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Hotter temperatures constrain movements in a top avian predator of the African Savanna

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Abstract

Under hotter conditions, some animals mitigate the physiological stress of heat by reducing activity or seeking shaded microrefugia. Additionally, parental care behaviour, such as brooding, may be adjusted to buffer offspring from extreme temperatures. However, it often comes with trade-offs, such as decreased foraging efficiency or increased heat exposure for adults. On the other hand, elevated temperatures can also reshape the energy landscape for soaring species by enhancing thermal uplift, thereby reducing the energetic costs of flight. We explore the influence of high temperatures on the movements of breeding adult Martial Eagles (*Polemaetus bellicosus*), a top avian predator of the African Savanna, using GPS tracking data from five females tracked over 13 successful breeding events between 2014 and 2024, in Kruger National Park, South Africa. We hypothesize that elevated temperatures can influence eagle movements in one of three ways: (a) reduced or limited movement to avoid heat stress and/or seek shade, (b) reduced or limited movement to provide shade for the chick at the nest, or (c) increased movement to exploit improved soaring conditions for foraging. We found that higher temperatures were associated with more limited movements (i.e., reduced step lengths and maximum distances from the nest, and lower flight heights) as well as decreased time spent moving and less time at the nest. Thus, eagle movements were constrained, and individuals spent less time moving, most likely to reduce their own heat exposure rather than to provide shade for their chicks at the nest. The relationships between step length, maximum distances from the nest, mean height, and proportion of time spent moving were quadratic, and the thresholds of these quadratic relationships with temperature, where changes in behaviour occurred, varied with chick age, suggesting that internal motivation interacts with environmental conditions. Worryingly, we detected significant increases in the proportion of days above these thresholds during most of the breeding months in our study area in the last 17 years. These shifts could be affecting the quality and regularity of the food provisioned to chicks, and has the potential to disrupt predator-prey dynamics across African savannas as global temperatures continue to rise.

Introduction

In the context of global climate warming, exposure to high temperatures, frequently referred to as thermal risk, is recognized as an important factor influencing the movement behaviour of both predators and prey with broad implications for ecosystems [1, 2]. Rising temperatures can have both lethal and sublethal effects on animals; while lethal effects refer to direct mortality of animals due to heatwaves [3], sub-lethal effects may have a more subtle impact on fitness in the mid- to long-term (e.g., through lower breeding success or survival; Woodroffe et al. 2017; Abrahms et al. 2022). These sub-lethal effects may arise as animals adjust their behaviour to mitigate the physiological impacts of elevated temperatures, for example, by ceasing activity, seeking shade or exhibiting more sinuous movement patterns [1, 2]. Such behavioural changes may incur opportunity costs, such as reduced foraging rates, with potentially large, but often overlooked, fitness and ecosystem consequences [1].

Animal movement patterns are influenced by both internal (e.g., requirements for parental care or self-maintenance) and external motivations (e.g., climatic conditions) [6]. For example, high temperatures can cause adults to reduce foraging either to reduce their own heat exposure to reduce physiological impacts (e.g., by seeking microrefugia or engaging in evaporative cooling) or to provide parental care (e.g., to shade their young from direct solar radiation) [1]. For example, Southern Fiscals (*Lanius collaris*) in the Kalahari Desert preferentially hunt from more exposed sunnier perches but move to shaded perches in hotter temperatures to stay cool, however, this change results in substantially lower foraging success [7]. Similarly, Yellow-billed Hornbills (*Tockus leucomelas*) spend more time in cooler microsites during hotter weather, but have lower foraging efficiency at these sites [8]. These studies, therefore, suggest negative changes in foraging behaviour (with corresponding costs) of some avian species in response to higher temperatures. However, an alternative hypothesis for the effects of higher temperatures on soaring birds, such as raptors, posits that warmer temperatures can benefit individuals through an improved ‘energy landscape’ resulting in lower costs of movement [9, 10].

Although several studies have explored movement patterns in raptors and other soaring species, in relation to temperature, these have principally focused on movements during migration, with far less research on resident species or during the breeding period. For example, hotter conditions were linked to faster flight speeds of migrating Turkey Vultures (*Catharthes aura*) [11] and White Storks (*Ciconia ciconia*) (Shamoun-Baranes etal. 2003). In one of the few studies exploring how temperatures can influence movements of resident raptors, it was found that California Condors (*Gymnogyps californianus*) were more likely to fly and soar at higher heights, when conditions promoted thermal updrafts, such as with high solar radiation (Poessel et al., 2018). Similarly, for

Verreaux's Eagles (*Aquila verreauxii*) in South Africa, warmer temperatures influenced their energy landscape by improving thermal lift availability but reducing orographic lift [10]. In a recent study, Naves-Alegre et al. (2025) explored the movements of three species of eagles in Spain (i.e., Golden Eagle (*Aquila chrysaetos)*, Bonelli's Eagle (*Aquila fasciata)* and Spanish Eagle (*Aquila adalberti*)), finding that responses to elevated temperatures varied between species.

The Martial Eagle is a top avian predator of the African Savanna, with research suggesting that they are positioned close to sympatric mammalian top predators in trophic pyramids, based on their kill rates and biomass recycling (Hatfield et al. 2024). They are generalist predators throughout their range, feeding on a variety of medium-sized mammals, and large birds and reptiles (Hatfield et al. 2024; Naude et al. 2019), despite that within in Kruger National Park it has been found they prey mainly on large reptiles, followed by medium sized mammals, and large birds [15, 16]. Adult Martial Eagles have a very large home range size, which in Kruger National Park is around 100 km^2 [17].

In this study, using different movement and nest attendance metrics derived from GPS tracking data from five female Martial Eagles we will explore how the movements of GPS-tagged adult female Martial Eagles are affected by high temperatures, specifically during the chick-rearing period, when energy demands are predicted to be greatest due to the requirements of the chick for food and thermoregulation [18–20]. We hypothesized (H) that higher temperatures may influence movements in one of three ways:

H1. Martial Eagles will reduce or limit their movements to seek shade and reduce their own heat exposure (physiological impacts of '*landscape of heat'*); if so, we would predict that all movement metrics would be reduced in hotter conditions.

H2. Martial Eagles will reduce or limit their movements to spend more time at their nests to provide shade from direct solar radiation to their chick; if so, we would again predict that in hotter conditions all movement metrics would be reduced, but that the amount of time birds spend at the nest would increase.

H3. Alternatively, Martial Eagles will increase their movements to take advantage of an improved *'energy landscape'* (e.g., thermals for soaring), thus reducing the physiological costs associated with movements. In that case, we would predict that movement metrics (particularly height) would increase in hotter conditions [21].

Materials and methods

Study species

Martial Eagles have a long breeding period (i.e., 12–14 months), including incubation of around 50 days, followed by an approximately 100-day nestling period and 7–9-month period of post-fledging dependency [19, 22]. In southern Africa, Martial Eagle breeding starts between April and July [18, 22]. The species breeds successfully only once per year and produces only one chick [18, 19]. Once successful the species usually does not breed in the following year [19].

Data collection

Between 2012 and 2020, five adult female Martial Eagles were caught and fitted with tracking devices in Kruger National Park, South Africa (Fig. 1). Some males were also tagged, but were excluded from this study due to their limited numbers [23]. Devices were PPT GPS trackers (Microwave Telemetry©), which when fitted weighed between 45 and 70g, representing < 2 % o the smallest adult female Martial Eagles (range: 4.5 to 5.0 kg). The tags were fitted using a Teflon backpack harness attached with a cotton weak-link [24]. Most loggers recorded a GPS fix once per hour during day light time, but there was some variation in the number and frequency of fixes. We therefore first regularized the data to include fixes that were at least 60 minutes apart (with a 5 min tolerance) in order to avoid shorter time intervals and also thereby reduce temporal autocorrelation in the data. Only fixes after sunrise and before sunset (i.e., daytime) were include applying the 'crepuscule' function of the package *maptools* in R, allowing sunrise and sunset to vary by month.

Breeding attempts

We used the '*nestR*' package [25] to establish or confirm nest locations, breeding success, and nestling period of our tagged females Martial Eagle. For this, we followed the same criteria defined by [23], which they applied to the same population and to some of the same data. This produced estimated start and end dates for each breeding attempt for the five eagles tracked between 2014 and 2024. We derived the estimated hatch date based on the estimated start of breeding plus 50 days of incubation [19]. From this, we determined the estimated chick age at each date for the duration of each breeding attempt. This variable was then used in our subsequent analysis to control for chick age when examining movement metrics. To define nesting success, we applied the same parameters in *nestR* as used by Murgatroyd et al. (2023), with the period being 50 days of incubation and considering success to be nests that reach 56 days (i.e., large chicks). For our analysis, we only used data collected while the eagles were actively rearing chicks. Additionally, we undertook extra checks to examine for any failures by monitoring the revisitation patterns of tagged females to nests from the proportion of fixes at the nest (see below for methods). From these data, in three cases it appears that a late failure occurred during the chick rearing period, with no time spent in the nest after the chicks were 38, 58, and 60 days old.days. In the case where no fixes at the nest were recorded after day 38 (G34492- 2021, Table S1), we did not obtain enough fixes to explore nest attendance between 56–75 days, so we opted to use 38 days as the nestling end date and thus no data were analysed after that point. Lastly, for each bird, we excluded any day during the chick rearing period with < 5 fixes for that day (i.e., < 4 steps per day), and excluded any breeding attempt with < 10 days of tracking data. Additionally, due to the malfunction of the tracking unit, we had missing height data for two individuals across a total of four breeding events (G32519: 2019, 2021, 2024, and G32554: 2015**)** (see Table S1). The final data set used in our analysis was collected from five female Martial Eagles in 13 breeding attempts (Table S1).

Movement metrics for tracking data

We used daily data as our unit for analysis, with the following five response variables describing daily movement behaviours: 1) *Mean step length*, estimated by taking the average distances between consecutive fixes (including if no movement occurred between fixes) in a day using the *st distance* function from *sf package* [26]. 2) *Maximum distances from the nest* (hereafter *maximum nest distance*), estimated by calculating the distance from the nest location to each GPS fix (obtained from *nestR*) and selecting the highest value in any one day. 3) *Mean height*, estimated as a daily mean of the difference between the height estimated by the GPS loggers (including both moving and non-moving fixes) and the land elevation (asl) underlying each GPS position from an 30-m digital elevation model (DEM) from the Shuttle Radar Topography Mission (SRTM; https://www.usgs.gov/centers/eros/science/usgs-eros-archive-digital-elevation-shuttle-radar-topography-mission-srtm-1-arc) using the *raster* package in R [27]. 4) *Relative time at nest*, estimated as the proportion of daily fixes that were within a 100 m radius of the nest location. 5) *Relative movement frequency*, estimated as the proportion of daily fixes which indicated that the bird was moving, this was estimated using the instantaneous speed of the tag. To classify whether the eagle was moving or not, we used the bimodal peak produced from a frequency plot of speeds for each individual eagle, and used the lowest value between the two peaks as the cutoff to define moving and non-moving fixes for each bird, respectively, following [28]

Temperature data

We downloaded hourly temperature data, available throughout the study period, from the Kruger Mpumalanga International Airport weather station (usaf code:109) using the *isd* function of the *rnoaa* package in R [29]. This weather station was located at an average distance of 128 km (range: 68–163; SD = 41) from the nests of the tracked Martial Eagles (Fig. 1). The temperature data are in degrees Centigrade (°C) as integer numbers. For each nesting attempt we extracted information on the daily maximum temperature for each day of the nestling period (chick age between 1 and 100 days) derived from this hourly weather data. Additionally, to explore whether there were changes in the proportion of 'hot' days (see below for the definition of a 'hot' day), we extracted these same data for each day in each of six months, from June to November from 2008 through 2024, which was the complete duration for which the weather data were available.

Statistical analyses

We analysed the effect of temperatures on the different movement metrics using Mixed Effect Models, running separate models for each movement metric. Three of our response variables (*mean step length, maximum nest distance*, and *mean height*) were

continuous and approximately normally distributed. Thus, for these we used a Linear Mixed Model (LMM) with a Gaussian error distribution. For *relative time at nest* and *relative movement frequency*, we fitted betabinomial distributions using Generalised Linear Mixed Models (GLMM), with the *cbind()* function, which uses the raw data (e.g. fixes at the nest, fixes not at the nest) to more effectively model the proportions. We controlled for *chick age* in all models, as we expected that it would have a strong effect on both motivation for foraging movements (older chicks requiring more food) and the amount of time spent brooding [20]. We tested for both linear or non-linear relationships with *daily Tmax* by fitting second-order polynomial terms, as quadratic relationships between behaviour and temperature are commonly encountered [30]. Models included both bird *ID* and *year* as random effects to control for repeated measures from the same bird, and repeated measures of different birds within the same year. Thus, our two base models (BM) were:

a. y ~ chick age + daily Tmax + (1|ID) + (1|year)

b. y ~ chick age + poly(daily Tmax, 2) + (1|ID) + (1|year)

where *y* represents each one of our five daily response variables (i.e., *mean step length, maximum nest distance, mean height, relative time at nest, and relative movement frequency*), *chick age* represents the age of the chick in days and *daily Tmax* represents the daily maximum temperature (ºC).

Through an information-theoretic approach using Akaike's Information Criterion corrected for small sample sizes (AICc) and Akaike weights (ωi), we determined our best BM (i.e., evidence of quadratic temperature effects if ΔAICc > 2 relative to the non-quadratic model) as well as the parsimony of our best BM compared to other alternative models (AM) (see Richards et al., 2011). The AMs included an interaction between *daily Tmax* and *chick age*, or a simpler AM that included only *chick age* (Table 1). We considered models where ΔAICc relative to the best model was < 2 as equally well supported models [31, 32]), in which case we chose the simplest model with the fewest terms. To improve model convergence and facilitate the interpretation of interaction terms, we z-standardized continuous predictors (*daily Tmax* and *chick age*) using the *scale()* function from the R base *stats* package, which centres variables to a mean of zero scaled by 1 SD. Model predictions were generated using the *ggeffects* package.

Where our BM included *daily Tmax* as a quadratic term, we then identified the temperature threshold values at which point the relationship directions changed. To do this, we identified the vertex of the fitted quadratic polynomial for each chick age (when there was an interaction with the *chick age*) using the formula:

$$\text{Threshold} = -\beta_1 / (2\beta_2)$$

where β_1 represents the linear coefficient and β_2 the quadratic coefficient of the temperature polynomial. Model predictions and thresholds were subsequently back-transformed to their original scales for visualization and interpretation, while statistical models retained the standardized variables.

Finally, we conducted two additional analyses. First, to test whether the quadratic relationship was underpinned by a consistent negative linear trend at high temperatures, we subsetted the data to include only days with Daily Tmax > 25°C and fitted linear models with additive effects and binomial distribution to assess the strength of this relationship (BMa; Table 1). Second, we explored whether the proportion of 'hot' days (i.e., those above our threshold value for the quadratic relationship) had increased over time. For this we analysed the relationship between the monthly proportion of days with maximum temperature above the lowest threshold identified for any of our movement response metrics. We used a Generalised Linear Model (GLM) with binomial distribution and logit link. For this analysis, we used data from the nestling period (but without considering extreme months: April and December) over a 17-year period, which was the complete duration that the weather data were available (i.e., from 2008 through to 2024). From these data, we used the monthly proportion of days above the lowest threshold as the response variable, again with the *cbind()* function and binomial distribution (i.e., number of days with temperature higher than the threshold, number of days with temperature equal or lower than the threshold), and *year* as the explanatory variable. For this analysis, because our temperature data were integers, we approximated our threshold to the closest integer. All analyses were performed in the R software version 3.6.3 (R Development Core Team, 2014).

Table 1
Base models (BM) and alternative models (AM) used to explore the effect of temperature (*daily Tmax*) and *chick age* on Martial Eagle movements during the first 100 days of the chick rearing period: a) *daily Tmax* considered as a linear variable, or b) *daily Tmax* considered as a non-linear quadratic variable. *y* represents one of our response variables: *mean step length; maximum nest distance; mean height, relative time at nest*, or *relative movement frequency. The ID* and *year* represent the individual female and year, considered as random terms in the model.

Model	Variables included
a.	
BMa	*y ~ daily Tmax + chick age + (1|ID) + (1|year)*
AM1a	*y ~ daily Tmax. * chick age + (1|ID) + (1|year*
AM2a	*y ~ chick age + (1|ID) + (1|year)*
b.	
BMb	*y ~ poly(daily Tmax, 2) + chick age + (1|ID) + (1|year)*
AM1b	*y ~ poly(daily Tmax, 2) * chick age + (1|ID) + (1|year*
AM2b	*y ~ chick age + (1|ID) + (1|year)*

Results

We had enough movement data for 13 breeding events from five female Martial Eagles, each having data from one to four breeding events with chicks in different years, between 2014 and 2024. Across all these breeding events, the daily average (± SD) distance between fixes was 1,011 ± 296 m (*mean step length)*, the daily average maximum nest distance was 3,661 ± 1509 m (*maximum nest distance*), the daily average mean height was 111 ± 51 m (*mean height*), the daily average time that birds spent in their nest was 57 ± 18% (*relative time at nest*), and the average percent of fixes per day classified as moving was 14 ± 5% (i.e., *relative movement frequency*) (Table 2). The dates with chicks aged 1 to 100 days spanned from 21 May to 17 December. During this full period with the chicks, the annual mean daily *Tmax* was 24.3 ± 5°C (range = 12 to 37), the earlier months (i.e., May to August) had lower maximum temperatures than the later month (Fig. 2).

Both maximum temperature and chick age were associated with all five metrics of movement (Table 3, Fig. 3). Only one response variable (*i.e., relative time at nest*) showed a negative linear relationship with *daily Tmax* and no interaction between *daily Tmax* and *chick age*. In contrast, for the other four variables (*mean step length, maximum nest distance, mean height*, and *relative movement frequency)*, there was a quadratic relationship with *daily Tmax.* For the first three variables, there was an interaction between *daily Tmax* and *chick age*, but not for the *relative movement frequency* (Table 3). For variables that showed quadratic relationships with *daily Tmax* and an interaction with *chick age*, the temperature threshold at which negative relationships with higher temperatures emerged ranged across the different ages. It was between 26.4°C and 29.7°C for the *mean step length*, 26.3°C and 28.9°C for the *mean height*, and 28.5°C and 33.1°C for the *maximum nest distance.* For the *relative movement frequency*, it was 27°C. The nature of the interaction with chick age also differed between variables; for *mean step length* and *maximum nest distance* the temperature thresholds where negative relationships emerged were lower for females tending older chicks, in contrast, for *mean height* this temperature threshold was lower for females with younger chicks (Fig. 3).

For these four variables with quadratic relationships, that we also explored a negative linear relationship with temperature on a subset of data, including only those hotter days with *daily Tmax* > 25° C. A significant negative trend for *relative movement frequency* was found as *daily Tmax* increased (Table S3), but no significant negative or positive linear relation was found for the *mean height, mean step*, and *maximum nest distance* (Table S3). Based on this analysis, we found that the *relative movement frequency* decreased from 20% at 26°C to 14.5% at 37°C, a reduction of nearly one third.

Examining the change in the proportion of 'hotter' days between 2008 and 2024, for all the main months of the nestling period, except September, there were significant annual increases (Fig. 4). Increases over this 17-year period were substantial, averaging a 16% absolute change (range: 10–20%; Fig. 4). For example, during August, the peak month for nestlings, based on our breeding data (Fig. 2), trends suggested more than doubling in the percentage of days exceeding the 26°C threshold, from 17% to more than 36% of days (Table S2). Additionally, these rising trends mean that in the hottest months (September, October, and November), on average more than 50% of days now exceeding the threshold temperature.

Table 2
Descriptive statistics of the response variables assessed. Data missing (-) due to the malfunction of the tracking unit for two individuals (G32554 in 2015 and G32519 in 2019, 2021, and 2024).

ID	Year	Assessed period (days)	Mean Step (m)		Maximum nest distance (m)		Mean Height (m)		Relative Time at Nest		Relative Movement Frequency	
			Mean	±SD	Mean	±SD	Mean	±SD	Mean	±SD	Mean	±SD
G32553	**2014**	100	1495	1288	8442	5931	70	74	0.40	0.39	0.13	0.11
G32554	**2014**	60	925	917	3709	3824	89	104	0.79	0.19	0.12	0.10
	2015	100	809	941	2942	2428	–	–	0.52	0.32	0.15	0.16
	2017	100	988	991	3087	2655	82	111	0.46	0.35	0.07	0.10
	2019	100	1196	1190	3574	3012	136	150	0.35	0.37	0.09	0.14
G32519	**2017**	100	761	688	2850	3144	62	78	0.69	0.23	0.15	0.13
	2019	100	852	753	2947	2149	–	–	0.46	0.36	0.16	0.14
	2021	100	574	690	2416	2214	–	–	0.53	0.36	0.11	0.11
	2024	58	764	887	3114	3731	–	–	0.73	0.32	0.12	0.13
G34492	**2018**	100	1274	999	4227	4505	231	164	0.27	0.27	0.24	0.16
	2021	38	815	1331	3632	9545	128	76	0.75	0.15	0.17	0.11
G34495	**2021**	100	1173	1249	3149	5275	96	73	0.84	0.12	0.11	0.11
	2023	100	1523	1387	3509	3070	104	127	0.61	0.29	0.22	0.21
Annual average		89	1011	243	3661	2040	111	106	0.57	0.09	0.14	0.03

Table 3
Performance of our Linear Mixed Models (LMM) and Generalized Linear Mixed Models (GLMM). Models are ranked according to the Akaike Information Criterion corrected for small sample sizes (AICc). Additionally, AICc, ΔAICc, Akaike weights (ωi), and the number of parameters (k) are provided. *Chick age* represents the age in days of the chick and the *Dmax T* refers to the daily maximum temperature (both were scaled). *Poly* refers to a second-degree polynomial transformation.

Model	Intercept	Chick Age	daily Tmax	poly(Tmax,2)	Chick Age × daily Tmax	Chick Age × poly(Tmax,2)	df	logLik	AICc	ΔAICc	ωi
Mean Step (m)											
AM1b	1125	285.5	NA	+	NA	+	9	-7589.8	15197.7	0	1
BMb	1122	287.1	NA	+	NA	NA	7	-7606.6	15227.4	29.6	0
AM2b	1125	293.2	NA	NA	NA	NA	5	-7635	15280.1	82.4	0
Maximum nest distance (km)											
AM1b	4.4	0.96	NA	+	NA	+	9	-2592.5	5203.2	0	0.9
BMb	4.4	0.96	NA	+	NA	NA	7	-2597.1	5208.4	5.2	0.1
AM2b	4.4	0.99	NA	NA	NA	NA	5	-2605.8	5221.7	18.5	0
Mean height (m)											
AM1b	123.9	32.44	NA	+	NA	+	9	-2888.1	5794.6	0	1
BMb	126.1	35.19	NA	+	NA	NA	7	-2901.5	5817.1	22.5	0
AM2b	128	35.92	NA	NA	NA	NA	5	-2926.5	5863.0	68.4	0
Relative time at nest											
BMa	-0.308	-1.339	-0.112	NA	NA	NA	6	-1795.8	3603.7	0	0.5
AM1a	-0.306	-1.340	-0.109	NA	-0.057	NA	7	-1795	3604.0	0.27	0.5
AM2b	-0.313	-1.353	NA	NA	NA	NA	5	-1799.8	3609.6	5.86	0
Relative movement frequency											
BMb	-1.5	0.251	NA	+	NA	NA	7	-1536.7	3087.5	0	0.8
AM1b	-1.5	0.276	NA	+	NA	+	9	-1536.1	3090.3	2.8	0.2
AM2b	-1.6	0.250	NA	NA	NA	NA	5	-1566.2	3142.5	55	0

Discussion

Our results revealed that higher temperatures significantly influence the movement behaviour of adult female Martial Eagles. For most movement metrics (i.e., *mean daily step length, maximum nest distance, mean height*, and *relative movement frequency*), we observed a quadratic relationship with *daily Tmax;* thus, eagles constrained their movements at higher temperatures. Our findings largely support our physiological impacts of the *'landscape of heat'* hypothesis (H1), which proposed that during hotter days, eagles should reduce or limit their activity to reduce their own heat exposure. Furthermore, behavioural responses differed by *chick age*, suggesting that eagles do not have fixed physiological limits but rather flexible behavioural responses modulated by both internal motivation (parental care) and external factors (ambient temperature).

We found variation in how different movement metrics responded to increasing ambient temperature, some of them interacting with chick age. For the *mean step length* and the *maximum nest distance*, females with older chicks exhibited lower temperature thresholds at which movements became constrained (~ 26°C and ~ 28°C, respectively; Fig. 3). This is likely because older chicks impose higher energetic demands that may force adults to continue foraging even under warmer conditions, causing females to

respond at lower *Tmax*. For mean height, the opposite pattern was observed: the lowest threshold (~ 26°C) occurred for females with younger chicks (Fig. 3). On the other hand, the relative movement frequency showed a quadratic relationship with temperature that did not interact with the age of the chicks and therefore had a unique thermal threshold at ~ 27°C (Table 3). However, when we restricted our analysis to hotter days, from the threshold where negative trends began to emerge (i.e., 26°C), only *relative movement frequency* showed a significant negative relationship with increasing temperature (Table S3). This suggests that the negative linear relationship for the remaining response variables on hotter days is likely weaker. Therefore, rather than an abrupt reduction in movement, eagle movements appear to be gradually constrained as temperature increases, with the strength of this effect depending strongly on chick age. This pattern likely reflects a trade-off between behavioural thermoregulation and the need to provision food for growing chicks [33].

Our results suggest that in hotter conditions, Martial Eagles respond by limiting the distances they moved and their flight heights, and reducing how often they moved. This response was particularly apparent when they had older chicks (Fig. 3). Therefore, we contend these changes are likely aimed at behavioural thermoregulation (e.g., Briscoe et al. 2014), with Martial Eagles in hotter conditions adjusting their behaviour to minimise activity-related thermogenesis or heat gain by solar exposure. Moving greater distances or at higher heights may incur higher energetic costs and, thus, in hotter conditions, such movements may be limit to reduced physiological stress from elevated heat loads generated by activity-related thermogenesis [34, 35]. Martial Eagles employ two main hunting strategies: perch scanning from treetops then swooping, and thermal soaring gaining height on thermals then gliding with head down to spot prey (i.e., similar to vultures foraging; [17, 36, 37]. At hotter temperatures, however, eagles may shift away from thermal soaring to more perch hunting, which is consistent with some observed constraints in flight height in our results. Furthermore, the decreased movement frequency suggests that they tend to stay perched more frequently at hotter temperatures. It may be that perch hunting allows for perching to occur in more shaded micro-refugia, as has been seen for other perching hunting species [7]. Finally, a tendency to reduce the distances away from the nest in hotter conditions when tending older chicks (but not with younger chicks) may reflect the need to avoid the high energetic cost of transporting prey back to the nest from further away following a successful capture [38].

Martial Eagles, as the largest species of eagle in Africa, may be particularly susceptible to activity-related thermogenesis, as larger birds generate metabolic heat more easily and find it harder to subsequently shed such heat burdens [39]. The quadratic relationships with our key movement variables suggest that at certain temperature thresholds there is a trade-off between the competing motivational forces of provisioning chicks and the need to safeguard their own physiological welfare [40]. These thermal thresholds varied by chick age, indicating that these are not fixed physiological limits, but rather flexible behavioural responses modulated by both internal factors (chick developmental stage) and external factors (ambient temperature) [41, 42]. When females have younger chicks, it is only at higher temperatures that they start to limit these movements (i.e., between 30 and 33°C), while with older chicks, these movements start to be constrained at lower temperature (i.e., between 26 and 28°C) (Fig. 3). This plasticity likely represents an adaptive strategy to optimize parental investment according to changing offspring requirements [42].

Our results suggest that the *chick age* dependent thresholds observed may be due to varying energy expenditure associated with foraging for chicks of different ages. Older chicks, being larger, have higher energy requirements, and thus the amount of food that the parents must supply also increases. Regardless of the relationship with temperatures, this pattern of generally longer and higher movements by female with older chicks, indicative of greater food demand from the chicks, is very apparent in our data (Fig. 3). For example, the average *maximum nest distance* and the *mean step length* were between 1.5 and 2 times greater in older chicks compared to younger chicks. Thus, it appears that the movements required, and thus energy expenditure, to capture sufficient prey when tending to young chicks are relatively low and that females can maintain this level of energy expenditure in hotter condition. However, when caring for older chicks, more energy expenditure is required to cover larger food areas in order to meet the dietary requirements of larger chicks. Thus, we contend that in order to minimise physiological costs associated with hyperthermia in hotter conditions, they curtail these larger movements at a lower temperature threshold to save energy and minimise their own physiological costs [1].

We found no support for our alternative hypothesis (H2) that Martial Eagles would reduce their movements in hotter conditions in order to provide shade for their chick. In direct contrast to the prediction associated with this hypothesis, we found that the females spent less time at the nest as the temperatures increased. This pattern likely reflects that the main purpose of brooding

is to provide warmth until the young can thermoregulate rather than to shield them from the solar heat gain and suggests that at higher temperatures this requirement is relaxed. This is presumably because the chicks can maintain an adequate body temperature at elevated ambient temperatures. We noted a strong pattern of time spent in the nest associated with *chick age*. Females with young chicks (i.e., 17 days old) spend around 75% of their time on the nest, likely brooding these chicks that would not be able to thermoregulate at that young age, and also to provide protection from potential predators. For chicks aged 46 days, the female spent less than 50% of her time at or around the nest, and by the time the chicks reach 74 days, the females spend less than 20% of their time near the nest. [20] reviewed the age when raptors usually stopped the intensive brooding period (defined as falling below 20% brooding) and produced a predictive model for different-sized raptors. Based on that model, the mass of female Martial Eagles' mass (ca. 5000 g) would be predicted to spend less than 20% of their time brooding after around 30 days. However, the higher values observed in our study (e.g. 50% at aged 46 days) are likely because we are capturing both female brooding and nest defence behaviours rather than temperature-dependent shading responses, because we set our definition of being at the nest and the fix being within 100 m of the nest site. To more accurately assess this aspect, camera footage filmed at the nest would be needed, to examine parental behaviour and attendance in relation to age and temperatures, rather than rely on less accurate tracking data.

We also found no support for our other alternative hypothesis (H3), that in hotter conditions, Martial Eagles would increase their movements to take advantage of an improved *'energy landscape'* (i.e., thermals for soaring). On the contrary, we saw decreases in the proportion of time spent moving (*relative movement frequency*), suggesting that more time was spent perching, which would not be predicted if they were taking advantage of improved conditions for soaring via thermals. Furthermore, temperature increases did not result in longer step lengths or longer distances from the nest, which might be expected from more soaring flights; instead, these two movements were constrained under hotter conditions. This contrasts with the results of [13] who found significant positive responses to temperature increase for three movement metrics (i.e., flight height, flight speed, and proportion of time flown per hour) for three eagle species in Spain. However, this discrepancy between their findings and our results may have arisen because they overlooked exploring a quadratic relationship with temperature [1, 30]. This notion is supported by an additional analysis of [13], which suggested that most of the movement metrics decrease during heat waves (in support of our H1 and, thus, a quadratic relationship between movement and temperature). This finding highlights the need to appropriately explore quadratic relationships when disentangling the links between temperature and animal behaviour responses by comparing a quadratic relationship as an alternative hypothesis to the 'improved energy landscape' (i.e., linear relationships) [1, 30].

A key outstanding question, and one that will ultimately define the impact of warming temperatures on this species, is what are the fitness consequences of these behavioural changes in hotter conditions for this species [1, 30]. In other species of raptors and carnivore mammals, it is known that changes in behaviour due to temperatures can affect breeding success due to changes in either food provisioning rates or prey quality [4, 5, 41, 42], features which are known to influence breeding success in other raptor species [43, 44]. Another study on the same Martial Eagle population indicates a complex situation with regard to prey provision and temperatures [33]. It found that on hotter days the frequency of prey deliveries declined, but overall biomass delivered was maintained due to a switch away from smaller bird prey to larger reptilian prey, particularly Rock and Nile Monitors (*Varanus albigularis* and *V. niloticus)* [33], which are known to be an important prey item for this population [15, 16, 33]. The findings between these two studies may be linked, with prey composition changes due to both changes in prey behaviour (e.g. reptiles being more active in hotter conditions), but also due to changes in Marial Eagle foraging documented in this study. For example, increases in perch hunting in hotter conditions may favour foraging for reptiles, whereas birds may be more often caught on during more active soaring and stooping foraging.

Our results suggest that the proportion of hot days during the chick-rearing period has increased substantially over the last two decades, with more than 50% of days now exceed the threshold temperature in the hottest months (i.e., September, October, and November) when chicks are older. Thus, a dietary shift toward reptiles in these hotter conditions [33] may have important implications for future fitness of fledged offspring. Reptile-based diets can reduce the accumulation of essential fatty acids and other nutrients that are more abundant in mammalian and avian prey [45–47]. Such nutritional deficits could alter chick development during this critical life stage and potentially decrease post-fledging survival [48, 49]. Additionally, these dietary changes may alter the predatory pressure of eagles between prey groups, potentially initiating trophic cascades that could ultimately disrupt ecosystem functioning [50–52].

As top predators, large raptors play key roles in ecosystems as regulators of prey communities through complex predator-prey dynamics [53], thus, it can be expected that behavioural changes in raptors due to climate change can also have an influence on their prey population [14] particularly through indirect (*i.e.*, landscape of fear) effects [54]. Higher temperatures can be also affecting prey species who need to keep cool [52], potentially resulting in ecosystem mismatch across the entire system. Thus, it will be key for future studies to simultaneously study the predator–prey system to better unravel how the likely changes that may occur as temperatures increase worldwide may affect ecosystems and ultimately society [55].

Conclusion

This study represents an important first step in understanding the mechanisms by which rising temperatures may affect top avian predator-prey systems worldwide. We tested three hypotheses related to how higher temperatures may influence the movements of an important aerial top predator of the African Savanna, the Martial Eagle. Our findings largely supported the physiological impacts of the 'landscape of heat' hypothesis, which proposed that during hotter days, eagles should reduce or limit their activity to minimize their own heat exposure. As temperature continue to rise, these constrained movements under hotter temperatures may potentially alter both chick development and post-fledging survival as well as the predatory pressure of eagles on different prey groups. Thus, it may initiate trophic cascades that could ultimately disrupt ecosystem functioning.

Declarations

Ethical statement

Ethical approval was granted by the University of Cape Town Biological Sciences Animal Ethics Committee (permits: 2013/V7/AA, 2016/v12/AA, 2019/V22/AA); South African National Parks Animal Use and Care Committee (AMAA1374, AMAA1651, AMAA165); Department of Environmental Affairs and Tourism: Threatened or Protected Species (ToPS) (Permit number WM 1297/2013). All GPS transmitters deployed on eagles followed the established rule of not exceeding 3% of the bird's body weight to ensure the bird remains healthy post-capture and that no factors compromise its survival.

Consent to publish

All authors have approved the manuscript for submission, and the content of the manuscript has not been published or submitted for publication elsewhere.

Conflict of interest

The authors have no financial or non-financial competing interests to declare.

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Author Contribution

M. Murgatroyd and A. Amar collected the data; S. Zuluaga, M. Murgatroyd, and A. Amar conceived the ideas, designed methodology, and analysed the data; S. Zuluaga, and A. Amar led the writing of the first draft of the manuscript. All authors contributed critically to review the drafts and gave final approval for publication.

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Data Availability

The GPS data obtained for this study are stored in Movebank (https://www.movebank.org; ID: 871804244). These data are not openly available due to information sensitivity, but are available from reasonable request. The datasets generated and/or analysed during the current study, derived from these GPS data, as well as the R code used for analyses, will be made available in the public repository Zenodo.

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Figures

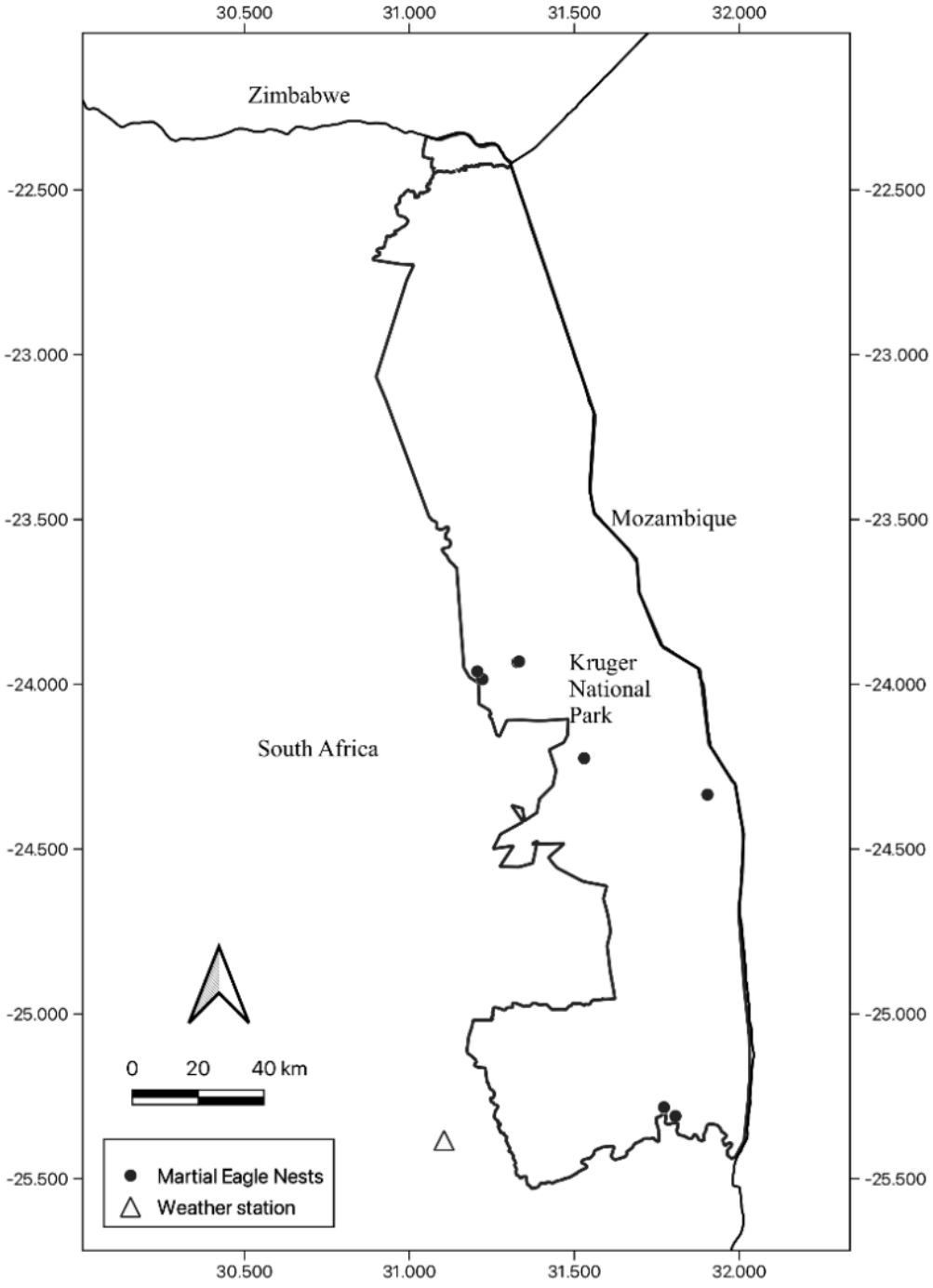


Figure 1

Study area and nest locations of the nests of the five GPS tracked female adult Martial Eagles (black circles) and the weather station (open triangle) in Kruger National Park, South Africa. For two birds, the nests used were different in different years.

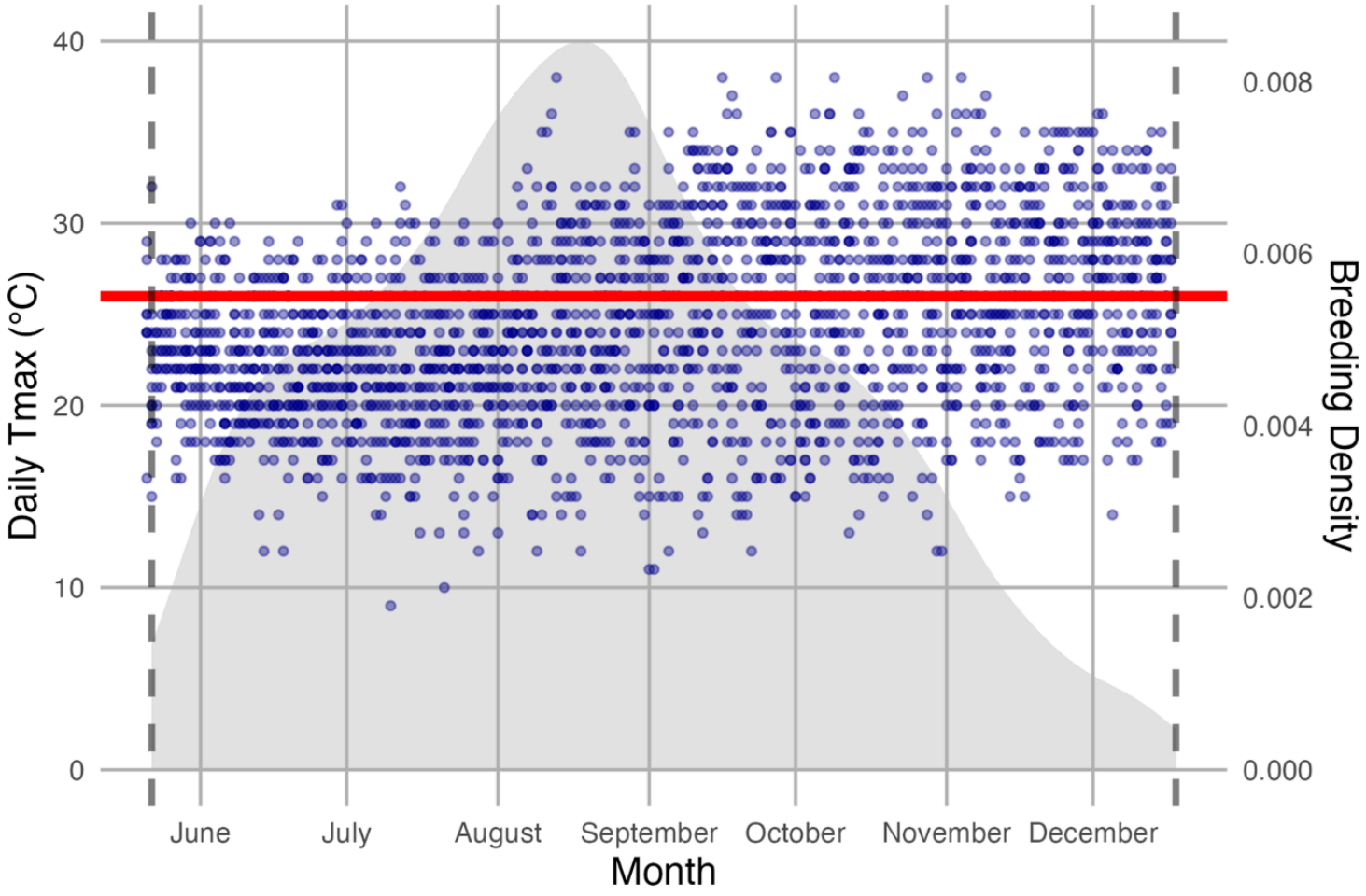


Figure 2

Distribution of daily maximum temperatures (*Daily Tmax*) during the nestling rearing period in our study area derived from a weather station over the 11-year period, 2014 to 2024. The red horizontal line indicates the critical thermal threshold (26°C) at which daily maximum temperatures begin to negatively influence eagle movement behaviour. The dashed black vertical lines delineate when the nestlings were present (21 May to 17 December). The grey shaded background represents the relative breeding density distribution (based on 10 complete breeding events spanning 100 days), showing the daily temporal concentration of reproductive events throughout the season.

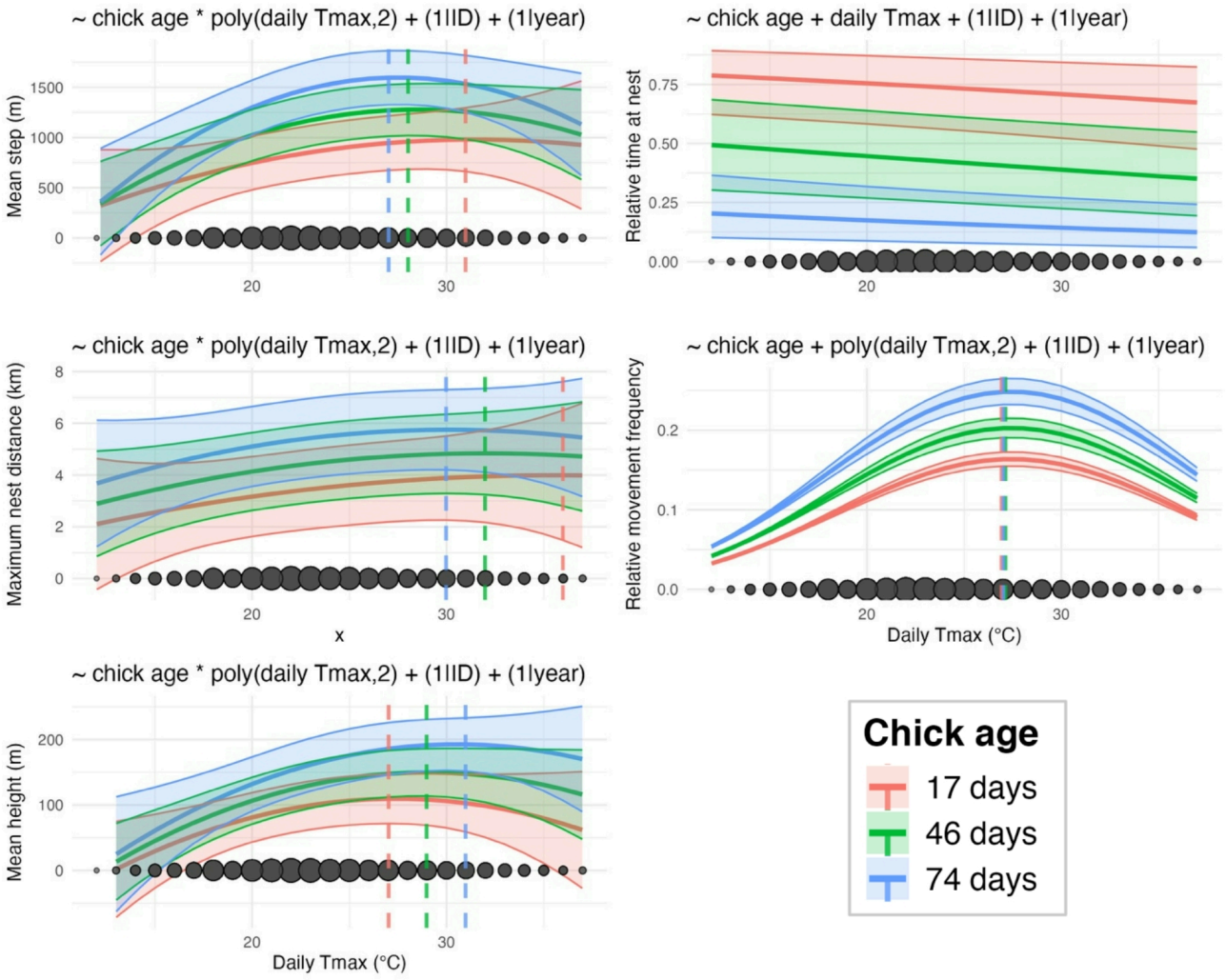


Figure 3

Relationship between daily maximum temperature (*Daily Tmax*) and *chick age* on five movement metrics, showing the fitted model (see Methods) and the thresholds of the *Tmax* value above which the trends negative relationships with temperature change across chick ages, representing: young (red), mid-aged (green), and older chicks (blue). Figures on the right are for those variables (*relative time at nest,* and *relative movement frequency*) which showed an additive effect of *chick age*. For all figures, the black circles at the bottom show the density of the *daily Tmax* data.

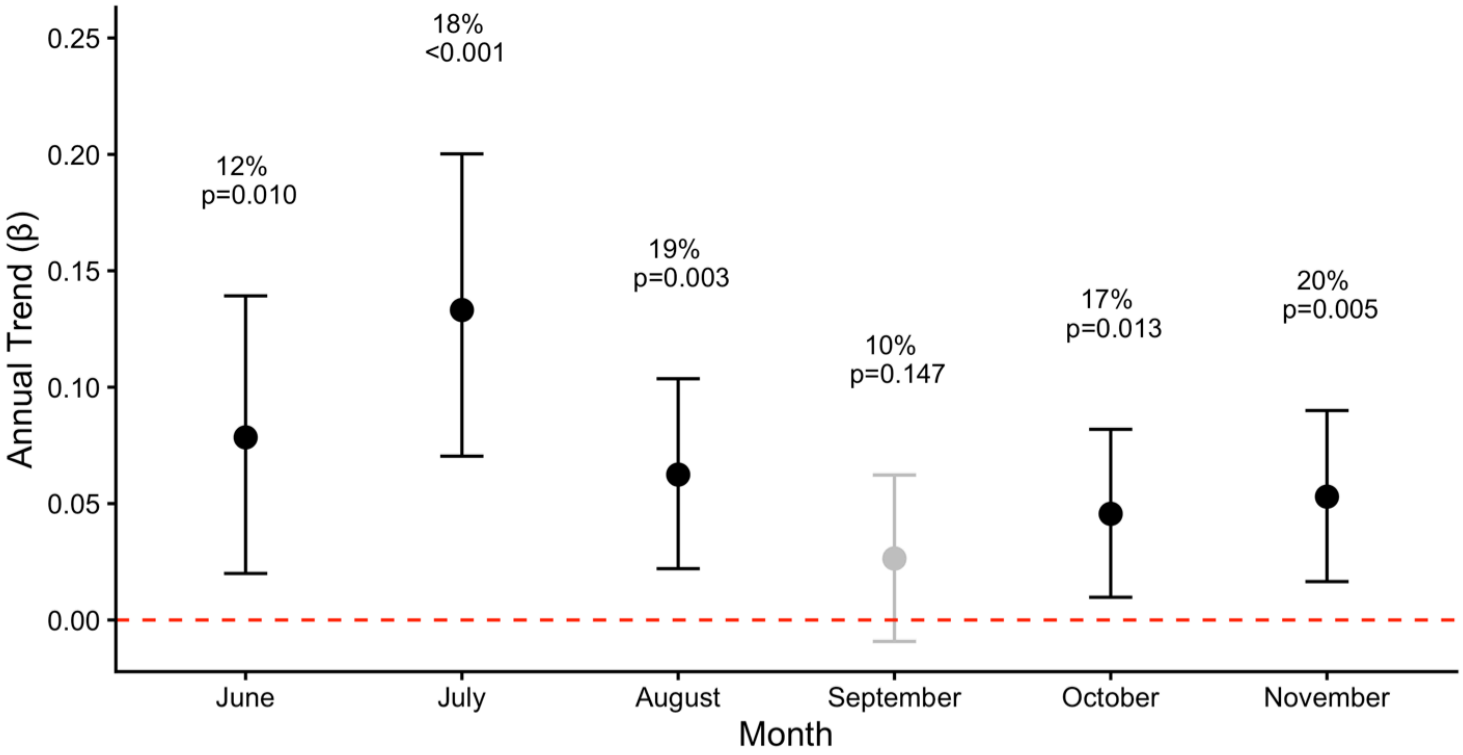


Figure 4

Monthly trends in the proportion of days that exceeded the minimum thermal threshold (>26°C) over the 17-year period from 2008 to 2024. Points represent beta coefficients from Generalized Linear Models for each month, and error bars show 95% confidence intervals. The absolute change in the percentage of days that exceed the threshold over the 17-year period and the corresponding p-values (p) are shown. The dashed red line indicates no annual change (β = 0). The black points and error bars represent statistically significant trends ($p < 0.05$).

Supplementary Files

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