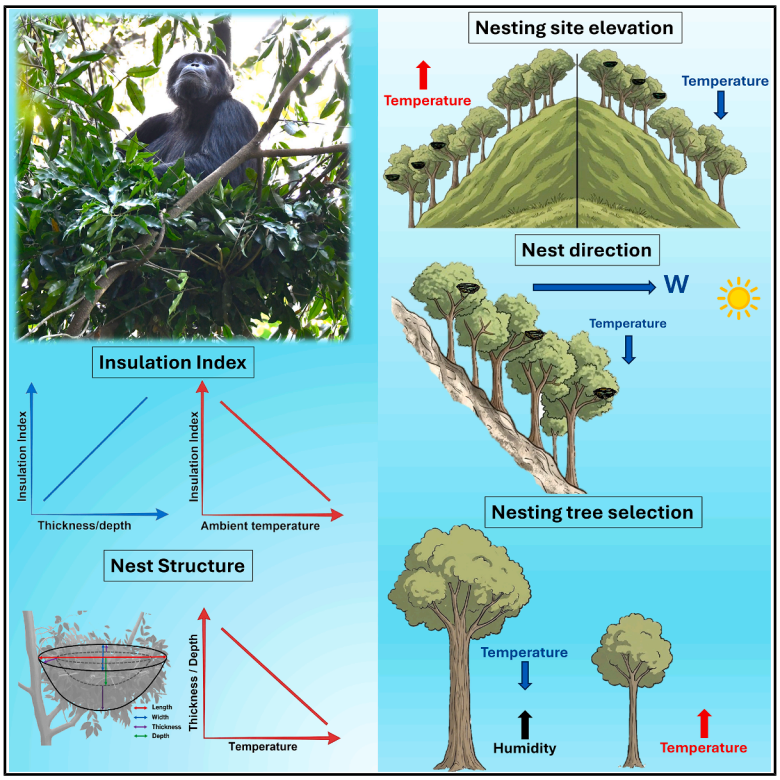
Report

Current Biology

Thermal adaptation and the potential anticipation of overnight weather in the nesting decisions of chimpanzees

Graphical abstract



Authors

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In brief

Al-Razi et al. show that chimpanzees adjust nest construction in relation to thermal conditions, with nesting decisions aligning more closely with overnight weather than with conditions at the time of construction, suggesting that nest building may integrate environmental cues linked to subsequent night-time conditions.

Highlights

- Chimpanzees adjust nest construction in relation to thermal conditions
- Nest structural traits contribute to variation in insulation performance
- Nesting decisions align more closely with overnight than immediate weather
- Nest building may integrate cues linked to subsequent overnight conditions

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Report

Thermal adaptation and the potential anticipation of overnight weather in the nesting decisions of chimpanzees

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SUMMARY

Animals employ behavioral strategies to buffer environmental stress,[1–4] yet it remains unclear whether such adjustments reflect reactive responses to current conditions or proactive anticipation of conditions yet to come. Nest building by great apes provides an ideal context in which to examine this distinction because nests function both as sleeping platforms and thermoregulatory structures.[5–13] We investigated the nesting behavior of eastern chimpanzees in relation to fine-scale microclimatic variation. We recorded *in situ* measurements of temperature, humidity, wind speed, and rainfall at the time of nest construction and during the subsequent overnight period. Then, we modeled how these microclimatic factors influenced the nesting site selection, nest structure, nest insulation, and the characteristics of the nesting tree. Chimpanzees preferentially constructed nests in warmer, less windy microclimates, built thicker and deeper nests under cooler or wetter conditions, and selected taller trees with denser canopy cover prior to rainy nights. Across analyses, models that incorporated overnight weather consistently outperformed those that incorporated weather variables at the time of nest construction, indicating that nesting decisions align more closely with overnight conditions than with conditions at the time of nest building. This outcome is consistent with the possibility that chimpanzees adjust nest-building behavior in relation to expected overnight thermal conditions, potentially using proximate cues, although it does not provide conclusive evidence of anticipatory decision-making. These findings suggest flexible thermoregulatory responses and possible integration of environmental cues in nesting decisions, offering new insight into the cognitive foundations of behavioral adaptation under variable climatic conditions.

RESULTS

Wild chimpanzees construct a new nest each evening for sleeping, and these nests play an important role in buffering individuals against environmental conditions.[5,6,12–20] Previous studies have shown that nest structure and nest-site selection vary with climatic factors such as temperature, humidity, wind, and rainfall, highlighting the thermoregulatory function of chimpanzee nests.[6,12,13,15,16,18–22] However, most previous studies have focused on low- to mid-elevation populations in relatively dry habitats and have primarily examined responses to prevailing conditions, leaving wet montane environments poorly studied.[12,13,15,16,23] Montane forests present distinct microclimatic challenges, characterized by cooler temperatures, higher rainfall, and persistently high humidity.[18,24] How chimpanzees adjust nesting behavior under such conditions remains unclear. More broadly, it is unknown whether nesting decisions reflect reactive responses to conditions already experienced or proactive adjustments in anticipation of forthcoming weather. Given their thermoregulatory function, the nests of chimpanzees provide an ideal context to test whether nesting decisions reflect reactive responses or proactive thermal adaptation. Although anticipatory responses to weather are documented in several non-primate taxa,[25–29] evidence for comparable anticipation in primates remains absent, with most weather-related behavioral adjustments interpreted as reactive. To address these gaps, we studied nesting behavior in a wild population of eastern

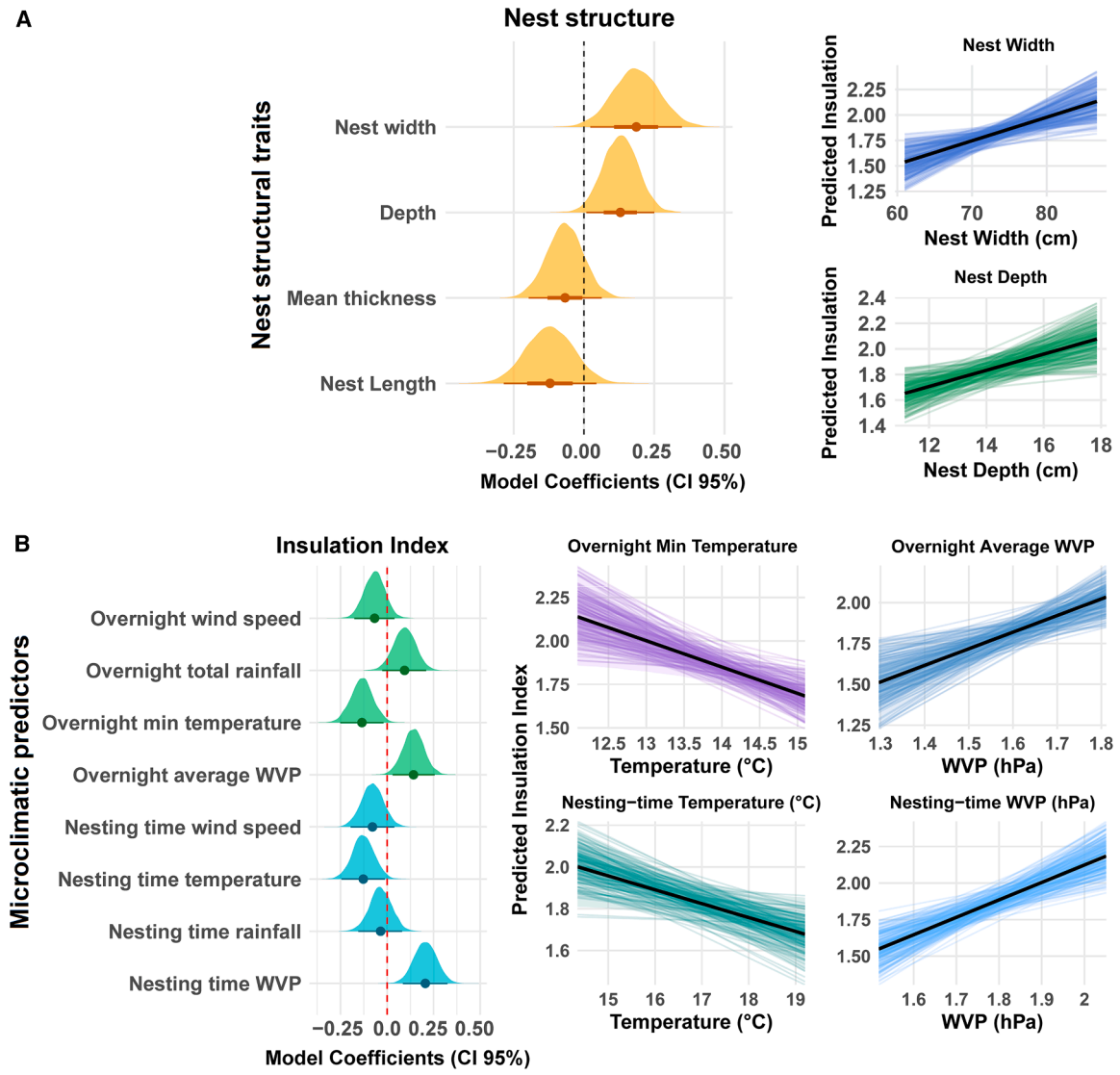

Figure 1. Weather sensitivity of chimpanzee nest structure and insulation

(A) Posterior effect distributions illustrating the relationships between nest structural traits (width, depth, thickness, and length) and predicted insulation.

(B) Effects of nesting time and overnight weather variables on the nest insulation index, with marginal effects showing predicted insulation responses to key temperature and water vapor pressure (WVP) variables. Shaded ribbons indicate 95% credible intervals.

See also Data S1B.

chimpanzees (*Pan troglodytes schweinfurthii*) in the cool, wet montane forest of Nyungwe National Park, Rwanda. By combining detailed measurements of nest structure, nesting-tree characteristics, nest insulation performance, and nest-site topography with fine-scale microclimatic data collected at nesting time and overnight, we asked three related questions. Do chimpanzees select nesting sites that provide thermally favorable microclimates in a cool, humid montane forest? Does weather variation influence nest structure, insulation, and nesting-tree characteristics in ways consistent with a thermoregulatory function? And are nesting decisions better explained by immediate conditions at construction or by environmental conditions occurring later during the night, consistent with anticipatory behavior?

Nest insulation

We tested the effects of nest structure, nesting time, and overnight weather conditions on the insulation index of the nests. The insulation index model converged well (all $\hat{R}$ = 1.00–1.01; effective sample sizes > 5,000) and provided an adequate fit, indicating that variation in nest insulation was partly driven by nest width and nest depth (Data S1B). Nest width had a positive effect on the insulation index (β = 0.19 ± 0.08, 95% CI: 0.02–0.35), as did nest depth (β = 0.13 ± 0.06, 95% confidence interval [CI]: 0.01–0.25). In contrast, nest length and mean thickness (hereafter thickness) showed no clear association with insulation (Figure 1A). We found no evidence that the insulation index differed among age-sex classes (Data S1B). The Bayesian R^2 was 0.19 (95% CI: 0.08–0.32), indicating that nest structural

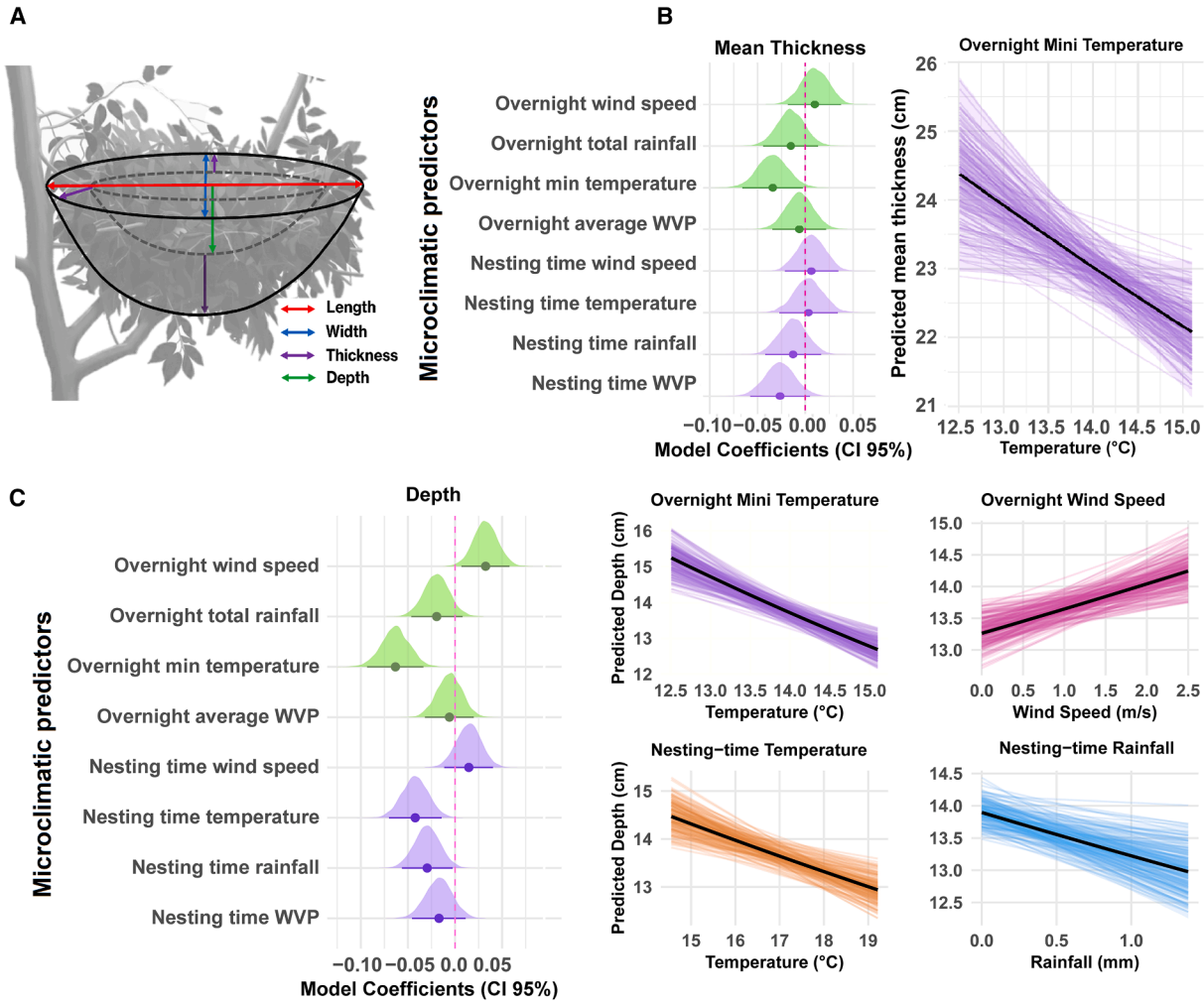

Figure 2. Nest structural measurements and weather effects on nest morphometrics

(A) Schematic illustrating how structural traits were measured directly from each chimpanzee nest, including length, width, thickness, and depth (colored arrows).

(B) Effects of nesting-time (pink) and overnight (green) weather variables on nest thickness. Left panels show posterior distributions of standardized effect sizes (points = posterior means; shaded areas = density; and vertical dashed line = zero effect). The right panel shows model-predicted relationships between thickness and key predictors, with thin lines representing posterior draws and the thick line the posterior mean.

(C) Effects of nesting-time (pink) and overnight (green) weather variables on nest depth, presented as posterior effect sizes (left) and model-predicted responses to selected predictors (right).

See also Data S1D.

traits explained approximately 19% of the variance in the insulation index (Data S1C).

When climatic variables were used as predictors in the nesting-time model, the insulation index was positively associated with water vapor pressure (WVP, β = 0.21 ± 0.06, 95% CI: 0.09–0.32, see STAR Methods) and negatively associated with temperature (β = −0.13 ± 0.06, 95% CI: −0.25 to −0.01, Figure 1B). Wind speed and rainfall showed no clear effects. In the overnight model, the insulation index was likewise negatively related to minimum temperature (β = −0.14 ± 0.06, 95% CI: −0.25 to −0.02) and positively related to average WVP (β = 0.14 ± 0.06, 95% CI: 0.03–0.26; Data S1B). Neither wind speed nor rainfall had a detectable association with insulation (Data S1B; Figure 1B). Both the nesting-time and overnight models showed good convergence (all $\widehat{R}$ = 1.00–1.01; effective sample sizes > 5,000), and posterior predictive checks indicated adequate model fit (Data S1B). Model comparison based on the leave-one-out information criterion (LOOIC) revealed that the overnight model (LOOIC = 76.2) performed better than the nesting-time model (LOOIC = 79.0) in explaining variation in the insulation index (Data S1C). The overnight model also exhibited a marginally higher Bayesian R^2 (0.31, 95% CI = 0.17–0.44) than the nesting-time model (0.28, 95% CI = 0.14–0.41), suggesting a modest improvement in explanatory power (Data S1C).

Variation of nest structure in relation to weather

Nest structure varied with both weather and age–sex class (adult males [AM], adult females [AF], subadult males [SAM], subadult females [SAF], and juveniles [Juv]) (Data S1D; Figure 2B). Nest

length was significantly shorter for SAF (β = −0.12, 95% CI: −0.21 to −0.04) and SAM (β = −0.17, 95% CI: −0.24 to −0.09) than it was for AM. Nest width showed a similar pattern, being narrower in SAF (β = −0.11, 95% CI: −0.18 to −0.04) and SAM (β = −0.15, 95% CI: −0.21 to −0.09). Among climatic factors, nest thickness decreased with increasing overnight minimum temperature (β = −0.03, 95% CI: −0.07 to −0.01), suggesting lower investment in insulation under warmer nocturnal conditions. Similarly, nest depth declined with increasing nesting-time temperature (β = −0.04, 95% CI: −0.07 to −0.01) and overnight minimum temperature (β = −0.06, 95% CI: −0.10 to −0.03), indicating that the chimpanzees built shallower nests on warmer nights (Data S1D; Figure 2C). Depth also decreased under higher nesting-time rainfall (β = −0.03, 95% CI: −0.06 to −0.01) but increased slightly with stronger overnight wind (β = 0.03, 95% CI: 0.01–0.06).

Model comparison based on LOOIC and Bayesian R^2 indicated broadly comparable fits between the nesting-time and overnight models for all structural components (Data S1D). For nest width, the nesting-time model showed a slightly lower LOOIC (−174.2 vs. −171.4) and marginally higher Bayesian R^2 (0.28, 95% CI: 0.16–0.39 vs. 0.27, 95% CI: 0.15–0.37). In contrast, for thickness and depth, the overnight model had lower LOOIC values (−20.7 vs. −19.5; −129.5 vs. −127.6) and slightly higher R^2 (0.13, 95% CI: 0.05–0.23 vs. 0.12, 95% CI: 0.04–0.21; and 0.26, 95% CI: 0.14–0.37 vs. 0.25, 95% CI: 0.13–0.36, respectively). However, LOOIC differences were small, and the credible intervals overlapped substantially, indicating only weak evidence for improved explanatory performance.

Nesting site selection

A comparison between the baseline weather, which we assume provided a measure of the general weather in the park, and the microclimate at each nesting site indicated that the chimpanzees consistently selected a location for their nest that provided warmer, more humid, and less windy conditions. Pairwise comparisons using Wilcoxon signed-rank tests showed that average overnight air temperature was significantly higher at the nesting site than at the baseline site (V = 555, $p < 0.0001$), as was WVP (V = 0, $p < 0.0001$). In contrast, wind speed (V = 0, $p < 0.0001$) and rainfall (V = 522, $p < 0.0001$) were significantly lower at the nesting sites (Figure 3A).

There was no clear evidence that the selection of slope was influenced by weather conditions (Data S1E). Both the nesting-time and overnight models exhibited low and comparable explanatory power (nesting-time R^2 = 0.24, 95% CI: 0.07–0.42; overnight R^2 = 0.22, 95% CI: 0.05–0.39; Data S1C). Model comparison likewise indicated nearly identical predictive performance between the nesting-time (LOOIC = 38.8) and overnight (LOOIC = 39.8) models. In contrast, elevation showed some clear associations with weather variables, particularly for the overnight conditions. The minimum overnight temperature was significantly and negatively associated with elevation (β = −0.033, 95% CI: −0.07 to −0.01), indicating that the chimpanzees nested at higher elevations on cooler nights (Figure 3B; Data S1E). Other overnight predictors showed weak and uncertain effects. Model comparison based on LOOIC and Bayesian R^2 indicated that the overnight model fit better than the nesting-time model (Data S1C). The overnight model showed a lower LOOIC (−62.6 vs. −57.4) and higher explanatory power (R^2 = 0.49, 95% CI: 0.26–0.63) than the nesting-time model (R^2 = 0.38, 95% CI: 0.15–0.55). Although the difference in model fit was moderate, credible intervals overlapped substantially, indicating that overnight conditions provided somewhat better explanatory performance for variation in nest elevation.

The multinomial model of nesting slope direction indicated several weather-dependent effects during nest construction (Data S1F). For north-facing slopes, the probability of nest occurrence increased with higher nesting-time temperature (β = 0.67, 95% CI: 0.17–1.22) and wind speed (β = 1.28, 95% CI: 0.19–2.42). No other predictors showed credible effects for this direction. For south-facing slopes, no parameter had a credible effect, although rainfall exhibited a weak negative trend (β = −1.38, −2.99 to 0.06). The chimpanzees were more likely to build their nest on a west-facing slope on cooler and drier evenings, as the probability of nest occurrence decreased with increasing temperature (β = −0.61, 95% CI: −1.07 to −0.18) and rainfall (β = −0.89, 95% CI: −1.69 to −0.07). In the overnight model, only total rainfall significantly influenced slope orientation, with a nest on a south-facing slope being less likely when the night was wetter (β = −1.32, −2.50 to −0.37; Figure 3C; Data S1F). Other overnight weather variables showed no meaningful effect on direction. Model comparison indicated that the nesting-time predictors provided a better overall fit (LOOIC = 209.7) than the overnight predictors (LOOIC = 252.1). Thus, environmental conditions experienced during nest construction better explained the choice of hill-slope direction than those measured overnight (Data S1C).

Characteristics of the nesting tree and nest position

For diameter at breast height (DBH), both the nesting-time and overnight models identified negative effects of temperature because the credible intervals excluded zero (nesting: β = −0.14, 95% CI: −0.26 to −0.02; overnight: β = −0.22, 95% CI: −0.35 to −0.10; Data S1G; Figure 4). Other weather predictors (WVP, wind speed, and rainfall) showed no consistent effect, and no age-sex category differed significantly from adult males (Data S1G). For tree height, crown height, and nest height, temperature again had a negative association, strongest for crown height (nesting: β = −0.25, 95% CI: −0.38 to −0.12; overnight: β = −0.26, 95% CI: −0.40 to −0.13). Overnight models also suggested small but statistically supported positive associations between average WVP and tree height (β = 0.13, 95% CI: 0.04–0.22) and crown height (β = 0.15, 95% CI: 0.02–0.28), whereas these effects were absent in the nesting-time models (Data S1G). For distance from the main trunk (DMT), none of the weather predictors or age-sex categories showed credible effects, as all 95% credible intervals overlapped zero. For leaf area, overnight minimum temperature was negatively associated (β = −0.17, 95% CI: −0.30 to −0.05), whereas other weather variables were uninformative. For canopy coverage, rainfall was positively associated at both time points (nesting: β = 0.28, 95% CI: 0.06 to 0.51; overnight: β = 0.26, 95% CI: 0.04 to 0.48), whereas other predictors were negligible (Data S1G; Figure 4).

Across the traits for nesting tree characteristics and nest position, the overnight models generally showed better predictive performance than did the nesting-time models (Data S1C), as indicated by lower LOOIC values and modestly higher Bayesian

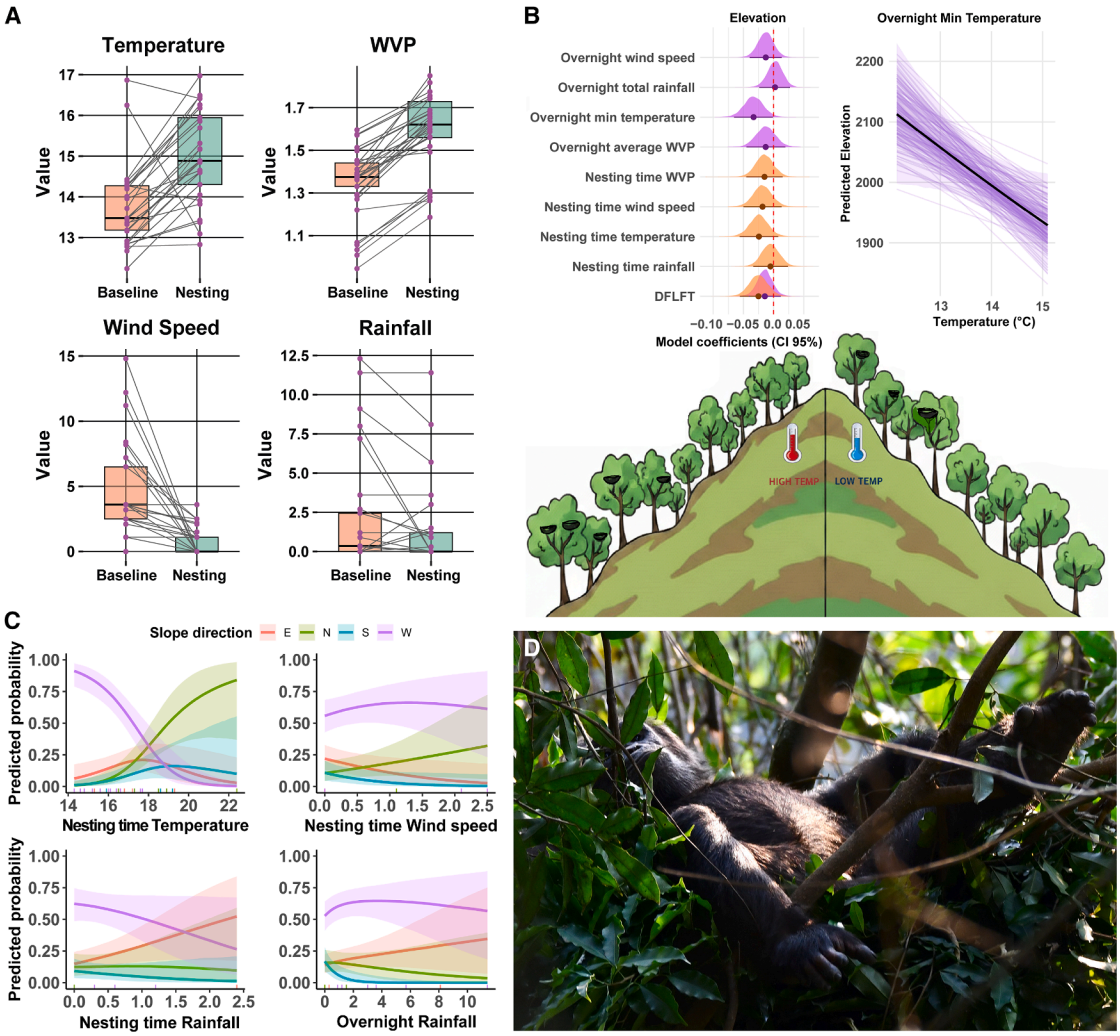

Figure 3. Microclimatic conditions, topography, and behavioral responses associated with chimpanzee nesting decisions

(A) Changes in local microclimatic conditions between baseline and nesting sites, showing temperature, water vapor pressure (WVP), wind speed, and rainfall (n = 26 paired nesting events). Boxplots display raw observed values; the central line represents the median, boxes indicate the interquartile range (25th–75th percentiles), and whiskers extend to 1.5 × IQR. Points represent individual paired measurements, and dashed lines connect baseline and nesting-site values from the same nesting event.

(B) Effects of nesting-time and overnight weather variables on nest-site elevation. The upper panels show the model results: posterior distributions of standardized coefficients (95% credible intervals) for nesting-time and overnight predictors (left), and the predicted relationship between overnight minimum temperature and nest elevation (right). DFLFT refers to the distance from the last feeding tree. The vertical dashed line at zero indicates no effect. The lower panel presents a conceptual illustration, based on our findings, showing how thermal conditions may influence the elevation at which nests are constructed.

(C) Predicted probabilities of selecting different slope directions derived from models including nesting-time and overnight temperature, WVP, wind speed, and rainfall. East-facing slopes were used as the reference category in the model, and only predictors with significant effects are shown. Lines represent posterior mean estimates, and shaded bands indicate 95% credible intervals.

(D) Representative photograph of a wild chimpanzee basking in the sun while lying on its night nest prior to sleeping.

See also Data S1E and S1F.

R^2 estimates. By contrast, DMT and nest coverage were better supported by the nesting-time models, showing comparable or slightly improved performance relative to overnight models. For DMT, Bayesian R^2 estimates were identical between model types (R^2 = 0.11, 95% CI: 0.04–0.20), and LOOIC values were nearly the same (128.2 vs. 128.6). For nest coverage, Bayesian R^2 estimates differed slightly but remained low for both models (nesting-time: R^2 = 0.11, 95% CI: 0.04–0.18; overnight: R^2 = 0.08, 95% CI: 0.03–0.15), with similarly close LOOIC values (−50.4 vs. −45.5).

Anticipation of overnight weather conditions

Nesting-time and overnight weather variables were strongly correlated, indicating that environmental conditions at the time of nest construction generally mirrored those experienced later during the night (see STAR Methods). Pearson's correlation

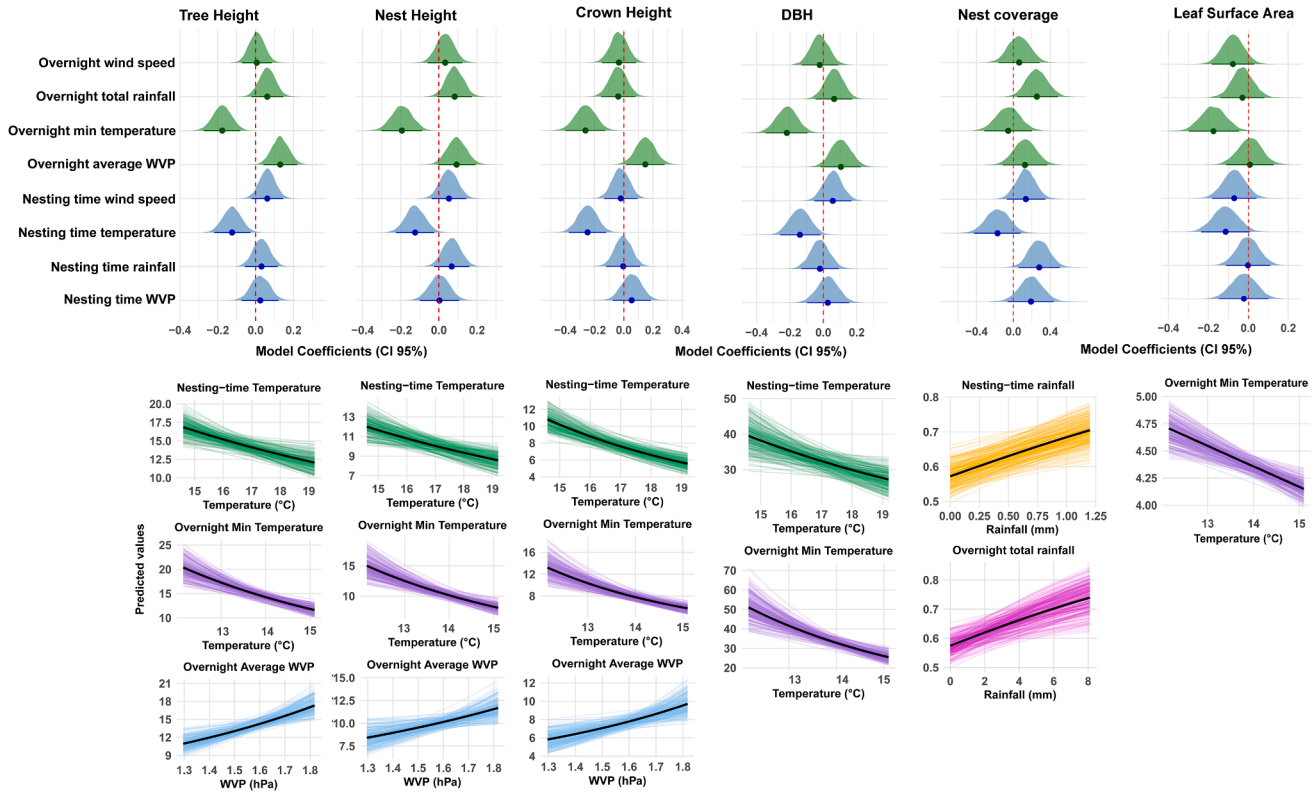

Figure 4. Effects of nesting time and overnight microclimate on nest tree characteristics and nest position

Posterior coefficient distributions (top) and model-predicted responses (bottom) showing effects of nesting-time (blue) and overnight (green) microclimate on nesting-tree characteristics and nest position on the tree. The dashed line indicates zero (no effect).

See also Data S1G.

analyses showed strong positive coupling between overnight and nesting-time temperature ($r = 0.71$, $p < 0.001$) and WVP ($r = 0.80$, $p < 0.001$), whereas wind speed ($r = 0.49$, $p < 0.001$) and rainfall ($r = 0.70$, $p < 0.001$) exhibited more moderate continuity. Despite these correlations, paired Wilcoxon signed-rank tests revealed significant diel differences across all weather parameters (all $p < 0.001$). Nesting-time temperature and WVP tended to exceed their overnight counterparts, whereas wind speed and rainfall were substantially greater overnight. A small number of outliers exerted a small influence on the overall trend (see STAR Methods). Across all model sets, overnight models explained more variance than did nesting-time models in most cases (9 of 14; 64%), showing higher Bayesian R^2 and lower LOOCI values for insulation, nest structural attributes, nesting-tree characteristics, and positional traits (Data S1C). Models that incorporated overnight weather variables showed stronger associations with nesting-site topography, nest structure, and nesting-tree characteristics than did the models that included nesting-time weather variables.

DISCUSSION

Our study revealed that chimpanzees in the montane forests of Nyungwe adjusted their nesting behavior in response to fine-scale microclimatic variation, demonstrating adaptive flexibility in thermoregulatory decision-making. By linking detailed nesting records with concurrent weather data, we showed that chimpanzees preferentially selected taller trees, a higher nesting position, and denser canopy cover on cooler or wetter nights. These patterns are consistent with the possibility that chimpanzees adjust their nesting behavior in relation to expected weather conditions, rather than reacting solely to immediate conditions, although our analysis does not provide conclusive evidence of anticipatory decision-making. Taken together, our findings highlight the capacity of great apes to integrate climatic information into their nesting decisions, offering new insight into the cognitive and ecological dimensions of behavioral adaptation.

Our study provides strong support for the thermoregulation hypothesis of nesting in great apes.[6,12,14,16,30–32] Although the thermoregulatory role of the chimpanzee nest has been demonstrated previously, our work offers the most detailed field-based evidence to date, incorporating microclimate measurements taken directly from natural nests under ambient forest conditions.[12,13,15] Earlier studies examined nesting microclimates across different habitats or elevations,[10,12,13,33,34] whereas we collected overnight weather data at the nesting site on each night. This fine-scale approach revealed a direct correspondence between local thermal conditions and chimpanzee nesting behavior. Furthermore, whereas Stewart et al.[13] used artificial nests with heat-retention experiments, we applied the

same method to freshly built natural nests and developed an insulation index to quantify how nest morphology performed as thermal protection across varying microclimatic conditions.

Our study not only supports previous findings on chimpanzee nesting behavior but also reveals several differences and novel insights. Our models indicate that, similar to the savanna chimpanzees at Fongoli, Senegal, the Mayebe chimpanzees built thicker and deeper nests on cooler nights.[13] However, unlike the Fongoli community, they also selected a higher nesting position in taller trees at high elevations under cooler conditions. This pattern likely reflects vertical stratification of temperature and humidity within the montane forest, where air near the forest floor is typically cooler and more saturated with moisture, whereas the upper canopy layers remain relatively drier and better ventilated.[18,20,24] Consequently, during nights with higher WVP, chimpanzees may prefer taller trees and higher crown positions to avoid a damp, moisture-laden microclimate near the ground and to maintain a drier, more thermally stable nest. Additionally, the model for nesting hill-slope orientation, together with field observations, revealed another intriguing behavioral difference from the Fongoli population that was described by Stewart et al.[13] In Mayebe, chimpanzees more frequently constructed nests on west-facing slopes during cooler nights. Such positioning may increase exposure to afternoon sunlight prior to nightfall, potentially allowing individuals to benefit from residual solar warmth before sleep (Figure 3D). Whereas sun-basking behavior is well documented in primates, including chimpanzees,[13,35] basking from the nest immediately prior to sleep has not previously been described. Nest placement on west-facing slopes may therefore facilitate passive heat gain before the nocturnal resting period, providing a simple behavioral mechanism that would buffer heat loss in the cool montane climate of Nyungwe. The Mayebe chimpanzees also built nests under denser canopy cover on rainy nights, reflecting adaptation to the cool, wet montane climate. By contrast, chimpanzees in Senegal and Equatorial Guinea nested in more open sites during the wet season,[21] likely favoring ventilation over insulation.

Nest building in great apes exemplifies environmental problem solving, involving the manipulation and organization of natural materials to meet ecological and physiological demands, and occurs more frequently than tool manufacture and use within and across species.[6,34] Nest construction by great apes is therefore not merely a resting or defensive behavior but reflects advanced cognitive processes, including object manipulation, decision-making, and social learning.[6,36–41] As several studies have observed, great apes adjust nest structure, height, and site selection in response to climatic and habitat variation, decisions that entail sensory evaluation, material manipulation, and spatial planning.[6,7,13,21,42,43] Such behavioral flexibility is consistent with the broader concept of ecological intelligence,[44,45] which posits that complex cognition evolves to address recurrent environmental challenges. The harsh climatic conditions of Nyungwe National Park likely drive adaptive decision-making by the Mayebe chimpanzees in their selection of thermally optimal nesting sites, exemplifying the ecological intelligence hypothesis. The closer alignment between nesting decisions and overnight weather conditions supports a hypothesis that chimpanzees use proximate atmospheric cues, such as shifts in humidity, temperature, or barometric pressure, to adjust nest construction in advance of nocturnal thermal conditions (Figures 1B, 2B, 2C, 3B, and 4). Under this framework, nest building would reflect predictive use of environmental information rather than purely reactive responses to prevailing conditions. However, because our analyses are correlational and nesting-time and overnight variables were partially coupled, the present data do not provide conclusive evidence of anticipatory behavior. Direct tests of this hypothesis will require fine-scale atmospheric monitoring, continuous behavioral observations, and approaches that are capable of disentangling predictive from reactive responses.

Although anticipatory responses to weather variation have been reported, such behaviors are uncommon across taxa and often originate from ethnobiological observations that link animal activity to approaching weather events.[46–48] However, several empirical studies have shown that some animals, including birds, bats, and amphibians, can detect changes in barometric pressure.[25–29,49–51] Barometric pressure is a useful tool to predict weather changes.[52] Because barometric pressure changes reflect atmospheric instability and are often accompanied by shifts in temperature and humidity, the ability to perceive these cues may enable animals to anticipate short-term (a few hours to a few days) weather fluctuations and respond adaptively.[53–56] For example, golden-winged warblers (*Vermivora chrysoptera*) vacate breeding territories up to 24 h before severe storms,[27] and migratory songbirds adjust departure decisions based on barometric pressure trends over the preceding 24 h, increasing the likelihood of favorable weather conditions.[28] Similarly, the close alignment between nesting decisions and overnight weather in the Mayebe chimpanzees suggests a sensitivity to proximate atmospheric cues, such as subtle changes in air pressure or humidity that precede temperature shifts, allowing them to adjust the structure of a nest in response to the region's rapidly fluctuating montane climate. In this context, anticipation refers to adjustments made at nest construction in the late afternoon that align with weather conditions occurring later that same night, rather than the prediction of specific meteorological events many hours in advance. However, because our data link nesting-time conditions to overnight summaries, we cannot determine whether chimpanzees are responding to very proximate cues (e.g., changes within 1–2 h) or to broader atmospheric shifts that precede conditions across the entire night. Another key limitation of this study is that we did not collect data on nocturnal activity and therefore cannot determine whether chimpanzees add to, modify, or reposition within their nests during the night in response to changing weather conditions. In orangutans, nocturnal repositioning within nests has been documented, particularly among immatures, although this behavior has not been linked to thermoregulatory outcomes.[40] However, recent work on nocturnal behavior in the Budongo Forest, Uganda, found no evidence that chimpanzees engage in nest modification after construction.[57] Future studies incorporating continuous nocturnal observations would help distinguish between anticipatory nest construction and potential within-night adjustments.

Together, our findings provide detailed field evidence that chimpanzees adjust their nesting behavior in response to changing thermal conditions, revealing a dynamic interaction between climate, cognition, and nest construction. Such flexibility

highlights how chimpanzees may buffer thermal challenges through adaptive nest-building behavior, in a way that promotes thermal comfort under variable climatic conditions. In addition, our results raise the possibility that chimpanzees may respond to atmospheric cues that are associated with forthcoming weather conditions, generating a testable hypothesis that decisions about nest construction could incorporate information about overnight environmental changes. Future work integrating fine-scale atmospheric monitoring, behavioral observations, and physiological measurements will be necessary to test whether chimpanzees detect specific meteorological cues, such as changes in barometric pressure, humidity, or wind speed, and how these cues influence their nesting decisions. Comparative studies across populations and habitats could further clarify whether such responses represent a widespread adaptive strategy or are a distinctive feature of montane chimpanzees living under highly variable climatic conditions.

RESOURCE AVAILABILITY

Lead contact

Requests for further information and resources should be directed to, and will be fulfilled by, the lead contact, Hassan Al-Razi (hassan.alrazi@research.uwa.edu.au).

Materials availability

This study did not generate new unique reagents.

Data and code availability

- All data connected to this paper are available at https://doi.org/10.6084/m9.figshare.31641877.
- All codes connected to this paper are available at https://doi.org/10.6084/m9.figshare.31641877.
- Any additional information required to reanalyze the data reported in this paper is available from the lead contact upon request.

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AUTHOR CONTRIBUTIONS

Conceptualization, H.A.-R. and C.C.G.; methodology, H.A.-R., C.C.G., and S.K.M.; data collection, H.A.-R., and F. Muhayeyezu; data curation, H.A.-R.; formal analysis, H.A.-R.; software, H.A.-R.; supervision, C.C.G., S.K.M., and B.A.K.; project administration, F. Mulindahabi, P. N., and D.A.B.; visualization, H.A.-R.; technical support, L.D.; funding acquisition, H.A.-R. and C.C.G.; writing—original draft, H.A.-R., C.C.G., and S.K.M.; writing—review and editing, all authors.

DECLARATION OF INTERESTS

The authors declare no competing interests.

STAR★METHODS

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SUPPLEMENTAL INFORMATION

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited data		
Repository data	This paper	https://doi.org/10.6084/m9.figshare.31641877
Eastern chimpanzee (*Pan troglodytes schweinfurthii*)	Wild chimpanzees: Mayebe chimpanzee community, Nyungwe National Park, Rwanda	https://www.africanparks.org/the-parks/nyungwe
Software and algorithms		
R 4.3.0	R Core Team	https://www.r-project.org/
ggplot2.	https://CRAN.R-project.org/package=ggplot2	RRID: SCR_014601
brms package	https://CRAN.R-project.org/package=brms	RRID: SCR_017029
Stan backend (v2.8.0)	https://mc-stan.org/	RRID: SCR_018343
loo package	https://mc-stan.org/loo/	N/A
terra package	https://cran.r-project.org/package=terra	N/A
Analysis code	This study	N/A
Other		
GPS	Garmin	eTrex 64s
Mini weather station	TESA Professional Weather Station	WS1081 Ver3
Temperature logger	Standard temperature loggers	https://www.loggermate.com/
Laser Rangefinder	Suaoki	Lw600GOLF

EXPERIMENTAL MODEL AND STUDY SUBJECT DETAILS

Study site

Nyungwe National Park (NNP) is located in Southwest Rwanda (2°17′-2°50′S and 29° 07′-29°26′E), covers 1,013 km^2, and spans an elevation range from 1,600 to 2,950 m. NNP is a cool, well-watered, tropical montane forest. The forest has two wet seasons each year (when monthly rainfall exceeds 100 mm). However, the timing and intensity of these wet seasons are not consistent, showing interannual variation in rainfall magnitude.[58–61] During our study, the climatic patterns of Nyungwe National Park exhibited seasonal variation (Figure S2). Monthly average air temperature was relatively stable throughout the year, ranging between approximately 14°C and 17°C, with slightly higher variability during the wetter months. The average wind speed also peaked during the dry season (June to September), reaching up to 5 km/h, and remained lower during the rest of the year. There were two distinct wet months: a major wet month in March (366 mm) and a minor wet month in November (260 mm), while the driest period occurred from June to August, with June receiving only 24 mm of rain.

Nyungwe National Park, combined with the adjacent Kibira National Park in Burundi to the south, is one of the largest remaining montane forests in Africa.[62] Nyungwe is regarded as one of the most biologically rich forests in the Albertine Rift.[62] Besides chimpanzees, 12 other non-human primate species are present in the park.[62] The forest is home to around 380 chimpanzees, which is the largest population of chimpanzees in Rwanda.[63] The vegetation in the national park is a mosaic of open and closed forests, bamboo forests, swamps, moorland, and grasslands. Due to the relatively open canopy coverage, the vegetation structure of the forest is of different types, with a dense herb layer in moist areas.[62,64,65]

Study subjects

We worked on the Mayebe chimpanzee community, which is well habituated to humans and contains around 67 individuals, including 14 adult and four subadult males, 18 adult and seven subadult females, 12 juveniles, and 12 infants. The community ranges between Uwinka and Mount Bigugu.[66] Depending on the method used to assess the home range of the Mayebe community, it varies from 38 to 48 km^2.[67] The home range of the Mayebe community includes the highest known altitudinal limit of chimpanzees (2,950m ASL). As is typical for chimpanzees, the Mayebe community exhibits a multimale-multifemale social organisation with parties that frequently change in size and composition.[68]

METHOD DETAILS

Chimpanzee tracking

We collected data on the nests made by chimpanzees on an average of seven days per month between March 2024 and February 2025 by random following of chimpanzee parties. H. Al-Razi collected the data with the assistance of one trained field assistant and an experienced chimpanzee tracker. Because the trees of Nyungwe National Park are tall and often remain wet, we employed an additional assistant to climb trees and collect nesting data. The climber had prior experience in this forest and was provided with two weeks of training in techniques to standardise nest measurements before the commencement of systematic data collection. During data collection, depending on tree characteristics, we used both single-rope climbing equipment and freehand climbing. To collect nest data, we followed chimpanzees from the afternoon until they made a nest. Individuals were classified into age classes using the method described by van Lawick-Goodall[69] (Data S1A). The logistical constraint of a need to carry equipment for weather-monitoring, together with food and water supplies, prevented us from tracking the chimpanzees continuously from morning until nesting. To minimise the risk of damage to sensitive instruments and to reduce the physical burden of transport, data collection was therefore restricted to targeted observation periods rather than full-day follow-ups.

Collection of weather data at nesting time and overnight

A weather station was deployed permanently in our camp to collect baseline weather data. We placed that weather station in an open area, 2,200 meters above sea level. When we observed any nesting activity of the chimpanzees, we waited at a minimum distance (from 5 to 15 meters, depending on vegetation type, topography, and party size) until they had completed the nest preparation. Once all of the nests had been completed, we deployed another mini weather station (WS1081 Ver3 TESA Professional Weather Station) close to the nesting site. Each night, the station was installed at a height that corresponded to the height at which most nests occurred to ensure comparable microclimatic measurements. We defined the nesting site as a 25 x 25 m area that enclosed the nesting trees (Figure S3). We placed the deployed weather station as close as possible to the sleeping party with minimal disturbance. The weather station collected weather data every 10 minutes overnight. During deployment, we avoided loud conversation and high-intensity headlamps; when illumination was necessary, we used red light. Only nests that were located within the defined area and used on that nesting night were included in the analyses.

Both weather stations collected data on temperature, relative humidity, wind speed, and rainfall. For the statistical analyses, the second reading that was recorded by the weather station after it was deployed each night was used to represent the weather conditions at nesting-time for all variables. To minimise the impact of our installation activities, we did not use the data from the first reading of the weather station. Weather conditions on the subsequent night (overnight) were quantified as the minimum temperature recorded during each night, the average relative humidity, and maximum wind speed, while overnight rainfall was expressed as the total accumulated rainfall. Relative humidity is strongly temperature-dependent, so we converted the relative humidity to water vapour pressure to reduce collinearity with temperature and improve the stability of statistical analyses.[70] Following Barenbrug,[71] we calculated the water vapour pressure as:

$$\text{Vapour pressure of water (WVP)} = 0.6105 \times \exp\left[\frac{17.27 \times T_a}{(237.3+T_a)}\right] \times \frac{RH}{100}$$

Where:

$$WVP = \textit{water vapour pressure (kPa)}$$

T_a = air temperature (°C)

$$RH = \text{relative humidity (\%)}$$

exp = exponential function (e^x)

Collection of data on the nesting tree and nest position

After the chimpanzees had vacated the nest the morning after, we recorded some characteristics of the nest and the tree that the nest was in. For the nest itself we assessed: (i) nest height from the ground, calculated as the vertical distance from the base of the nesting tree trunk directly below the nest to the base of the nest, (ii) nest position within the crown, calculated as the difference between nest height and the height of the lowest branch, and (iii) perpendicular distance of the nest from the main trunk of the nesting tree.

For the tree we recorded: plant species, diameter at breast height (DBH; stem diameter measured at 1.3 m above ground), total tree height (from the base of the tree to top of crown), lowest branch height (base to lowest branch), crown height (distance between the lowest branch and the top of the tree), and percentage canopy cover. The DBH was measured with a measuring tape, and other measurements were made using a handheld Laser Range Finder (SUAOKI Lw600GOLF). We estimated the surface area of leaves from nesting trees by placing leaves on a grid board (0.25 × 0.25 cm squares), tracing their outlines, and counting the enclosed grid squares to calculate leaf area. We averaged measurements from 28 leaves to obtain a mean leaf surface area. When a tree had compound leaves, the size of each leaflet was used as the average for the species. We estimated nest coverage visually as a percentage. If no branches or leaves were present above a nest, coverage was recorded as 0%, whereas nests directly beneath dense foliage

were recorded as 100%. Intermediate values were assigned when partial cover was present, with 25% indicating sparse cover, 50% representing moderate cover, and 75% denoting dense but not complete cover.

Nest morphology

Although chimpanzees very occasionally reuse old nests,[6,17,72] we did not bring any nests down from trees or destroy them in order to avoid creating ecological hazards. Because of that, we measured only the morphology of the nest and did not collect data on the nest architecture, such as the number of linings, the number of mattress layers, or the number and size of used branches. We measured the length, width, thickness, and depth of each nest (Figure 2A) using a measuring stick. We measured nest thickness at five locations, including the centre and each of the four sides, and then calculated the mean of these measurements.

Nest insulation

We measured nest insulation in 64 of 98 fresh nests that were recorded during the study. The remaining nests were not tested due to logistical constraints, including limited personnel and occasional equipment limitations (e.g., rapid cooling of the heated water in the thermal flask on some sampling days). To measure the insulation of each nest, we followed the method of Stewart et al.[13] with modifications. We used two 200 ml bottles made of flexible plastic that were filled with hot water for each assessment. We carried hot water (> 50°C) with us in vacuum thermos flasks. We compared the rate of temperature decline (caused by heat loss from the bottles) of a bottle within the nest to the rate of temperature decline of a bottle hung outside of the nest. Each bottle contained one temperature logger (Standard model, loggermate.com) that measured the temperature of the water within the bottle every 40 seconds. To protect the loggers from water, each logger was sealed inside a thin glass tube (same thickness for all loggers). Prior to and after deployment, the temperature loggers were calibrated to the nearest 0.1°C against a certified (National Association of Testing Authorities, Australia) platinum thermometer (Centre 376) in a water bath that was maintained at temperatures between 4°C and 60°C in 5°C steps.

For the assessment of nest insulation, we used only fresh nests that had been used by the chimpanzees the previous night. Although Stewart et al.[13] found that the leaves in a nest dried rapidly in dry, mosaic environments, which could potentially alter the insulation properties of the nest, our study was conducted in a wet rainforest with consistently high humidity, meaning that leaves remained fresh for longer and dried much more slowly. To maintain consistency and minimise any potential variation due to leaf drying, we examined a nest only the day after it was used, ensuring that it was freshly built. At the same time, we initiated the experiments as early as possible and completed them before noon.

Each time a bottle was used, it began with a temperature above 50°C. For each deployment, we applied an exponential decay model to the data from 45 to 30°C, the logic being that midway through that range is the average body temperature of a chimpanzee.[73]

$$Y = A_o \cdot e^{-kt}$$

where Y represents the temperature recorded at time t, A_0 is the initial temperature (at time zero), and k is the decay constant that describes the rate of temperature decrease.

To linearise the exponential decay function and facilitate statistical analysis, we applied a natural logarithmic transformation to the temperature data:

$$\log(Y) = \log(A_o) - kt$$

For each nest, we calculated the natural logarithm of the temperature values and then fitted a simple linear regression model with time as the independent variable and log-transformed temperature as the dependent variable. This was done separately for the "inside nest" and "outside nest" datasets. The slope of the fitted line was extracted using the SLOPE function in Excel. The resulting slope value represents the negative of the decay constant (−k), which we used as an indicator of the rate of temperature decline.

Although only the slope values (−k) were required to calculate the insulation index, we validated the reliability of each slope by reconstructing the modelled temperature trajectories using the exponential function. These modelled curves closely tracked the observed data, confirming that the fitted slopes accurately reflected the cooling dynamics. The resulting slope values were then used to calculate an insulation index for each nest, defined as the ratio of the slope from the bottle outside of the nest to the slope from the bottle inside the nest (outside slope / inside slope). The index reflects how effectively the nest insulated the bottle from heat loss relative to the ambient conditions, and a larger value of the index indicates that better insulation was provided by the nest.

Nesting site topography

We collected the elevation of each nesting site using a hand-held GPS (Garmin GPSMAP 64s), which provided values for latitude / longitude and elevation. To quantify the steepness of a nest location, we derived slope values from a digital elevation model (DEM). A freely available DEM (Copernicus GLO-30; 30 m spatial resolution) that covered Nyungwe National Park, Rwanda, was obtained from the European Space Agency.[74] The DEM was imported into R using the *terra* package, and a slope raster was generated with the terrain function, which calculates the maximum rate of elevation change between each raster cell and its neighbours. Nest coordinates were converted to spatial points and overlaid on the slope raster. The slope value at each nest location was extracted with the

extract() function (terra package) and appended to the nest dataset for subsequent analyses. Following Hernandez-Aguilar et al.,[75] we recorded the orientation of the hill slopes where chimpanzees constructed their nests to assess potential preferences for specific slope direction.

QUANTIFICATION AND STATISTICAL ANALYSIS

General approach

Data analysis focused on the effect of weather conditions either at the time that the nest was constructed or the subsequent overnight conditions on the selection of nesting site (elevation and slope, n = 26), nest structure (n = 98), insulation (n = 64), characteristics of the nesting tree (n = 106), and the position of the nest in a tree (n = 106). Initially, we tested the normality of each dependent variable before any statistical analysis was conducted. We assessed normality using a two-step approach: first, we visualised the Q-Q plots to identify major deviations from a theoretical normal distribution, and then we used the Shapiro-Wilk test to statistically evaluate normality. To meet the assumptions of Gaussian modelling and improve the normality of residuals, we log-transformed all continuous response variables related to nest structure, characteristics of the nesting tree, and nest position.

To facilitate convergence, reduce scaling issues, and allow direct comparison of effect sizes across variables, prior to modelling, we standardised (Z-transformed) all weather predictors to a mean of zero and a standard deviation of one.[76] To assess potential multicollinearity, we examined interactions among the predictor variables. We detected high collinearity between overnight average water vapour pressure (WVP) and nesting-time WVP, where Variance Inflation Factors (VIFs) were more than 5.[77,78] However, after including them in separate models, no substantial multicollinearity was observed among the remaining variables within each model. All analyses were conducted in R (version 4.3.0)[79] using RStudio version 2023.3.0.386.[80] To graphically present the results, we used the R package ggplot2.[81]

Analysing climatic effects on nesting behaviour

To examine the effect of weather conditions either at the time that the nest was constructed (hereafter, ''nesting-time'' weather) or the overnight conditions (hereafter, ''overnight'' weather) on the nesting behaviour, we fitted two separate models. To assess which set of weather conditions (nesting-time vs. overnight) provided better predictive performance for each response variable, we later compared the two competing models. To assess how weather conditions at nesting-time influenced nest site selection, nest structure, insulation, direction of nesting hill slopes, tree characteristics, and nest position on the tree, we included four weather variables: air temperature at nesting-time (hereafter, nesting-time temperature), wind speed at nesting-time, rainfall at nesting-time, and WVP at nesting-time in the first model. Chimpanzee age-sex category was included as a categorical predictor in all models to account for potential variation in nest construction among demographic classes. Factor levels were coded to ensure compatibility with the modelling framework, and adult males (AM) were set as the reference category, allowing all other age-sex coefficients to be interpreted relative to this group.[82]

Model 1(*nesting time model*) : *Response variable* $\sim$ *Nesting* $-$ *time temperature* + *Nesting* $-$ *time rainfall* + *Nesting* $-$ *time WVP* + *Nesting* $-$ *time wind speed* + *age* $-$ *sex*

The second model was established to assess the impact of overnight weather conditions on the nesting behaviour of the Mayebe chimpanzee community. We used the overnight minimum air temperature (hereafter, overnight minimum temperature), average WVP, maximum wind speed, and overnight total rainfall.

Model 2(*overnight model*) : *Response variable* $\sim$ *overnight minimum temperature* + *Overnight total rainfall* + *Overnight average WVP* + *Overnight average wind speed* + *age* $-$ *sex*

We applied the same model structure to all response categories- nest structure, insulation, and nesting tree characteristics, except for nesting site selection. For the models of Insulation index, we fitted a separate model to assess the effect of nest structure on nest insulation. Here, we used the insulation index as the response variable and the nest length, nest width, thickness, and depth as predictor variables. The intercept was centred on the observed mean of the insulation index (Normal[μ, 0.5]), slopes for standardised predictors followed a Normal prior (0, 0.3), and the residual standard deviation had an Exponential(2) prior. Here, we also kept age-sex category as a categorical predictor in the models.

Insulation Index $\sim$ *Nest Length* + *Nest Width* + *Thickness* + *Depth* + *age* $-$ *sex*

Previous studies have demonstrated that feeding trees can influence the selection of chimpanzee nesting sites across different habitats.[83–87] Therefore, for elevation and slope, two topographic variables, we included an additional predictor: the distance from the nesting site to the feeding tree that was the last to be used the prior day (hereafter referred to as DFLFT in the models and tables), along with the weather variables. This variable was incorporated into both the nesting-time and the overnight model. We did not use the age-sex categories as a control variable in these models.

Nesting-time model: *Response variable* (*Slope value* /*elevation*) $\sim$ *Nesting* $-$ *time temperature* + *Nesting* $-$ *time WVP* + *Nesting* $-$ *time wind speed* + *Nesting* $-$ *time rainfall* + *DFLFT*

Overnight model: *Response variable* (*Slope value* /*elevation*) $\sim$ *Overnight minimum temperature* + *Overnight average WVP* + *Overnight wind speed* + *Overnight total rainfall* + *DFLFT*

To examine how weather variables might modulate the selection of hill-slope direction for a nesting site by chimpanzees, we fitted Bayesian multinomial logistic regression models using the brms package in R. Nest direction (categorical: E, N, S, W) was used as the response variable. A Bayesian framework was used to flexibly model this multi-level categorical outcome and to obtain probabilistic

parameter estimates while incorporating weakly informative priors to regularise estimates. We specified two separate models: one incorporating nesting-time weather predictors and another using overnight predictors. Weakly informative priors were placed on all parameters, with Normal(0, 1) priors for slopes and Normal(0, 2) priors for intercepts. In both models, East was used as the reference category.

We conducted regression analyses using Bayesian generalised linear models in R with the brms package[88] running on the Stan backend (v2.8.0,[89]). For continuous responses, we used a Gaussian likelihood with an identity link; for proportion outcomes bounded in (0, 1), we used a Beta likelihood with a logit link. Nest coverage (recorded as percentages) was rescaled to proportions and adjusted to lie strictly within the open unit interval (0,1) following Smithson and Verkuilen,[90] ensuring suitability for beta regression. Models were fitted with four Markov chain Monte Carlo (MCMC) chains (4,000 iterations per chain, including 2,000 warm-ups), yielding 8,000 post-warm-up draws. We used weakly informative priors to regularise parameter estimates while remaining consistent with the scale of our data (Data S1H). MCMC accuracy was assessed using visual diagnostics (trace plots, chain-wise posterior density overlays, and MCMC autocorrelation plots) and by verifying convergence statistics, including the rank-normalised split $\widehat{R}$ (≤ 1.01) and large bulk and tail effective sample sizes (ESS[91]). We compared the relative fit of the nesting-time and overnight Bayesian GLMs using approximate leave-one-out cross-validation (LOO-CV), quantified by the leave-one-out information criterion (LOOIC) computed with the loo() function in the loo package.[92] For each model, we assessed explanatory power using Bayesian R^2 with 95% credible intervals.[93] As the models included only fixed effects, the reported R^2 values represent the marginal R^2, indicating the variance explained by the fixed predictors (Data S1C).

Analysing nesting site and baseline weather

To evaluate differences in weather conditions between the baseline and the nesting sites for each nesting night, we compared the overnight minimum temperature, average water vapour pressure, maximum wind speed, and total rainfall. Because the paired differences for all of the variables deviated significantly from normality (Shapiro-Wilk tests: average temperature $W = 0.773$, $p < 0.0001$; water vapor pressure $W = 0.957$, $p = 0.0016$; wind speed $W = 0.797$, $p < 0.0001$; rainfall $W = 0.764$, $p < 0.0001$), we applied non-parametric Wilcoxon signed-rank tests using the Wilcox test function from the stats package.

Identification of outliers

We investigated the relationship between nesting-time weather variables and those recorded overnight by fitting simple linear regression models for each variable pair: temperature (nesting-time vs overnight minimum), water vapour pressure (nesting-time vs overnight average), wind speed (nesting-time vs overnight peak), and rainfall (nesting-time vs overnight total). For each regression model, we extracted fitted values and residuals using the broom package. Standardised (studentized) residuals were calculated to allow direct comparison across models, as they account for differences in residual variance. Observations with standardised residuals greater than 2 were classified as outliers, a threshold that is commonly used to identify extreme values in regression diagnostics.[94] Outlier observations were identified and exported together with the corresponding nights on which they occurred. To visualise the relationships and the influence of potential outliers, we created scatterplots with fitted regression lines and 95% confidence intervals for each weather variable pair (Figure S1).