



## OPEN Influence of season, sex, and interspecific interactions on the diel activity patterns of two sympatric African small carnivores

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Animal activity patterns vary seasonally and between species, facilitating species coexistence. In Africa, however, factors affecting the activity of many small carnivores remain poorly understood, especially for congeneric and sympatric species whose similar sizes may lead to interspecific competition. Here, we investigated differences and variations in the activity patterns of two sympatric Viverridae species in a seasonal African landscape. We continuously radio-tracked 15 small-spotted genets (*Genetta genetta*) and five Cape genets (*G. tigrina*) over 24-h cycles throughout the year. We analysed the effects of season, sex, and interspecific interactions on circadian rhythms using multi-cosinor regression models. Both species maintained a nocturnal activity pattern year-round, decreasing activity significantly during the cold-dry season. This pattern aligns with the thermoregulatory hypothesis—especially for species with an elongated body like genets—suggesting decreased activity under extreme cold weather conditions to conserve energy. Females in both species were less active than males, possibly due to their smaller home ranges, especially during the cold-dry season. These effects were particularly pronounced in Cape genets, which primarily inhabit riverine forests. Female Cape genets adjusted their activity onset, possibly to minimize encounters with males, mostly during the hot-wet season when caring for their offspring. Small-spotted genets shifted their activity onset and peak in riverine forests—areas of potential contact with Cape genets—compared to areas without Cape genets. Overall, our study underscores the critical role of seasonal environmental changes and interspecific interactions in shaping the activity patterns of two carnivore species within a semi-arid Albany Thicket landscape.

Understanding the timing of vital behaviours such as foraging and resting in animals, as well as the factors influencing them, is pivotal for deciphering the mechanisms governing species coexistence and survival<sup>1,2</sup>. Animal endogenous circadian rhythms are usually synchronized with the light–dark cycle, with three primary diel activity patterns identified: nocturnal, diurnal, and crepuscular (dusk and dawn hours)<sup>3</sup>. Occasionally, animals exhibit a cathemeral pattern, engaging in both day- and night-time activity<sup>4</sup>. Given the impact of photoperiod on activity patterns, species living far from the equator may exhibit heightened sensitivity to seasonal changes and need to adapt accordingly<sup>3,5</sup>.

Variations in day length throughout the year have indeed been identified as the main factor influencing the onset/offset and peaks of activity in many animals<sup>2,6</sup>. They also reflect seasonal climatic changes, which greatly affect the capacity of small animals with slender bodies to cope with extreme low temperatures (owing to faster heat loss resulting from their higher surface-area-to-volume ratio) and can lead to death<sup>3,7,8</sup>. Sexual differences have also been recognized as a significant driver of diverse activity responses<sup>4,9,10</sup>. For instance, sexual dimorphism may manifest in different activity patterns as a response to seasonal weather changes, with larger males potentially better equipped to handle extreme conditions than smaller females<sup>4,11</sup>. However, species lacking sexual dimorphism may exhibit fewer sex-based effects in seasonal activity variations<sup>4</sup>. Additionally, reproductive status has been implicated in sexual differences in activity, with females reducing activity away from the natal area during the rearing season to protect offspring from predators, harsh conditions, and male

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intruders<sup>10,12</sup>. Conversely, males may intensify territory patrolling, particularly during the breeding season, prioritizing female protection over foraging<sup>10,13</sup>. Furthermore, interactions among animals have been identified as a critical factor influencing activity, with limited resources and the risk of intra-guild predation prompting smaller carnivores to adjust their activity patterns to avoid competition and predation by larger species<sup>14–16</sup>.

Among mammalian carnivores, for example, studies on two sympatric marten species have suggested nocturnal behaviour in the stone marten (*Martes foina*) compared to cathemeral or diurnal behaviour in the pine marten (*M. martes*), when other larger carnivores are present<sup>17</sup>. Gerber and colleagues<sup>18</sup> found that two similar-sized Eupleridae (*Galidia elegans* and *Galidictis fasciata*) in Madagascar showed almost no temporal overlap when living in sympatry, due to an identical generalist diet, forcing them to diverge temporally. Similarly, research on sympatric skunks (*Mephitis* spp.) has highlighted the importance of temporal segregation in resource use, indicating that species may not share foraging and resting sites simultaneously<sup>19</sup>.

Although information exists on the activity patterns of small carnivores (species with a body mass <21.5 kg *sensu* Do Linh San et al.<sup>20</sup>), the specifics of their adaptations and the primary factors influencing their diel activity rhythms in the wild remain poorly understood<sup>21</sup>. Small carnivores have been predominantly studied through laboratory experiments, potentially misrepresenting their natural behaviours<sup>22,23</sup>. Additionally, limited attention has been given to assessing the potential effects of interactions between similar species on their activity patterns<sup>11,24</sup>. These knowledge gaps may be particularly pronounced in sympatric, congeneric small carnivores such as genets (*Genetta* spp.; Viverridae), providing an excellent opportunity to explore these interactions in the wild<sup>24,25</sup>. Whether full or partial temporal activity segregation occurs between sympatric genet species under the influence of a complex African carnivore assemblage remains unknown. Most activity studies on genets have been carried out in Southwestern Europe for the small-spotted genet (*Genetta genetta*)<sup>7,17,26–28</sup>, while a few emanate from central and South Africa for the large-spotted genet *sensu lato* (*G. maculata*)<sup>29–33</sup>. The lack of studies is especially true for the Cape genet (*G. tigrina*), endemic to South Africa, for which only one study was conducted and mostly focused on activity at latrine sites in a coastal area<sup>34</sup>. All studies on genets describe them as strictly nocturnal<sup>29–34</sup>. However, some daytime activity occasionally occurs—as recorded for a young female in Spain<sup>26</sup>, and in some individuals from the large-spotted genet complex (*G. tigrina* and *G. maculata*)<sup>24,29,30</sup>.

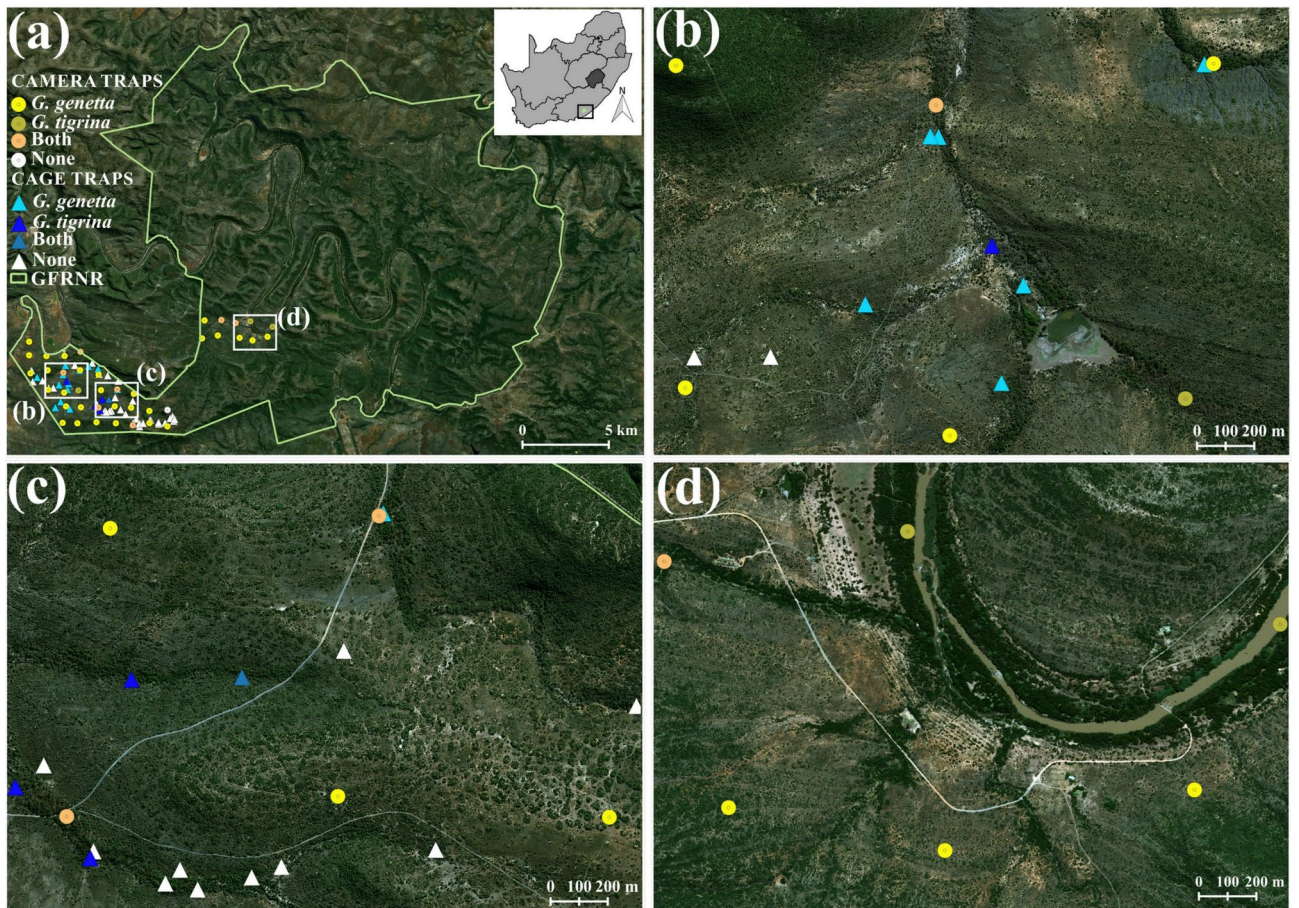
To address the knowledge gap on the temporal ecology of sympatric African small carnivores, we investigated the factors influencing the activity patterns of sympatric small-spotted and Cape genets by radio-tracking wild adult males and females over the annual cycle in an African Albany Thicket landscape. The selected genet species were deemed suitable for investigating activity patterns due to their anticipated responses to the pronounced seasonality of the semi-arid climate in the study area<sup>7,35</sup>. Furthermore, small-spotted genets' distribution is wider (i.e., they are superior exploiters *sensu* Amarasekare<sup>36</sup>), occupying most of the habitats except for open areas<sup>37</sup>, [FC, unpublished data]. In contrast, Cape genets show a patchier distribution in the area and are confined to large riverine forests, where they might compete (i.e., they are superior interferers *sensu* Amarasekare<sup>36</sup>) with the small-spotted genets in contact areas<sup>38</sup>, [FC, unpublished data]. Intensive individual activity monitoring was facilitated through motion-sensor-equipped collars and a car roof antenna for continuous signal reception. This method enabled comprehensive activity monitoring compared to the recent increased use of camera trapping technology, which captures only snapshots of animal activity, potentially missing significant activity periods<sup>39</sup>. Gathering the full activity during tracking sessions provides robust data to be analysed using curve-fitting rhythmometric techniques tailored to trace complex activity waveforms and simultaneously tackle several research questions<sup>40,41</sup>. We also assessed the potential effects of seasons, sex, and interspecific interactions on circadian activity rhythms<sup>6,42</sup>.

In this study, we explored three sets of predictions. (1) Thermal energetic costs in small carnivores with elongated and skinny bodies like genets are high under harsh cold weather<sup>7</sup>. Accordingly, extreme cold temperatures have been described as a limiting factor for genet expansion in Europe<sup>8</sup>. However, small-spotted genets may be more resilient to temperature variations, and cope better with extreme cold weather<sup>25</sup>, compared to Cape genets, which favour milder coastal climates<sup>24,43</sup>. Therefore, we anticipated a more pronounced seasonal response in activity patterns for Cape genets due to weather constraints<sup>7</sup>. (2) Although no significant sexual size differences have been observed for both species<sup>24,35,43</sup>, we predicted longer activity periods for males throughout the year, driven by territorial patrols and mate-seeking behaviours<sup>7,44</sup>. Conversely, females were expected to reduce activity following parturition, concentrating efforts to maximize resource acquisition while minimizing time away from cubs<sup>45,46</sup>. Additionally, competition for resources among males and females of the same species may lead to activity shifts and occasional diurnal behaviours, particularly in territorial carnivores such as viverrids<sup>13</sup>. We anticipated more pronounced differences in Cape genets due to their constrained distribution in the study area. Since female Cape genets select high-quality habitats, their activity bouts to acquire resources are expected to be shorter compared to males, which have larger home ranges to include more females<sup>47</sup>, [FC, unpublished data]. (3) While no species dominance was expected due to their similar sizes, we predicted that Cape genets, with their patchier distribution, may outcompete small-spotted genets in riverine forests, potentially prompting activity adjustments in small-spotted genets to avoid direct confrontations<sup>48,49</sup>. The detailed activity data collected in this study provide valuable insights into the drivers of activity patterns, essential for informing species conservation strategies amidst a contemporary scenario of habitat fragmentation, climate change, and biodiversity loss.

## Methods

### Study area and genet populations

The study was carried out in the southwest part of the Great Fish River Nature Reserve (GFRNR; between 33°04' and 33°09' S and 26°37' and 26°49' E; Fig. 1), a 455 km<sup>2</sup> medium size conservation area located in the Eastern Cape province of South Africa. Data collection occurred during different periods (2005–2007, 2010–2011, 2017–2019), using the same methodologies. The climate is semi-arid, with warm summers (December–



**Fig. 1.** Study area showing: (a) location of the Great Fish River Nature Reserve (GFRNR), South Africa; (b–d) details of different sectors showing the general distribution of small-spotted genets (*Genetta genetta*) and Cape genets (*G. tigrina*) determined from camera-trapping and live-trapping surveys (only traps with captured genets are shown). Maps created using the Free and Open Source QGIS 3.16.0 ‘Hannover’ software (<https://www.qgis.org>).

February) when maximum daily temperatures often exceed 35°C, with a mean monthly maximum of 39.6°C in January. In contrast, minimum night-time temperatures often drop below 0°C in June–August, with a mean monthly minimum of 2.1°C in July<sup>50</sup>. Rainfall is variable, with peaks occurring in October and March. The mean annual rainfall is 435 mm. Hence, in this study, we defined a hot-wet season spanning October to March and a cold-dry season from April to September<sup>51</sup>. The mean (range) day length was 10 h 46 min (9 h 57 min–12 h 23 min) during the cold-dry season, and 13 h 26 min (11 h 44 min–14 h 52 min) during the hot-wet season (data obtained from the National Aeronautics and Space Administration [NASA] database (<https://www.usno.navy.mil/>)). The southern part of the GFRNR is mostly flat, with rolling hills. These topographic features were important for the choice of this area for our study, allowing the radio-tracking of genets, which would have been impossible to undertake in the steep valleys of the northern Great Fish River. The landscape belongs to the Albany Thicket Biome and is dominated by the Great Fish Thicket<sup>50</sup>. In the study area, based on multiyear telemetry and camera-trap data, we found that the small-spotted genet selects areas with medium to high vegetation cover, such as bush clump shrublands and secondary narrow riverine habitats without large trees and avoids only open grassland areas (Fig. 1). The Cape genet shows a more patchy and constrained distribution, relying exclusively on wild and dense *Combretum cafrum* and *Vachellia* (formerly *Acacia*) *karroo* forests along dry riverbeds (Fig. 1), where large hollow trees thrive, and milder temperatures and higher humidity are maintained<sup>38</sup> [FC, unpublished data].

### Animal capture and handling procedures

All capture and animal handling procedures were reviewed and approved by the South African National Health Research Ethics Council (NHREC), by the University of Fort Hare’s Research Ethics Committee (Ethical Clearance Number: DOL001) and by the Eastern Cape Parks and Tourism Agency (Permit Number: RA0259), which is the custodian of the Great Fish River Nature Reserve. All capture and handling procedures were also in accordance with guidelines endorsed by the American Society of Mammalogists<sup>52</sup>.

Trapping was performed throughout the calendar year, except during the hot months of December–February due to logistic constraints and extremely low capture success recorded during the hot season. During this period, genets are less active due to the shorter nights and females avoid being away from their cubs for long periods,

as reported from study areas in southwestern Europe subjected to similar climatic conditions<sup>53</sup>. We used 10 cage traps of 80 × 30 × 30 cm in size (Model AHATSD, Animal Handling Support Systems, Johannesburg, South Africa), set at > 500 m from each other, and baited with sardines in oil, as well as fresh game meat (e.g., common warthog *Phacochoerus africanus* legally eradicated as an alien invasive in the region). Trap groups were spread all over the study area, in potential genet habitats, e.g., forest areas, riparian areas and shrubland areas (Fig. 1), following Galantinho and Mira<sup>54</sup> and Carvalho and colleagues<sup>34,55</sup>. Each trap group remained active for 2 weeks; however, if the resident genet pair (adult male and female) was trapped earlier, the trap group was relocated to another area. Traps were active for 24 h and were checked every morning after sunrise to minimize animal stress after their nocturnal activity period, and to minimize potential observer impact (e.g., leaving human scent next to the trap) while replacing the bait.

Once an animal was captured, we covered the cage trap with a blanket and contacted the veterinarian. Whenever the veterinarian could not come immediately, we took the animal to the veterinary clinic to minimise the time the animal spent in the cage. After being removed from the box, the genets were immobilised by the veterinarian and injected intramuscularly with a mixture of ketamine hydrochloride (ca. 22 mg/kg) and medetomidine (ca. 0.05 mg/kg; Lion Bridge, Pretoria, South Africa), drugs usually used to anaesthetise small carnivores<sup>56</sup>. Animals were weighed, sexed, and checked for sanitary disorders (e.g., parasites). Individuals were classified as juveniles, sub-adults, or adults by analyzing a combination of morphological traits such as tooth wear, body size, sexual development, and overall body condition<sup>57</sup>. Adult genets were equipped with motion-sensor radio-collars (Model M1940B, Advanced Telemetry Systems, Isanti, MN, USA), weighing ≈ 35 g, i.e., from 1.5 to 2.9% of their body mass (1.2–2.3 kg), which is a crucial range of weights for a skilled semi-arboreal small carnivore and considerably less than the guideline weight for mammals (< 5–10%)<sup>52</sup>. After handling, the individuals were released at the capture location once they had fully recovered their reflexes and started moving normally (1–3 h).

### Activity sampling data collection design

The activity signal of each animal was recorded constantly during tracking sessions from a field vehicle, using a telemetry receiver (R-1000, Communication Specialists, Inc., Orange, CA, USA) and an omnidirectional roof antenna (Telonics, Inc., Mesa, AZ, USA). After selecting an animal for sampling, we approached its location by car, maintaining a distance within 300 m to minimise animal disturbance. Activity was then monitored by noting whether the radio-signal was pulsing regularly and with the same intensity (animal resting) or was fluctuating in frequency and/or intensity (animal moving), relying on the motion-sensor integrated in each radio-collar. To ensure that genet movement matched effective activity (travelling/foraging vs. small movements at resting sites), we assessed the animal's position through triangulation every 30 min or more frequently when a large signal variation was detected. Tracking sessions targeted both night- and day-time periods for each animal, with an average (± SD) of 11.5 ± 3.4 h<sup>46</sup>. When two animals shared the same area, both were tracked simultaneously (two receivers and antennas were used). Therefore, we repeatedly sampled different time intervals covering several 24 h cycles per animal. This enabled rhythm components to be summarized across all sampled individuals to obtain an overall assessment of the diel activity rhythms of both genet populations<sup>40</sup>. For our analyses, we divided the 24 h cycle into 5-min intervals ( $n = 288$ ). We considered a 5-min interval as “active” when the animal moved for 4–5 min and “rest” when no movement or only residual movement occurred (< 1 min). This allowed us to increase the resolution of the data compared with other studies that used 15-min or 1-hour intervals<sup>6,42</sup>. In > 90% of the cases, however, genets were either moving or resting during the whole of the 5-min intervals.

### Statistical analysis

The diel activity rhythms of genets were analysed using mixed-effects logistic regression models implemented through the *glmer* function of the ‘lme4’ R package<sup>58</sup>. Because we modelled time as pairs of sine and cosine functions, these models fall into the population-mean multi-cosinor regressions models<sup>6,59</sup>. We then used a multiple parameters approach to incorporate complex ecological time-dependent factors, where perfect sinusoidal waves might not exist, and thus to improve the quality of fit compared to single-cosinor models<sup>41,60</sup>. The lack of independence among tracked animals with specific activity idiosyncrasies was accounted for by specifying each animal and track session as random effects (RE) under the mixed-effects model context<sup>61,62</sup>.

We first analysed circadian activity for each species with all annual data by running a global model incorporating the main periodic components that might affect genets' activity<sup>7,23,35,54</sup>. The global model included the main circadian cycle (CD; 24 h), a hemircadian cycle (HCD; 12 h; to reflect sunrise and sunset periods) and an ultradian period (UD; 6 h; to reflect feeding, marking or territory patrolling behaviours). Prior to the above analyses, four UD periods (2 h, 4 h, 6 h and 8 h) were tested, and the UD period with the lowest Akaike information criterion (AIC)<sup>63</sup> was included in the global model. The models incorporating the circadian cycle plus several period components in the cosine waveforms allow many shapes to be fitted and reflect genets' activity patterns. A general mixed-effect activity model was described as:

$$\log \text{it} (Y_{(t)}) = I + MC + FE + RE = I + \sum_{c=1}^C [\beta_i \cdot \sin\left(\frac{2 \cdot \pi \cdot t}{T}\right) + \gamma_i \cdot \cos\left(\frac{2 \cdot \pi \cdot t}{T}\right)] + FE (\text{season} \mid \text{sex} \mid \text{CG pres}) + RE + \varepsilon_t$$

where  $Y_{(t)}$  is the probability of activity (hereafter referred to activity) at time  $t$ ,  $I$  is the intercept,  $MC$  are the multiple components,  $FE$  are the fixed effects (cold-dry/hot-wet seasons, sex and presence/absence of Cape genets (CG)),  $RE$  are the random effects (collared individuals and tracking sessions),  $C$  is the number of sinusoidal components (here CD, HCD and UD components, thus  $C = 3$ ), and  $T$  is the time (h) of each fitted period (24 h, 12 h and 6 h).

We evaluated the performance of each species model by comparing their AIC with the null model incorporating only the random effects (*RE*). Each waveform obtained was then compared using the midline estimating statistic of rhythm (MESOR), which corresponds to the average value over the period of the waveform. Moreover, we compared each cosine waveform amplitude (*A*), which corresponds to half the difference between the highest and lowest values of the waveforms. Finally, we obtained the acrophases for each cosine waveform component (*C*) that corresponds to the time (h) of the activity peak in each waveform<sup>41,62</sup>. We approximated the time for the acrophases to the 5-min intervals we used to record activity. To assess possible shape differences (peaks, bimodality, short bouts) among species' waveforms, we also compared the amplitudes and acrophases for each harmonic component (CD, HCD and UD). We used bootstrapped analysis to get model parameters with 95% confidence intervals (CI) as an alternative to the delta method since bootstrapping does not assume any particular distribution, and to account for any potential bias due to unbalanced data among species<sup>41</sup>. Overall differences between species were considered significant when 95% CI estimates did not overlap<sup>64</sup>.

Seasonal effects on genets' activity were analysed by fitting three alternative activity *MC* models: one with no seasonal variation in circadian rhythms ( $Y = MC + RE$ ); one accounting for seasonal variations in mean activity but no variations in circadian rhythms ( $Y = Season + MC + RE$ ); and one considering interactions effects on the differences between seasons in circadian rhythms ( $Y = Season * MC + RE$ ), following the work from Pita and Colleagues<sup>6</sup>. Alternative models were then compared through AIC and respective Akaike weights. We then used evidence ratios to quantify model parsimony<sup>63</sup>. Akaike weights were considered as the approximate probabilities that a model is the best compared to the alternative ones, while evidence ratios reflect the log of the odds of the best model over another<sup>63</sup>. The same procedure was used to test for possible seasonal effects of sex and the presence of Cape genets. For factors showing interaction effects, we ran a model for each group (e.g., cold-dry season vs. hot-dry season), and bootstrapped 95% CI of *MC* parameters were estimated to describe and compare the respective waveforms. All models were checked for overdispersion and residual normality (Table S2 and Fig. S1 and Fig. S2)<sup>65</sup>. All modelling analysis were run in the R 3.6.1 software<sup>66</sup>. Bootstrap analyses ( $n = 1000$  simulations) were performed by using *predictInterval* and *add-ci* functions from 'merTools' and 'ciTools' packages<sup>67,68</sup>.

## Results

### Animal trapping and activity sampling efforts

Overall, 19 small-spotted genet individuals were captured 33 times, and six Cape genets were captured 13 times, from a total of 178 small carnivore captures made during the study. Mean ( $\pm$  SE) sampling effort per trap station was  $33.9 \pm 0.8$  trap nights (581 total operative trap nights) in the hot-wet season, and  $123.0 \pm 4.4$  trap nights (690 total operative trap nights) in the cold-dry season. From those genets, we fitted a radio-collar to 18 adult (11 males and 7 females) small-spotted genets and six adult (three males and three females) Cape genets. All the tracked genets appeared healthy. The mean weight of collared small-spotted genets was  $1548 \pm 61$  g, while Cape genets weighed  $1461 \pm 46$  g. All Cape genets were captured at sites where small-spotted genets co-occurred, while 47% of small-spotted genets were captured outside the known places where Cape genets live in the GFRNR. We tracked 82% of all collared small-spotted genets during the cold-dry season and 53% in the hot-wet season. Similarly, we tracked 80% of the radio-tagged Cape genets during the cold-dry season and 67% in the hot-wet season. Unfortunately, we registered one collar failure a few days after a female Cape genet was released and a female small-spotted genet was found dead on a dirt road 2 weeks after release. From the remaining animals tracked for at least 2 months, we recorded four predation events by black-backed jackals (*Canis mesomelas*)—determined by the presence of fresh jackal tracks and scats around the genet remnants—for three male small-spotted genets and one male Cape genet. Lastly, one female small-spotted genet stopped moving in the surroundings of the Great Fish River, outside the reserve, and it was impossible to trace the fate of that animal, or to recover the collar.

Radio-telemetry returned 35,989 activity records (5-min intervals) matching 3000 h, and the mean ( $\pm$  SE) number of activity records per animal was  $1587 \pm 239$  (equivalent to  $132 \pm 20$  h) for small-spotted genets and  $2438 \pm 442$  ( $203 \pm 37$  h) for Cape genets. For the hot-wet season, the mean number of activity records per animal was  $1395 \pm 202$  ( $116 \pm 17$  h) for small-spotted genets and  $1566 \pm 379$  ( $130 \pm 32$  h) for Cape genets. In the cold-dry season, we obtained  $803 \pm 141$  ( $67 \pm 12$  h) activity records for small-spotted genets and  $1185 \pm 253$  activity records ( $99 \pm 21$  h) for Cape genets.

### Annual circadian activity

Annual circadian activity for both genet species determined from multi-cosinor models based on pooled annual data showed clear rhythmicity when compared to the null model with only the random effects (*G. genetta*: AIC = 16234 [best model] vs. 22390 [null model] and *G. tigrina*: AIC = 9379 [best model] vs. 11551 [null model]) (Table S1). Mean activity (MESOR) was higher for Cape genets when compared to small-spotted genets, although the differences were not significant (Table 1). Regarding the global amplitude, it was significantly lower for Cape genets than small-spotted genets (Table 1 and see supplementary Table S3 for the amplitudes and acrophases of each individual periodic parameter). Both species showed similar early night activity peaks (20:30–21:30), but small-spotted genets reduced their activity earlier (Fig. 2). Sunrise-related activity trends were similar for both species, but Cape genets exhibited a higher probability of activity during that period. For the sunset period, both species started activity just before sunset, albeit slightly earlier for Cape genets (see supplementary Fig. S3 for activity boxplots comparing the different diel periods for both species). Cape genets retained some daylight activity during early mornings, while small-spotted genets almost ceased activity (Fig. 2). The beginning of the night was the only period where small-spotted genets were more active than Cape genets (Fig. 2).

| Effects                      | MESOR | 95% CI      | Amplitude | 95% CI      | Acrophase |
|------------------------------|-------|-------------|-----------|-------------|-----------|
| Annual                       |       |             |           |             |           |
| <i>G. genetta</i>            | 0.408 | 0.367–0.449 | 0.481     | 0.476–0.485 | 21:20     |
| <i>G. tigrina</i>            | 0.461 | 0.421–0.501 | 0.439     | 0.429–0.446 | 21:05     |
| Seasonal                     |       |             |           |             |           |
| <i>G. genetta</i> (Cold-dry) | 0.361 | 0.318–0.406 | 0.475     | 0.466–0.483 | 20:35     |
| <i>G. genetta</i> (Hot-wet)  | 0.454 | 0.416–0.494 | 0.493     | 0.492–0.494 | 21:35     |
| <i>G. tigrina</i> (Cold-dry) | 0.410 | 0.358–0.465 | 0.451     | 0.439–0.459 | 19:35     |
| <i>G. tigrina</i> (Hot-wet)  | 0.501 | 0.455–0.547 | 0.468     | 0.464–0.472 | 22:30     |
| Seasonal: sex                |       |             |           |             |           |
| <i>G. genetta</i> (Cold-dry) |       |             |           |             |           |
| Male                         | 0.371 | 0.325–0.421 | 0.462     | 0.450–0.472 | 20:30     |
| Female                       | 0.348 | 0.307–0.391 | 0.487     | 0.480–0.493 | 20:30     |
| <i>G. genetta</i> (Hot-wet)  |       |             |           |             |           |
| Male                         | 0.463 | 0.428–0.501 | 0.495     | 0.494–0.496 | 21:25     |
| Female                       | 0.422 | 0.375–0.473 | 0.490     | 0.489–0.491 | 21:40     |
| <i>G. tigrina</i> (Cold-dry) |       |             |           |             |           |
| Male                         | 0.491 | 0.442–0.541 | 0.484     | 0.476–0.488 | 01:20     |
| Female                       | 0.359 | 0.304–0.416 | 0.454     | 0.443–0.458 | 19:15     |
| <i>G. tigrina</i> (Hot-wet)  |       |             |           |             |           |
| Male                         | 0.534 | 0.481–0.589 | 0.456     | 0.446–0.464 | 22:20     |
| Female                       | 0.452 | 0.412–0.493 | 0.497     | 0.495–0.499 | 01:05     |
| Seasonal: interspecific      |       |             |           |             |           |
| <i>G. genetta</i> (Cold-dry) |       |             |           |             |           |
| <i>G. tigrina</i> absent     | 0.371 | 0.326–0.419 | 0.475     | 0.466–0.483 | 20:20     |
| <i>G. tigrina</i> present    | 0.346 | 0.303–0.391 | 0.476     | 0.464–0.485 | 20:40     |
| <i>G. genetta</i> (Hot-wet)  |       |             |           |             |           |
| <i>G. tigrina</i> absent     | 0.471 | 0.438–0.508 | 0.482     | 0.469–0.491 | 00:25     |
| <i>G. tigrina</i> present    | 0.423 | 0.389–0.458 | 0.496     | 0.494–0.498 | 21:15     |

**Table 1.** MESORs (average value over the period of the waveforms and confidence intervals—CIs), amplitudes (and CIs), and acrophases of diel activity rhythms of both genet species (*Genetta genetta* and *G. tigrina*) radio-tracked at GFRNR, South Africa. Annual, seasonal, seasonal sex and seasonal interspecific effects were estimated from the best mixed-effects multiperiodic logistic regression models.

### Seasonal effects on activity patterns

The model for each genet species, including the interaction between season and rhythm components (*MC*), had much stronger support than alternative models (Table 2 and Table S1). Indeed, small-spotted genets showed significantly higher activity and amplitude during the hot-wet season than in the cold-dry season (Table 1).

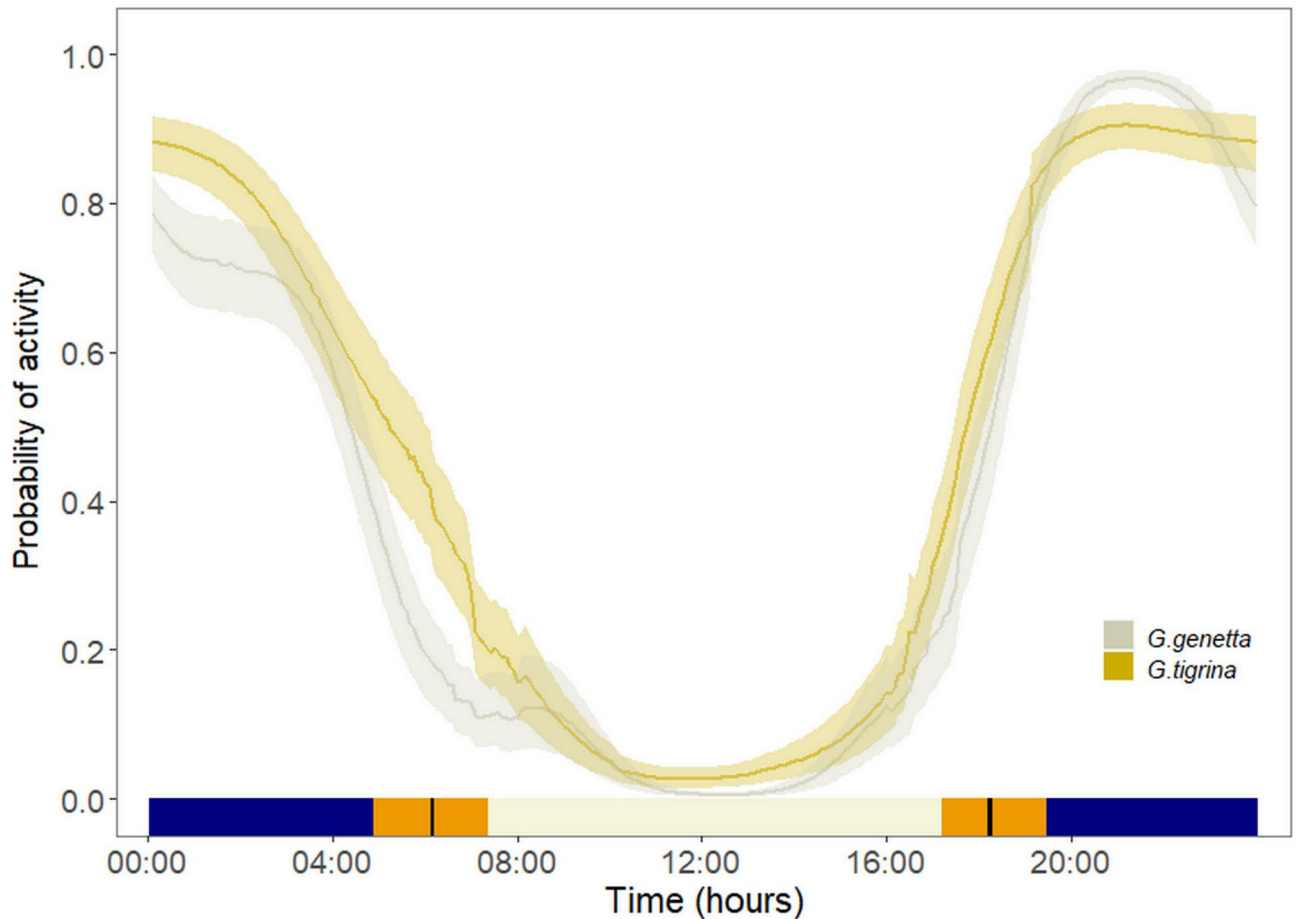
In the hot-wet season, small-spotted genets extended their activity throughout the night with lightly marked bimodal peaks during the early and late-night hours (Fig. 3a; Table S4). They also displayed some diurnal activity just after and before twilight hours. During the cold-dry season, they had high levels of activity at the beginning of the night, reaching a peak in the early hours of the night (20:00–21:00; Fig. 3a), but then decreased considerably till sunrise. In this season, diurnal activity was residual except for the activity start, which occurred before sunset hours (Fig. 3a; Fig. S4a).

Cape genets mean activity was higher in the hot-wet season than in the cold-dry season (Table 1; Fig. 3b and Fig. S4b), although the difference was not significant (95CI%, Table 1). Mean global amplitudes were significantly higher in the hot-wet season than in the cold-dry season (Table 1; see also Table S4). Cape genets in the hot-wet season showed an extended nocturnal activity peak (21:00–03:00) followed by a sharp decrease just before sunrise (Fig. 3b). For the cold-dry season, Cape genets had a short peak of activity in the evening hours (19:30–20:30) followed by a gradual decrease till 04:00 (Fig. 3b). During both seasons diurnal activity was recorded just after sunrise and before sunset, although activity virtually ceased around midday but increased sharply after 16:00 (Fig. 3b). Among species, Cape genets showed a higher average activity in both seasons compared to small-spotted genets, but the opposite pattern was found for the amplitude (Table 1; Fig. 3a and b).

### Sex effects on seasonal activity patterns

The models, including the interaction of sex with the rhythm components (*MC*) for each species, had much stronger support than alternative models for both the cold-dry and hot-wet seasons (Table 3 and Table S1).

Male small-spotted genets were more active on average than females in both seasons, although the differences between the sexes were not significant (Table 1; Fig. 4a, b). However, in the cold-dry season, although the shape of the activity waveform was similar for both sexes, males' activity had significantly lower amplitudes than

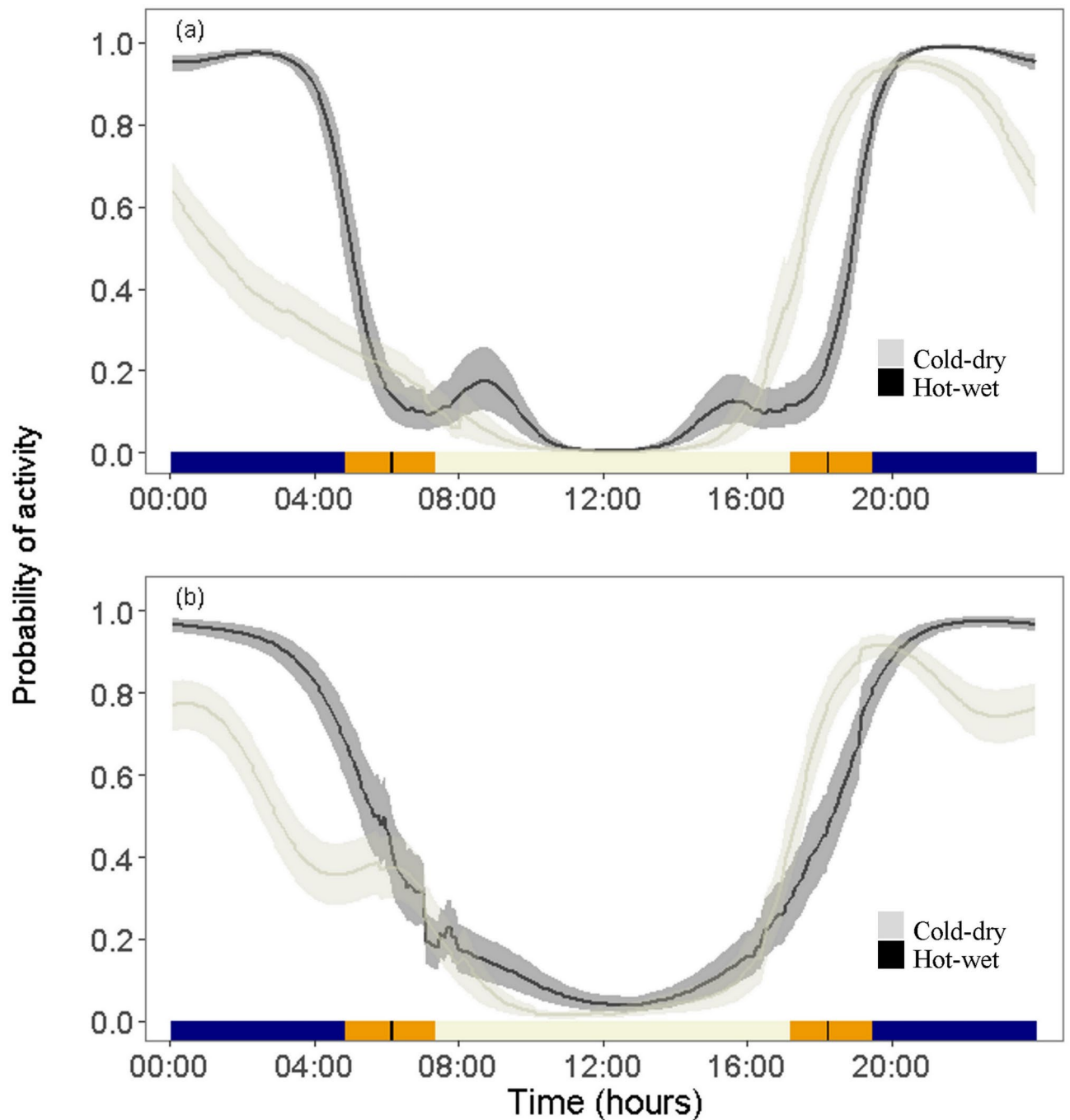


**Fig. 2.** Composite waveforms showing the overall circadian activity rhythms of small-spotted and Cape genets based on pooled annual data, derived from mixed-effects multiperiodic logistic regression models. Error bands are 95% confidence intervals of predicted probability of activity. Bars at the bottom represent night-time (navy), daytime (beige), minimal and maximal timings of sunrise and sunset (orange) and respective means (vertical lines), considering the overall days of activity sampling.

| Candidate models   | No. of components | Small-spotted genets |                |                |      | Cape genets   |                |                |      |
|--------------------|-------------------|----------------------|----------------|----------------|------|---------------|----------------|----------------|------|
|                    |                   | $\Delta$ AICc        | Akaike weights | Evidence ratio | Rank | $\Delta$ AICc | Akaike weights | Evidence ratio | Rank |
| MC + RE            | 9                 | 2360.72              | 0              | $\infty$       | 3    | 616.84        | 0              | $\infty$       | 2    |
| S + MC + RE        | 10                | 2359.64              | 0              | $\infty$       | 2    | 618.76        | 0              | $\infty$       | 3    |
| S $\times$ MC + RE | 16                | 0                    | $\approx 1$    | 1              | 1    | 0             | $\approx 1$    | 1              | 1    |

**Table 2.** Summary results of model selection for both species, comparing alternative models reflecting the effects of season on circadian rhythms of small-spotted and Cape genets. S: season effects; MC: multi-cosinor function; RE: random effects.

females (Table 1; Fig. 4a; Table S5). Both sexes were almost strictly nocturnal showing a clear activity peak at the beginning of the night (20:00–21:00; Fig. 4a; see also Fig. S5a for activity boxplots). After the nocturnal peak, both males and females showed a gradual decrease in activity till the end of the sunrise period. In the cold-dry season, females were slightly more active than males at the beginning of the night when both reached the peak, as well as before and after twilight periods (Fig. 4a). For the hot-wet season, the shape of the activity waveform was significantly higher for males than for females (Table 1; Fig. 4b). Both sexes were mainly nocturnal, except for a small bout of female activity during the morning after sunrise (08:30–09:30, Fig. 4b). Indeed, females were only more active than males in the hot-wet season during daylight hours (Fig. 4b and Fig. S5b). Overall, both sexes in the hot-wet season were highly active during the whole night, but with higher activity levels during the first and last hours of the night (20:45–22:00 and 02:00–03:00; Fig. 4b). During the hot-wet season, sunrise and sunset hours matched the cessation and onset of activity for both sexes, respectively (Fig. 4b).



**Fig. 3.** Composite waveforms, showing the circadian activity rhythms of **(a)** small-spotted and **(b)** Cape genets during the cold-dry and hot-wet seasons, derived from mixed-effects multiperiodic logistic regression models. Error bands are 95% confidence intervals of predicted probability of activity. Bars at the bottom represent night-time (navy), daytime (beige), minimal and maximal timings of sunrise and sunset (orange) and respective means (vertical lines), considering the overall days of activity sampling.

In the cold-dry season, male Cape genets were significantly more active on average and showed a greater amplitude in activity than females (Table 1; Fig. 5a and Table S6). Differences among sexes were also clear in their activity waveforms. Males were highly active throughout the night, reaching the highest peak at 01:30 (Fig. 5a). On the other hand, females were more active at the beginning of the night, reaching a peak at 19:15, followed by a gentle decline in activity and a plateau that lasted till midnight (Fig. 5a). After midnight, females' activity decreased sharply till 04:00. Females had a second small bout of activity around the sunrise hours and stopped moving after that (Fig. 5a). Both sexes ceased activity after 10:00 and started again activity just before sunset (Fig. 5a and see also Fig. S6a for activity boxplots). In the hot-wet season, males were more active than females, but the differences were not significant (Table 1). However, global amplitudes significantly differed among sexes

| Candidate models     | No. of components | Cold-dry season |                |                |      | Hot-wet season |                |                |      |
|----------------------|-------------------|-----------------|----------------|----------------|------|----------------|----------------|----------------|------|
|                      |                   | $\Delta$ AICc   | Akaike weights | Evidence ratio | Rank | $\Delta$ AICc  | Akaike weights | Evidence ratio | Rank |
| Small-spotted genets |                   |                 |                |                |      |                |                |                |      |
| MC + RE              | 9                 | 55.16           | 0              | $\infty$       | 2    | 65.35          | 0              | $\infty$       | 2    |
| SEX + MC + RE        | 10                | 56.86           | 0              | $\infty$       | 3    | 66.73          | 0              | $\infty$       | 3    |
| SEX $\times$ MC + RE | 16                | 0               | 1              | 1              | 1    | 0              | $\approx 1$    | 1              | 1    |
| Cape genets          |                   |                 |                |                |      |                |                |                |      |
| MC + RE              | 9                 | 274.00          | 0              | $\infty$       | 2    | 104.05         | 0              | $\infty$       | 2    |
| SEX + MC + RE        | 10                | 274.71          | 0              | $\infty$       | 3    | 105.73         | 0              | $\infty$       | 3    |
| SEX $\times$ MC + RE | 16                | 0               | $\approx 1$    | 1              | 1    | 0              | $\approx 1$    | 1              | 1    |

**Table 3.** Summary results of model selection for both species, comparing alternative models reflecting the effects of sex on seasonal circadian rhythms of small-spotted and Cape genets. *SEX*: sex effects; *MC*: multi-cosinor function; *RE*: random effects.

(Table 1; Fig. 5b and Table S6). Females in the hot-wet season kept high levels of activity throughout the night, but it decreased sharply before sunrise (Fig. 5b). Males reached a peak of activity before midnight (22:00–23:00). After that, they decreased activity more gently, and kept some levels of diurnal activity until midday. Males also started activity earlier than females in the middle of the afternoon. Females almost ceased activity during the day and started activity before sunset (Fig. 5b and Fig. S6b). When comparing both species and sexes, we found that, in both seasons, male and female Cape genets exhibited higher average activity than male and female small-spotted genets (Table 1). During the cold-dry season, male Cape genets displayed a greater activity amplitude compared to male small-spotted genets, while the opposite was observed for females. In the hot-wet season, these patterns were reversed (Table 1).

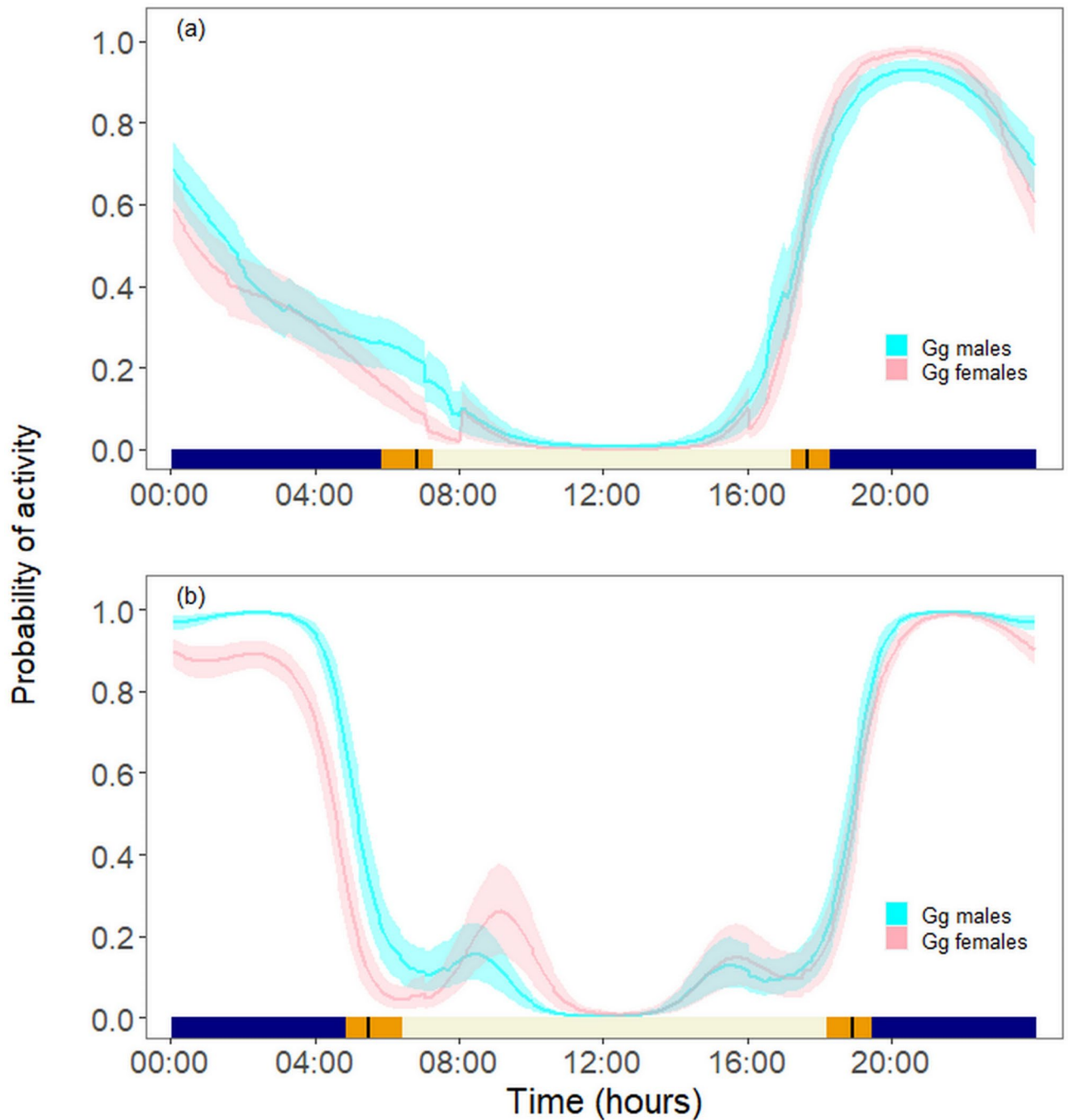
### Interspecific effects on seasonal activity patterns

Cape genets affected small-spotted genets' activity rhythms. Indeed, the best model for both seasons included the interaction between the presence of the Cape genet and the rhythm components of the small-spotted genet (Table 4 and Table S1). During the cold-dry season, small-spotted genets had a similar mean activity and activity pattern independently of the presence of Cape genets (Table 1; Fig. 6a and Fig. S7a). They were highly active at the beginning of the night with a high peak around 20:00–21:00, then progressively decreased activity till sunrise hours (Fig. 6a). In places without Cape genets, small-spotted genets also showed some daily activity bouts just after sunrise and before sunset (Fig. 6a). During the hot-wet season, the mean activity of small-spotted genets in areas where Cape genets co-occurred was lower, although the 95% CI overlapped slightly (Table 1; Fig. 6b and Fig. S7b). When Cape genets were present, small-spotted genets were more active just after sunset and before sunrise (Fig. 6b). During the day, small-spotted genets ceased activity when Cape genets were present but showed small activity bouts during the morning and afternoon, except during the midday hot hours (Fig. 6b). Finally, there were significant differences in the amplitude of all the periodic components between areas with and without Cape genets in the hot-wet season, but only for the 6 h ultradian period (UD) in the cold-dry season (see supplementary Table S7).

### Discussion

Both genet species displayed nocturnal activity consistently throughout the year, exhibiting a distinct seasonal pattern, with reduced activity during the cold-dry season amid harsh weather conditions. Males of both species exhibited higher average activity levels than females, potentially reflecting their larger home ranges<sup>7,9,47</sup>. This effect was more pronounced and significant for Cape genets, which are predominantly confined to dense riverine forests. Female Cape genets adjusted their activity start, likely to avoid encounters with males; this was particularly prominent during the hot-wet season when they were probably caring for cubs<sup>45,46</sup>. Additionally, small-spotted genets avoided encounters with Cape genets in riverine forests, as indicated by shifts in their activity onset and peaks compared to areas without Cape genets.

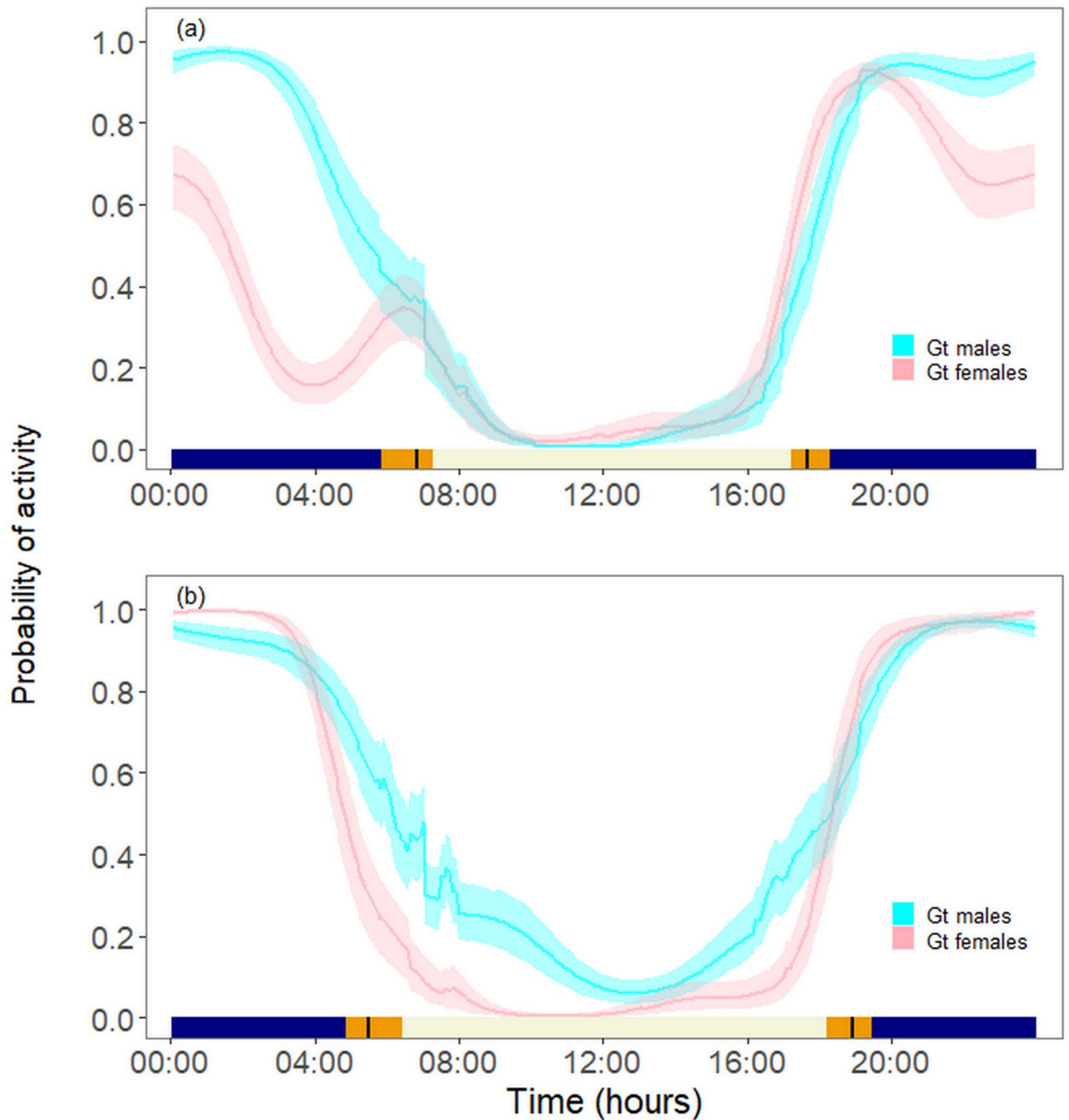
Our work supports the thermoregulatory hypothesis, as both genet species reduced their activity during the cold-dry season (winter months), probably to conserve heat<sup>5,7,8</sup>. This behaviour has been observed for small carnivores like the pine marten<sup>11,12</sup> and the least weasel (*Mustela nivalis*)<sup>69</sup>, as well as for other small mammals such as the red squirrel (*Sciurus vulgaris*)<sup>70</sup>. However, under low temperatures, Cape genets were, on average, more active at dawn and in the early hours of the day (Fig. 3b) than small-spotted genets (Fig. 3a), suggesting an advantage of occupying riverine forests, where more complex vegetation structures buffer extreme temperatures<sup>71,72</sup>. Small-spotted genets' activity peaks usually occurred earlier in the cold-dry season but occurred virtually at the same time as Cape genets during the hot-wet season (Table S2). This shift of activity peaks, especially during harsh cold weather, might allow the local coexistence of these two genet species in our study area<sup>48</sup>. During the hot-wet season, the apparent lack of temporal segregation among genet species might reflect their diet divergence. Indeed, during this period, small-spotted genets prey mostly on arthropods [Plaatjie et al., unpublished data], while Cape genets predominantly prey on small mammals and arthropods (see more details regarding the diet below)<sup>73</sup>. We thus suggest that the main factors driving activity patterns are concurrently thermoregulation and resource availability. Small-spotted genets might obtain resources at a higher cost than Cape genets. In fact, small-spotted genets use a larger area (and different habitats) with scattered resources,



**Fig. 4.** Composite waveforms, showing the circadian activity rhythms of small-spotted genet (Gg) males and females during the (a) cold-dry and (b) the hot-wet seasons, derived from mixed-effects multiperiodic logistic regression models. Error bands are 95% confidence intervals of predicted probability of activity. Bars at the bottom represent night-time (navy), daytime (beige), minimal and maximal timings of sunrise and sunset (orange) and respective means (vertical lines), considering overall days of activity sampled during both the cold-dry and hot-wet seasons.

while Cape genets use riverine forests where food, shelter, and protection against harsh weather are easier to obtain<sup>45,74</sup>. Altogether, our results support that coexistence among genets in riverine contact zones is driven by subtle shifts in the onset of activity, space use or seasonal dietary composition.

Mean activity levels for male small-spotted genets were not significantly higher than that of females during the cold-dry season (Table 1; Fig. 4a, Fig. S5a), contradicting other studies where males were significantly more active than females, reflecting their larger home ranges<sup>10</sup>. In fact, the average home ranges (95% MCP  $\pm$  SD) are larger for males (361.8 ha  $\pm$  165.0,  $n=8$ ) than for females (234.1 ha  $\pm$  87.1,  $n=4$ ) [FC, unpublished data]. Whether larger home ranges result in higher activity levels may not depend solely on the size of the home



**Fig. 5.** Composite waveforms, showing the circadian activity rhythms of Cape genet (Gt) males and females during the (a) cold-dry and (b) hot-wet seasons, derived from mixed-effects multiperiodic logistic regression models. Error bands are 95% confidence intervals of predicted probability of activity. Bars at the bottom represent night-time (navy), daytime (beige), minimal and maximal timings of sunrise and sunset (orange) and respective means (vertical lines), considering overall days of activity sampled during both the cold-dry and hot-wet seasons.

range itself, but rather on factors such as the number and distance between focal areas, as well as environmental conditions (e.g., extreme cold, predation risk) that the animals may face<sup>7,9</sup>. Consequently, during the longer and cooler nights of the cold-dry season, both males and females concentrated their activity during the first hours of the night, when temperatures were milder, as shown in Europe for pine martens and American minks (*Neovison vison*)<sup>11,13</sup>. However, females began activity significantly earlier and had significantly higher activity peaks than males (Fig. 4a and Table S3). Females might avoid confrontations with males when facing harsh conditions and/or to protect their cubs<sup>13,46</sup>. This behaviour was also described for similar-sized carnivores like pine martens, polecats (*Mustela putorius*), and European mink (*Mustela lutreola*)<sup>11–13,47</sup>. The hot-wet season is also the mating

| Candidate models    | No. of components | Cold-dry season |                |                |      | Hot-wet season |                |                |      |
|---------------------|-------------------|-----------------|----------------|----------------|------|----------------|----------------|----------------|------|
|                     |                   | $\Delta$ AICc   | Akaike weights | Evidence ratio | Rank | $\Delta$ AICc  | Akaike weights | Evidence ratio | Rank |
| MC + RE             | 9                 | 177.04          | 0              | $\infty$       | 2    | 406.15         | 0              | $\infty$       | 2    |
| CG + MC + RE        | 10                | 178.89          | 0              | $\infty$       | 3    | 407.03         | 0              | $\infty$       | 3    |
| CG $\times$ MC + RE | 16                | 0               | $\approx 1$    | 1              | 1    | 0              | $\approx 1$    | 1              | 1    |

**Table 4.** Summary results of model selection for both species, comparing alternative models reflecting the effects of the presence of Cape genets on seasonal circadian rhythms of small-spotted genets. CG: Cape genet effects; MC: multi-cosinor function; RE: random effects.

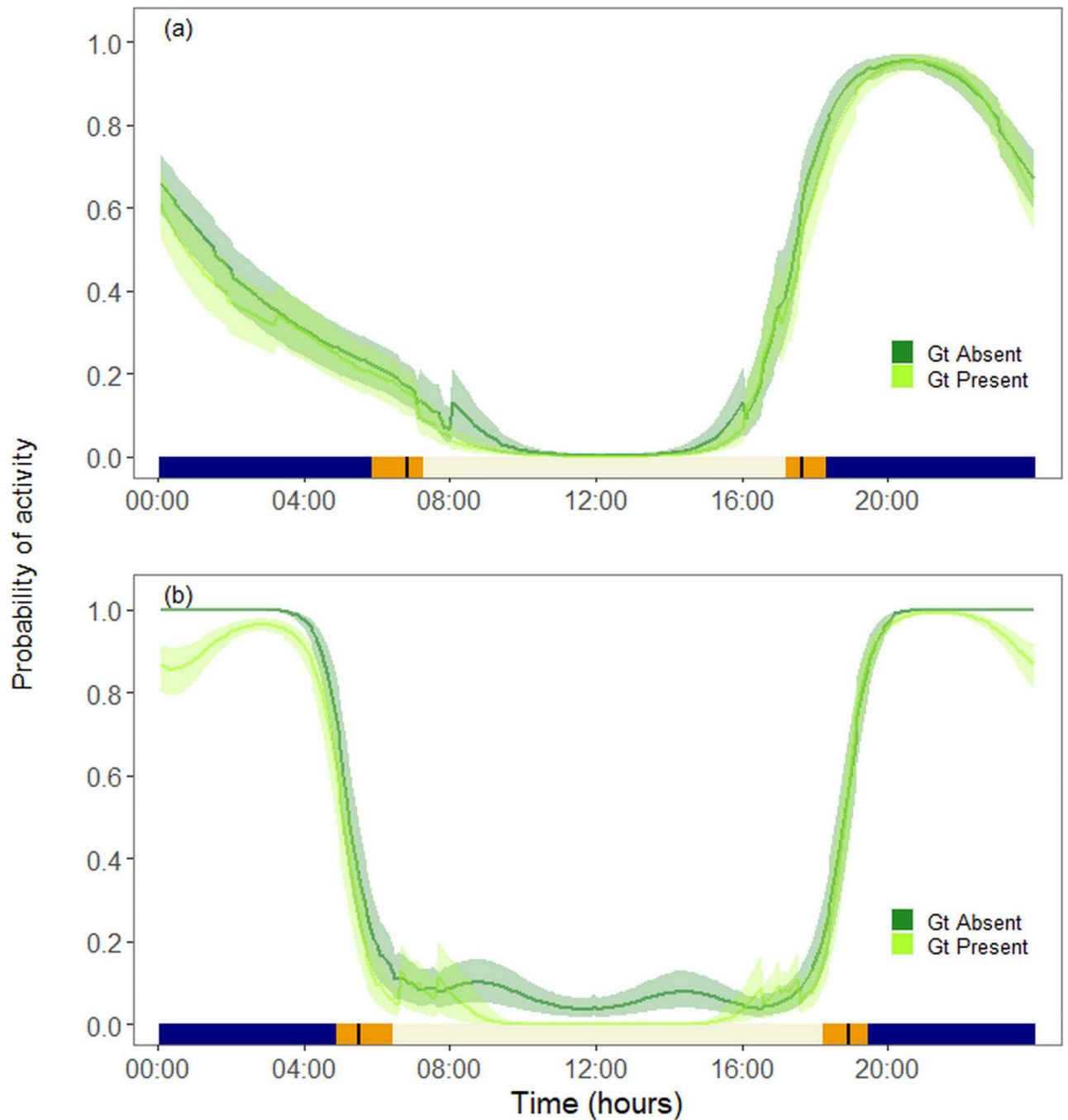
season<sup>25</sup>. Therefore, males may become more active in the hot-wet season (Fig. 4b; Table 3S) to patrol their larger territories and to mate with as many receptive females as possible during the shorter nights<sup>9,10,13</sup>. In turn, females reduce both the number and duration of activity bouts to minimise the time spent away from cubs<sup>10,11</sup>. In the hot-wet season, small-spotted genets, but mostly females, were active during the day for short periods. Diurnal activity in females might reflect the need for extra resources (e.g., high arthropod availability) to feed the cubs and/or to compensate for the shorter night-length and/or to avoid confrontation with males when raising the cubs<sup>13,26</sup>.

Female Cape genets were significantly less active than males during the cold-dry season (Table 1; Fig. 5a). Male Cape genets have much larger average home ranges (95% MCP  $\pm$  SD) (197.2 ha  $\pm$  173.0,  $n = 3$ ) than females (104.7 ha  $\pm$  55.8,  $n = 3$ ) [FC, unpublished data]. Therefore, males need to be active for longer periods to patrol their whole territory, and to find food, shelters, and mates<sup>47</sup>. Female Cape genets also started activity and reached the peak earlier, compared to males (Table 1; Fig. 5a). Again, this might allow females to avoid confrontation with males while foraging<sup>46</sup>. Their smaller home ranges are confined to riverine forests, where resources (prey, resting sites and latrine sites) are abundant and easier to access<sup>35,54,75</sup>. However, the linear nature (corridor) of riverine forests might increase the confluence of competitors—and possible predators—and, accordingly, also potential competition for resources<sup>76</sup>. In the hot-wet season, due to the shorter night length, male Cape genets also engaged in some diurnal activity to access extra resources across their larger territories<sup>77</sup>. Contrary to males, females were not active during the day but maintained higher activity levels throughout the night (Fig. 5b), which seem to match their feeding needs and avoid leaving their cubs unattended for too long<sup>13,26</sup>.

Both male and female Cape genets maintained high average activity levels throughout the cold-dry and hot-wet seasons, compared to male and female small-spotted genets. This might reflect the buffering effects of riverine forests against extreme weather, coupled with the high resource availability, which enables prolonged periods of activity<sup>71,72</sup>. In addition, defending high quality linear habitats, such as riverine forests, is energetically costly, requiring sustained activity levels<sup>74</sup>. In contrast, small-spotted genets, particularly females, struggle to keep constant levels of activity in low quality habitats. This results in longer rest periods and alternating peaks of activity under favourable conditions in harsh weather<sup>7,37</sup>. Alternatively, they may spend less time patrolling lower-quality areas within their larger home ranges<sup>46,47</sup>.

Temporal activity shifts in similar-sized and syntopic species have been reported as a mechanism to avoid confrontation<sup>17,19,48,78</sup>. Indeed, small-spotted genets started and decreased activity at different times in the presence of Cape genets, especially during the hot-wet season (Fig. 6b and Fig. S6b; Table S5). Those temporal shifts may become residual under high energetic costs due to extreme cold weather (Fig. 6a and Fig. S6a)<sup>3</sup>. Small-spotted genets have larger home ranges (superior exploiters) than Cape genets but exploit lower quality habitats<sup>7,36,75</sup>. Thus, small-spotted genets may opt to concentrate their activity in the best habitat patches (e.g., riverine forest) of their home range<sup>3</sup>. In this shared habitat, both species probably compete for resources. In these circumstances, Cape genets, constrained to these habitats, are the superior interferers<sup>19,36</sup>. Superior interferers induce aggressive confrontations to defend the territory (resources) against congeneric species or similar-sized carnivores<sup>13,79</sup>. Additionally, the diets of both genet species overlap considerably in our study area<sup>73</sup>. Thus, diet overlap is a proxy for direct competition and dangerous confrontations<sup>49</sup>. Small mammals are more abundant in the riverine forests, which is Cape genets' main habitat, compared to the other main habitats at the GFRNR<sup>80</sup>. Although Cape genets rely heavily on small mammals throughout the year, arthropods become an important prey during the hot-wet season<sup>73</sup>. Concurrently, small-spotted genets feed mostly on small mammals during the cold-dry season and arthropods during the hot-wet season [Plaatjie et al., unpublished data]. Arthropods are smaller and less nutritious than small mammals. Therefore, small-spotted genets would need to feed for longer periods, including part of the day (Fig. 6b), and their efficiency would increase in areas without direct competitors. In addition, Cape genets face a lower predation risk in riverine forests (intraguild killing)<sup>81,82</sup>, although there might be a higher confluence of predators. In fact, Cape genets' climbing skills allow them to evade predators easily in the presence of trees<sup>77</sup>. During our telemetry study at GFRNR, one Cape genet was killed (at the riverine edge), whereas three small-spotted genets were killed by jackals outside riverine forests, where trees are scarce [FC, unpublished data]. Predation by jackals on genets has been regularly recorded at GFRNR and elsewhere<sup>83,84</sup>. Jackals' predation pressure prevails outside riparian corridors, as they hunt easily in the open and avoid being killed by larger predators such as leopards (*Panthera pardus*) in the riverine areas<sup>85</sup>.

In this paper, we demonstrated that continuous radio-tracking activity data combined with multi-cosinor temporal mixed-model analysis can yield important insights into the activity patterns of two sympatric genets. These insights would be challenging to obtain with sparser activity data gathered by camera traps or sporadic telemetry sessions<sup>39</sup>. Our models enabled us to estimate not only the probability of activity but also its amplitude (rhythms) and time of peaks (acrophase), allowing us to infer the effects of seasonal changes, sexual differences



**Fig. 6.** Composite waveforms, showing the circadian activity rhythms of small-spotted genets during the (a) cold-dry and (b) the hot-wet seasons when Cape genets (Gt) are absent or present, derived from mixed-effects multiperiodic logistic regression models. Error bands are 95% confidence intervals of predicted probability of activity. Bars at the bottom represent night-time (navy), daytime (beige), minimal and maximal timings of sunrise and sunset (orange) and respective means (vertical lines), considering overall days of activity sampling.

and interspecific interactions (Table S2). However, these models require a large quantity of data evenly distributed throughout the 24-h cycle for different individuals and sexes. Consequently, due to our smaller sample for Cape genets, and despite our long-term ecological knowledge of both species' populations, our results need to be interpreted with caution. In the future, increasing the number of individuals and tracking sessions could enhance accuracy. This will become possible by developing lighter, more durable, and affordable GPS collars for small carnivores (< 2 kg)<sup>86</sup>. Furthermore, these models would benefit from incorporating more detailed activity data and weather data (e.g., temperature and precipitation) sampled at the same scale, providing insights into possible seasonal thresholds and the use of microclimate refugia<sup>87</sup>. Unfortunately, to date, detailed and accurate

weather data remain challenging to obtain systematically, particularly at the fine scale, as no weather stations exist near our study area.

Altogether, our results suggest that conserving riverine *Combretum* forests in Albany Thicket landscapes is paramount for the coexistence of both genet species and the survival of the endemic Cape genet. These areas serve as a refuge for Cape genets, buffering harsh weather, providing abundant prey and shelters, and experiencing less predator pressure<sup>19</sup>. Therefore, we recommend maintaining the structural complexity of these habitats, especially when crossing a matrix of open habitat<sup>55</sup>. Additionally, management in more open habitats should maintain patches of trees and bush cover. This approach would enable small-spotted genets to adjust their activity more easily, potentially reducing their dependence on riverine *Combretum* forests and competition with Cape genets. Such conservation efforts are particularly crucial for females of both species, increasing their chances of adjusting their activity and enhancing their survival and that of their offspring.

## Data availability

The datasets used and/or analysed during the current study are available from the corresponding author, on reasonable request as other related papers are also being prepared by the authors.

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## Author contributions

F.C., M.J.S. and E.D.L.S. conceived and planned the study. F.C. planned and coordinated the sampling design and data collection. F.C., E.D.L.S. and A.G. collected the data. F.C. conducted GIS and statistical analyses and wrote the first draft. All authors commented and reviewed the final manuscript.

## Declarations

### Competing interests

The authors declare no competing interests.

## Additional information

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