot patterns may be related to sexual differences in behaviour or energetic demands. Adult females have high energy requirements most of their lifetime as gestation time lasts about 15 months and suckling about 12 months, and they can be pregnant and nursing at the same time (Deacon et al., 2015). It may explain why spot patterns only weakly affected their survival rate and all females suffered from anomalously high temperatures. Females with smaller spots suffered slightly more from 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). Future studies would need to link physiological measures to spot traits to understand these individual differences. Moreover, 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 (Carter et al., 2013; Lavista Ferres et al., 2021; Pratt & Anderson, 1985b; VanderWaal et al., 2014). Colour polymorphism has been shown in several taxa to correlate with other traits, such as body size, body condition, metabolism or behaviour (Ducrest et al., 2008). Melanin-based colouration generally correlates with greater energetic balance but also positively with higher activity and aggressiveness levels. If males having larger spots 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. If their aggressiveness and dominance give them access to better 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 coat spots in giraffes. We suggest that spot patterns may help with thermoregulation in calves, but experimental work is needed to demonstrate a causal effect of temperature and determine its importance compared to other mechanisms such as camouflage. Thermoregulation by colour or shape patterns 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; D. Mitchell et al., 2018; Stuart-Fox et al., 2017). Sexual differences in viability selection on spot patterns with temperature suggest that, in adult giraffes, spot patterns may have another function than thermoregulation that remains to be determined. This study highlights the importance of considering variation in spot patterns alongside the impact of climate change when developing giraffe conservation plans. For instance, understanding how temperature trends influence survival linked to specific spot patterns could guide habitat protection strategies or population management efforts to support genetic exchange enabling the evolution of phenotypes best adapted to predicted climate scenarios.

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Author contribution

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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Data availability statement

Data and code used in this study are available on Figshare repository: dataset with encounter history and individual traits (10.6084/m9.figshare.28450583), dataset with temperature anomalies (10.6084/m9.figshare.28450547) and R script (10.6084/m9.figshare.28450958).

Competing interests

The authors declare no competing interests.

Supporting Information

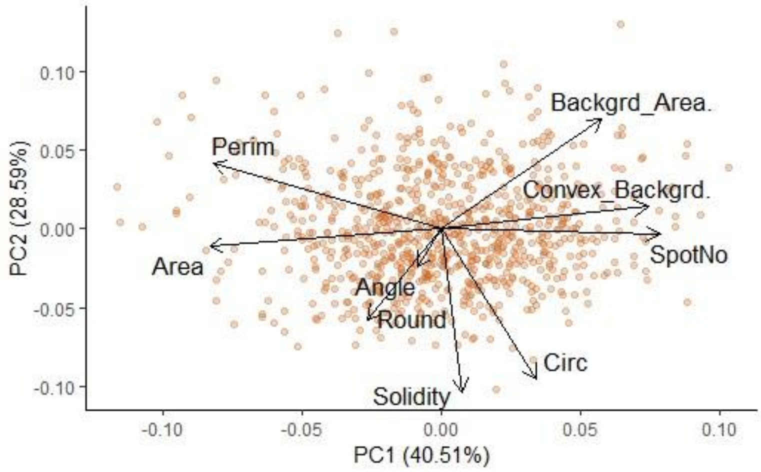

Figure S1. Loading plot of the principal component analysis (PCA) of giraffe spot traits. The spot traits extracted explained most of the variation in spot patterns along two dimensions, PC1 gathering traits related to spot size (from large to small) and PC2 gathering traits related to spot shape (from convex polygonal to lobate).

Table S1. Model estimates of the most parsimonious model of the effect of spot patterns on seasonal apparent survival. The most parsimonious model comprised spot traits as principal components (PC1 and PC2) and their interaction with life-stages [Age-Sex with five categories calf (reference), subadult male (SAM) and female (SAF), and adult male (AM) and female (AF)]. Results for subadults should be ignored as the model cannot properly estimate survival for this category, likely due to low sample size. Effect of linear age was estimated for each life-stage in number of seasons, calf for the first 3 seasons (i.e., one year; reference category), subadult for the next 6 seasons (year 1 to 3) and adult stage. MeanDistPA stands for the mean distance of the individual to the edge of the protected area. Shown are the model estimates for apparent survival (estimate), the standard error (se) and the lower (lcl) and upper confidence limits (ucl).

	estimate	se	lcl	ucl
S:(Intercept)	-2.951	1.28	-5.46	-0.44
S:MeanDistPA	3.358	1.24	0.93	5.788
S:PC1	0.042	0.04	-0.04	0.121
S:PC2	-0.005	0.065	-0.13	0.122
S:seasonLongRain	5.153	1.282	2.64	7.665
S:seasonShortRain	4.54	1.247	2.1	6.984
S:age[3,9)	1.639	0.273	1.1	2.173
S:age[9,35]	2.284	0.354	1.59	2.978
S:Age-SexMSA	-61.4	785.6	-1601	1478
S:Age-SexFSA	640.5	0	640	640.5
S: Age-SexMA	-0.522	0.378	-1.26	0.22
S: Age-SexFA	0.312	0.371	-0.41	1.039
S:PC1:PC2	0.021	0.021	-0.02	0.062
S:PC1:Age-SexSAM	151.1	1952	-3674	3976
S:PC1:Age-SexSAF	-271.3	0	-271	-271
S:PC1:Age-SexAM	-0.086	0.073	-0.23	0.058
S:PC1:Age-SexAF	-0.098	0.07	-0.23	0.039
S:PC2:Age-SexSAM	10.69	125	-234	255.8
S:PC2:Age-SexSAF	35.51	258.8	-472	542.7
S:PC2:Age-SexAM	-0.053	0.102	-0.25	0.147
S:PC2:Age-SexAF	-0.068	0.093	-0.25	0.113
S:MeanDistPA:seasonLongRain	-3.472	1.236	-5.89	-1.05
S:MeanDistPA:seasonShortRain	-3.398	1.233	-5.81	-0.98
S:PC1:PC2:Age-SexSAM	-263.8	3418	-6963	6435
S:PC1:PC2:Age-SexSAF	-28.8	107.6	-240	182
S:PC1:PC2:Age-SexAM	0.015	0.036	-0.05	0.086
S:PC1:PC2:Age-SexAF	-0.02	0.037	-0.09	0.053

Table S2. Model comparison for the effect of giraffe spot traits on apparent survival. All models with individual spot traits had a ΔAICc >2 compared to the most parsimonious model with spot traits as principal components (PC). Age-Sex includes life-stage categories calf, subadult male and female, and adult male and female; Season is a three-level factor for short rain, long rain and dry season; MeanDistPA stands for the mean distance of the individual to the edge of the protected area.

Model	df	loglik	ΔAICc	Weight
S(Age-Sex+Age+Season+MeanDistPA+MeanDistPA:Season+PC1+PC2+PC1:PC2+PC1:Age-Sex + PC2:Age-Sex +PC1:PC2:Age-Sex)	53	-18058.43	0	0.99
S(Age-Sex+Age+Season+MeanDistPA+MeanDistPA:Season+Perimeter+Perimeter:Age-Sex)	43	-18074.18	-11.296	0.003
S(Age-Sex+Age+Season+MeanDistPA+MeanDistPA:Season+Area+Area:Age-Sex)	43	-18074.84	-12.608	0.002
S(Age-Sex+Age+Season+MeanDistPA+MeanDistPA:Season+SpotNumber+ SpotNumber:Age-Sex)	43	-18075.18	-13.287	0.001
S(Age-Sex+Age+Season+MeanDistPA+MeanDistPA:Season+Angle)	39	-18079.86	-14.571	0.0007
S(Age-Sex+Age+Season+MeanDistPA+MeanDistPA:Season+Roudness+Roundness:Age-Sex)	43	-18076.08	-15.089	0.0005
S(Age-Sex+Age+Season+MeanDistPA+MeanDistPA:Season+BackgroundArea)	39	-18080.25	-15.367	0.0004
S(Age-Sex+Age+Season+MeanDistPA+MeanDistPA:Season+Solidity)	39	-18080.56	-15.974	0.0003
S(Age-Sex+Age+Season+MeanDistPA+MeanDistPA:Season+ConvexBckgdArea+ ConvexBckgdArea:Age-Sex)	43	-18076.8	-16.523	0.0002
S(Age-Sex+Age+Season+MeanDistPA+MeanDistPA:Season+Circularity)	39	-18081.15	-17.162	0.0002

Table S3. Model estimates of the most parsimonious model of the effect of temperature anomalies on viability selection on spot patterns. The most parsimonious model comprised an effect of temperature anomalies on viability selection on spot traits related to spot size (PC1:Temp). The effect of temperature anomalies on apparent survival also differed among life-stages [Age-Sex with five categories calf (reference), subadult male (SAM) and female (SAF), and adult male (AM) and female (AF)]. Results for subadults should be ignored as the model cannot properly estimate survival for this category, likely due to low sample size. Effect of linear age was estimated for each life-stage in number of seasons, calf for the first 3 seasons (i.e., one year; reference category), subadult for the next 6 seasons (year 1 to 3) and adult stage. MeanDistPA stands for the mean distance of the individuals to the edge of the protected area.

	estimate	se	lcl	ucl
S:(Intercept)	-3.572	1.66	-6.83	-0.31
S:MeanDistPA	4.2683	1.64	1.048	7.488
S:PC1	0.0059	0.06	-0.11	0.123
S:PC2	0.0002	0.07	-0.14	0.14
S:seasonLongRain	5.5817	1.64	2.359	8.804
S:seasonShortRain	5.4544	1.64	2.247	8.661
S:Age-SexSAM	-0.603	1.23	-3.01	1.802
S:Age-SexSAF	639.17	0	639.2	639.2
S:Age-SexAM	-1.115	0.62	-2.33	0.101
S:Age-SexAF	2.3624	0.92	0.56	4.164
S:Temp	-0.927	0.59	-2.09	0.232
S:age[3,9)	1.6774	0.3	1.089	2.266
S:age[9,35]	2.7793	0.53	1.732	3.827
S:PC1:PC2	0.042	0.03	-0.02	0.101
S:PC1:Age-SexSAM	3.3741	1.78	-0.12	6.87
S:PC1:Age-SexSAF	-276.2	0	-276	-276
S:PC1:Age-SexAM	-0.054	0.1	-0.25	0.146
S:PC1:Age-SexAF	-0.258	0.13	-0.51	-0.01
S:PC1:Temp	0.1798	0.12	-0.05	0.408
S:PC2:Age-SexSAM	7.4798	3.22	1.176	13.78
S:PC2:Age-SexSAF	129.39	524	-898	1157
S:PC2:Age-SexAM	-0.085	0.11	-0.31	0.135
S:PC2:Age-SexAF	-0.056	0.1	-0.25	0.138
S:Age-SexSAM:Temp	3.2515	1.56	0.195	6.308
S:Age-SexSAF:Temp	-154.1	1307	-2716	2408
S:Age-SexAM:Temp	1.1376	0.72	-0.28	2.557
S:Age-SexAF:Temp	-2.633	0.86	-4.32	-0.94
S:MeanDistPA:seasonLongRain	-4.346	1.64	-7.56	-1.13
S:MeanDistPA:seasonShortRain	-4.322	1.64	-7.54	-1.11
S:PC1:PC2:Age-SexSAM	-8.301	4.1	-16.3	-0.26
S:PC1:PC2:Age-SexSAF	-56.14	644	-1319	1207
S:PC1:PC2:Age-SexAM	-0.01	0.05	-0.11	0.089
S:PC1:PC2:Age-SexAF	-0.03	0.05	-0.12	0.063