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Grouping Behaviour and Anti-Predator Responses in the Helmeted Guineafowl *Numida meleagris*

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Simple Summary: This study deals with the role of predator pressure on group formation in the Helmeted Guineafowl, a large sub-Saharan highly social galliform. We focused on a population from South Africa exposed to the frequent chase of both aerial and terrestrial predators, namely, eagles and jackals, recording prey and predator behaviour along with the outcome of predatory encounters. While all attacks were directed to prey aggregates rather than lone individuals, a tendency for chasing groups of a larger size seemingly emerged in jackals. However, unlike aerial predators, these do not seem to induce high fear in guineafowl, eliciting hardly predictable anti-predator responses. This arguably suggests that these galliforms perceive eagles and jackals differently despite the comparable hunting success. While the high predator-induced fear points to a well-established predator–prey system in the case of aerial predators, jackals, mostly carrion eaters, are perceived as a minor threat accounting for the failure in eliciting a well-defined defensive behaviour.

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Abstract: Little is known about landbird group dynamics in response to predation. Here, we describe the interactions between the Helmeted Guineafowl (*Numida meleagris*) and its predators regarding the survival advantages grouping behaviour may provide. Livestream webcam observations were conducted in Madikwe Game Reserve (South Africa) from August 2020 to August 2021. Emphasis was placed on predator–prey interaction and its effect on group size and structure in a spatial framework. We hypothesise that while grouping is crucial for a number of daily activities in this highly social species, it might turn into a higher predatory pressure. We found, indeed, that the probability of attacks by black-backed jackals (*Lupulella mesomelas*) significantly increased with guineafowl group size, unlike what happened with raptors. Moreover, when attacked by jackals, the birds responded by standing close to each other. These results suggest, in line with the proposed hypothesis, that a trade-off occurs between the defensive function of grouping in this galliform and the probability of jackal attack that increases as a function of prey group size. Nevertheless, we argue that Helmeted Guineafowl cooperative social groups also play a role as a defensive strategy against predators, with the many-eyes and dilution effects likely compensating for the higher predatory pressure.

Keywords: antipredator model; collective behaviour; terrestrial and aerial predation; *Lupulella mesomelas*; predator–prey ecology

1. Introduction

Grouping behaviour in birds has traditionally been ascribed to feeding strategies, reproduction, parasite control, thermal benefits and energy saving [1,2]. Nevertheless, over the last decades, there has been growing interest in understanding how anti-predator strategies shape and drive collective behaviour, which contributed to laying the foundation of the many-eyes [3] and the confusion effect [4] hypotheses, among others. In several studies, predation has been primarily considered in ecological terms, with predators limiting the numbers of their prey in a regulated (density-dependent) or unregulated (density-independent) manner [5,6]. More recently, growing attention has been paid to the costs and benefits underlying collective behaviour as a defensive strategy [2,7–10].

Increased protection from predators has been invoked as the rationale behind group formation in several avian predator–prey systems. For example, the Common Redshank (*Tringa totanus*) is known to benefit from the lower risk of Sparrowhawk (*Accipiter nisus*) and Peregrine Falcon (*Falco peregrinus*) attacks by living in larger groups because of the "dilution" effect, increased vigilance (which is a direct consequence of group size) and, possibly, the "confusion" effect [11]. Likewise, significantly higher frequencies of large and dense flocks were found in European Starling (*Sturnus vulgaris*) roosts under high predation pressure [12]. However, although predator presence has been described as a crucial factor behind grouping behaviour as an anti-predator strategy in several animal species [13], other hypotheses suggest that grouping serves other important functions, such as defence against parasites. For example, a specific case of what is generally referred to as the selfish herd effect [14] postulates that individuals on the edges of an aggregation will be less frequently attacked by predators and some parasites. Moreover, grouping behaviour is often associated with thermoregulation and, more specifically, with heat loss reduction, as seen in birds huddling during cold spells [15]. Additionally, foraging in a group could reduce the energetic costs of movement [16] and increase individual feeding rates thanks to the information shared among group members [17] while lessening the time allocated to vigilance [18]. Nevertheless, there is a trade-off between resource intake rate and both vigilance rate and group size, suggesting the occurrence of an optimum number of foraging individuals that maximises individual fitness [19]. Indeed, if constantly harassed by predators while having to compete for food, prey may substantially decrease their feeding rates, with detrimental effects on their fitness [17]. While antipredator strategies seem to be influenced by specific predator traits, it has also been argued that the selection and intensity of antipredator behaviours are also driven by hunting style, such as, for instance, that of aerial or terrestrial predators stalking groups of birds on the ground [20]. Moreover, habitat structure can affect anti-predator behaviour [21]. For example, landscape fragmentation impacts the structure of mixed-species flocks of forest passerines and, hence, both energy management strategies and behavioural responses to predators [22].

Finally, the activities (and the location) of prey when chased may also influence the anti-predator response, whether collective or not [23]. More specifically, vegetation structure and landscape configuration are crucial factors in determining how prey respond to predators. For example, in territories with lush vegetation, small prey like the Rufous-and-White Wren (*Thryophilus rufalbus*) and the Banded Wren (*T. pleurostictus*) rely on acoustic, rather than visual, signals [24]. Yet another experiment on the foraging of granivorous birds evidenced that more food leftovers occurred in the open than under cover, meaning that feeding therein was preferred presumably because it provided an effective anti-predator shield [25]. Moreover, larger group sizes are often associated with increased escape behaviour [26] even if they have little effect on flight initiation distance [27].

However, the grouping behaviour response to predation is still poorly known in landfowl [28,29]. This also applies to the Helmeted Guineafowl (*Numida meleagris*), a widespread Afrotropical galliform that responds overtly to predator attacks by adopting a suite of defensive strategies, including loud alarm calls, fleeing, mobbing and associating with other species in response to predation [30–33]. The Helmeted Guineafowl is territorial and highly sociable, living in close-knit groups of 8 to 15 birds and seasonally joining neighbouring groups into larger units that can sum up to 50 birds [34]. These stable social systems are led by a dominant male initiating the foraging direction and warding off male intruders attempting to enter its territory, wherein cooperative breeding also occurs [35,36].

Such large units break into pairs that disperse over a wide area during the breeding season, when guineafowl remain near their nests on the ground, reluctant to leave the trophic resources (mostly invertebrates) and concealment provided by summer cover [34,35]. However, during winter, when they form large groups, they roost communally in trees [37].

Although social interactions between individuals within these aggregates have been previously investigated [34,35,38], little attention has been paid to the collective response to predation and group formation. Filling this knowledge gap is a management concern because the Helmeted Guineafowl is a valuable game bird in South Africa and neighbouring countries [39]. Noteworthy, this species has recently expanded to anthropised areas—such as the South African inland plateau known as Highveld [37]—which might lack the resources they need to escape predators [37,39]. Moreover, by being large-sized, noisy and mostly foraging in the open, the Helmeted Guineafowl represents a good model for examining the driving forces underlying grouping and anti-predator responses cf. [2,9].

We hypothesise that while grouping behaviour is beneficial for raising keets and finding food [35], it could also increase the risk of predator attacks (cf. [30]). This could, in turn, lead to the establishment of collective defensive mechanisms. This hypothesis will be supported if (i) an increased surveillance of predators occurs in larger groups. However, group formation bears additional costs with prey being detected more easily in larger aggregates; thus, (ii) there should be a threshold beyond which the number of attacks by predators increases with group size [7].

2. Material and Methods

2.1. Study Area

All the data were obtained from videos taken at Tau Waterhole in the 75,000 ha Madikwe Game Reserve (hereafter referred to as Tau; 24 42′33.24 S 26 12′19.17 E: Figure 1), from August 2020 to August 2021. The climate of the study area is characterised by warm summers and moderate to warm winters, with humidity peaking during the rainy months (January to March). In summer (October to March), the dry barren plain—where guineafowl can be observed easily—turns into a green weed patch thanks to the compound effect of nitrates in animal dung and rainfalls (500 mm per year on average). Guineafowl, which form breeding pairs, are hardly seen during this period because of the tall grasses. The study site, covering 6.6 ha, consists of a waterhole, an open plain, roosting trees, a scrub area and dense bush of the resin tree (*Grewia* spp.), acacia thorn tree (*Acacia karoo*), umbrella thorn tree (*A. tortilis*), black thorn tree (*A. mellifera*), camel thorn tree (*A. erioloba*) and sickle bush (*Dichrostachys cinerea*). Local vegetation is classified as Dwaalboom Thornveld [40]. The plain was visited daily by herds of 30 to 100 African bush elephants (*Loxodonta africana*), 20 to 100 African buffalos (*Syncerus caffer*), 10 to 15 greater kudus (*Tragelaphus strepsiceros*), 50 to 100 impalas (*Aepyceros melampus*), 30 to 50 blue wildebeests (*Connochaetes taurinus*), 10 to 30 Burchell's zebras (*Equus burchelli*) and giraffes (*Giraffa giraffa*). Chacma baboons (*Papio comatus*) and carnivores such as African lions (*Panthera leo*), spotted hyenas (*Crocuta crocuta*) and black-backed jackals (*Lupulella mesomelas*) also roam the plain.

2.2. Livestream Camera Observations

This work relies on the recordings obtained through a stationary DS-2DF8236IX-AELW livestream webcam (Hikvision Digital Technology Co. Ltd., Hangzhou, Cina) installed at Tau by AfriCam and operated remotely by volunteers. Audible sounds were recorded through HD 435 headphones (Sennheiser electronic SE & Co. KG, Wedemark-Wennebostel, Germany) plugged into an Pavilion computer (HP Inc., Palo Alto, CA, USA) fitted with a Bang and Olufsen (B&O) sound system. These devices had been previously used to observe guineafowl drinking at the waterhole, where they primarily formed guilds with impalas and blue wildebeest [41], between 7:00 and 10:00 as well as between 16:00 and 18:00. The webcam scanned the entire plain and neighbouring scrub from left to right and back again with 5-min sweeps nine times daily from 6:00 to 19:00. If a sweep was unsatisfactory (for instance, when the camera was not rolling correctly or when the inclement weather caused temporary interference leading to a blurry optic), we logged in again to find a suitable sweep from which it was possible to obtain clear images.

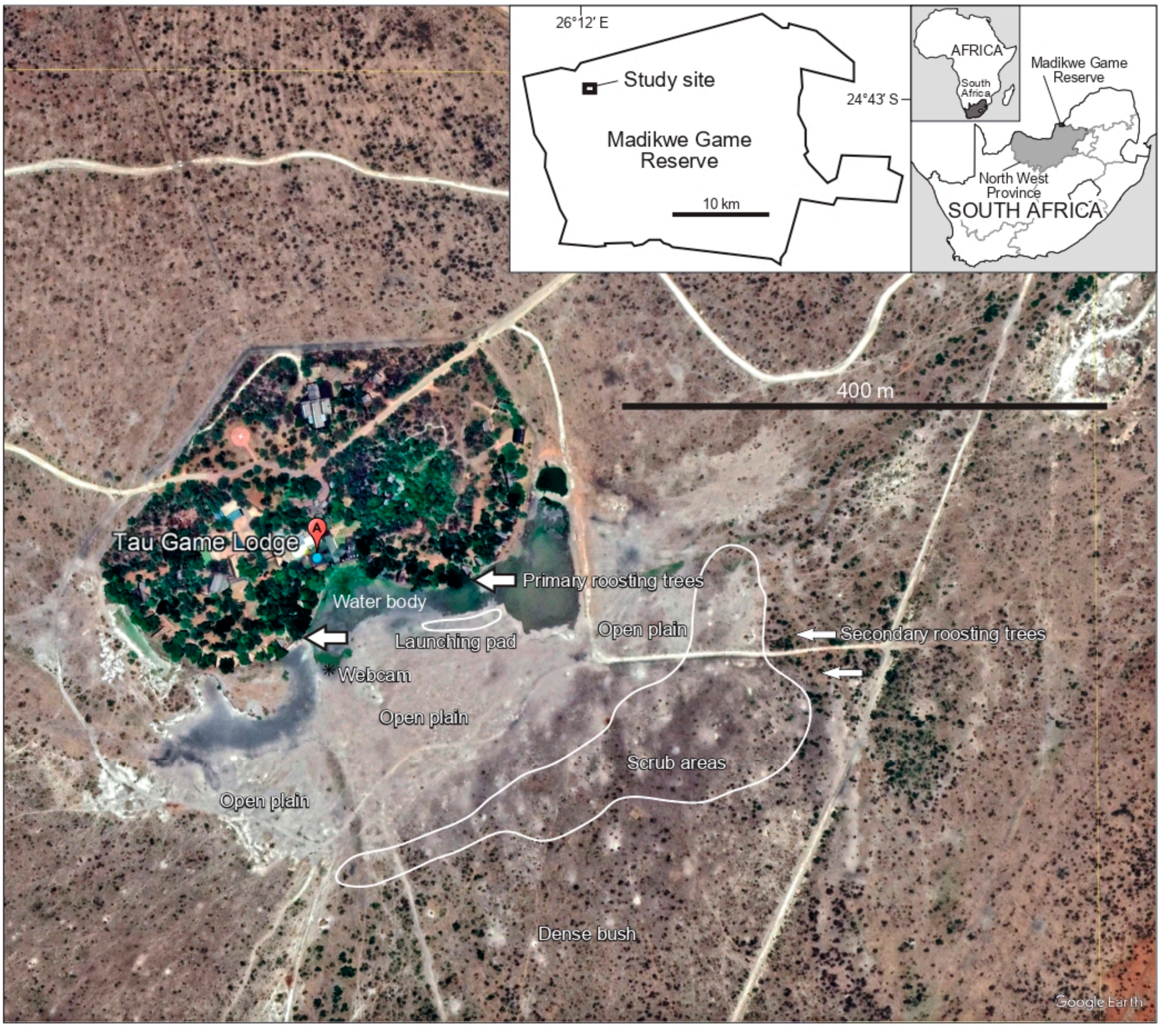

Figure 1. Aerial footage of the study area showing different habitat features: water body (2.5 ha), open plain (ca. 3 ha) and scrub (ca. 2.5 ha). The launching pad was situated where all the groups converged to fly up into the primary roosting trees. The insets at the top right corner show a map of the study area and the position of Madikwe Game Reserve in South Africa.

Out of the overall number of guineafowl group recordings obtained from August 2020 to August 2021 (see Results; for clarity, the core data about grouping behaviour and predation were obtained from April to August 2021, while measures for social distance were obtained across the entire study period), suitable (i.e., images not blurry with easily countable individuals) sub-samples were selected to conduct downstream statistical analyses. Different groups generally remained from 50 m to 200 m apart, with the camera usually spotting several of them during the five 5-min sweeps. In the afternoons, these distinct social units commingle to the open plain from three directions (which led us to assume we were dealing with at least three different groups). When the birds gathered for communal roosting, they also arrived from different directions, allowing us to distinguish these social units. Group size and location were recorded daily. The guineafowl were easily observable on the plain and in the scrub further away from the water during the dry winter. For clarity, we could accurately determine group sizes in the scrub as the camera captured all the birds at once, momentarily moving to less vegetated areas.

Predator approaches by jackals and raptors were recorded during the scans along with guineafowl response behaviours. More specifically, the camera was brought to a standstill by the remote controller to capture the scene when a predator-prey interaction was about to occur. This extra time was added to the standardised 5-min calculation sweeps. Suitable photos were selected to determine the social distance (SoD) in groups. The following data were recorded in a matrix for each SoD calculated (see below): date, time of day, number of birds, guineafowl scale (i.e., the broadside bird length in mm), location in the study area and number of birds in a straight line perpendicular to the viewing direction. In this case, we used a vernier calliper to measure group spread (i.e., the distance between two proximal guineafowl on either side of a straight line, as seen in mm on the computer screen). For drinking birds, the scale referred to the (frontal) breadth of the birds. In this case, SoD was determined between birds standing side by side.

To study predator surveillance behaviour, the head-up postures adopted by members of guineafowl groups were photographed from April to August 2021 [42]. An independent Pentax K-5 camera with a Sigma EX 10 to 20 mm wide-angle lens was used to take and download photographs via the computer screen. For this purpose, a random group was sampled in the scrub, on the open plain, during a huddle (i.e., a tight-knit group forming during cold spells or under a predator chase) and when drinking water. Every 2 s, a photograph was taken. Although screenshots would have also been possible, the camera automatically supplied a 2 s interval between images for consistency. For each sampling effort, 30 photographs were taken in 60 s (i.e., when a group was generally visible during a sweep). All the data were used to convert the head-up postures to percentages.

2.3. Statistical Methods

Kruskal–Wallis tests were used to determine differences in (i) group size during different times of the day; (ii) SoD in different habitats/activities; (iii) SoD during different feeding times; (iv) roosting group sizes during winter months and (v) time needed for a group to ascend a communal roosting tree (from the first to the last bird in the group) with time needed to descend from it in the morning. We focused on (iv) and (v) because grouping behaviour at roost and roost departure time are known as anti-predator responses in other species [43,44]. We conducted Dunn's post hoc tests to assess significant pairwise differences based on the overall significance indicated by Kruskal–Wallis H statistics. Since group size is also driven by time of day, and different habitat features are used depending on it, we carried out a generalised linear model fitted with a Poisson residual distribution and log linking function that had group size as the response variable, habitat feature as the factor predictor and time of the day as the continuous predictor to account for possible confounding effects. We also used a likelihood ratio test to analyse a multinomial model with predatory event (i.e., jackal, raptor, no predator) as the response variable and group size, month and time of the day as the predictors.

Surveillance behaviour was measured in terms of head-up counts per group, which were converted to percentages for comparison among groups engaging in different activities (i.e., during drinking or huddling) and across different locations in the study area (i.e., scrub vs. open plain) by chi-square tests: https://www.socscistatistics.com/tests/kruskal/default.aspx (accessed on 15 August 2024). Spearman rank correlation (Statistics Kingdom.com (accessed on 15 August 2024) was used to correlate jackals/hour vs. mean sizes of groups stalked by jackals. The number of guineafowl groups in different time slots of the day was also compared using chi-square tests. The SoD between individuals was calculated using the following algorithm:

$$\{[((s/\text{scale}) \times \text{constant}) - (f \times \text{constant})]/(f - 1)\} = \text{SoD},$$

where "s" is the spread of the birds standing in a straight line; "scale" is the size of one or more representative guineafowl in the line determined by measuring the broadside size or the frontal breadth of the bird(s) (with the average being calculated in the case of the measuring more than one bird); "constant" is either 0.350 m, corresponding to the average broadside size of a live guineafowl, or 0.175 m, in the case of drinking birds (i.e., the frontal breadth of the birds); and"f-1" is the number of birds in a straight line minus 1, because the focus was on the average distance between birds in the group.

3. Results

In total, we obtained 586 video recordings of guineafowl groups (mean size = 34.07; range = 2–200; SD = 34.57) over the entire study period. The number of recordings selected for each theme that was analysed is given in Table S1, and livestream camera observation times are given in Table S2.

3.1. Spatiotemporal Group Size Dynamics

Average group sizes were minimal from November to February (mean = 2.5, range = 2–5, SD = 1, n = 13) during the breeding season, during summer when very few birds could be spotted. During winter, group dynamics changed monthly and daily, being maximal in midwinter late afternoons and evenings (Figure 2). During the day, the webcam clearly showed how the birds descended from their roost as a relatively large collective group, breaking down into smaller ones, with the opposite behaviour occurring during the late afternoon when they were about to roost again (Figure 2). The difference in mean group size between morning (9:00) and afternoons (16:00 to 18:00) was statistically significant ($p < 0.01$; Table 1).

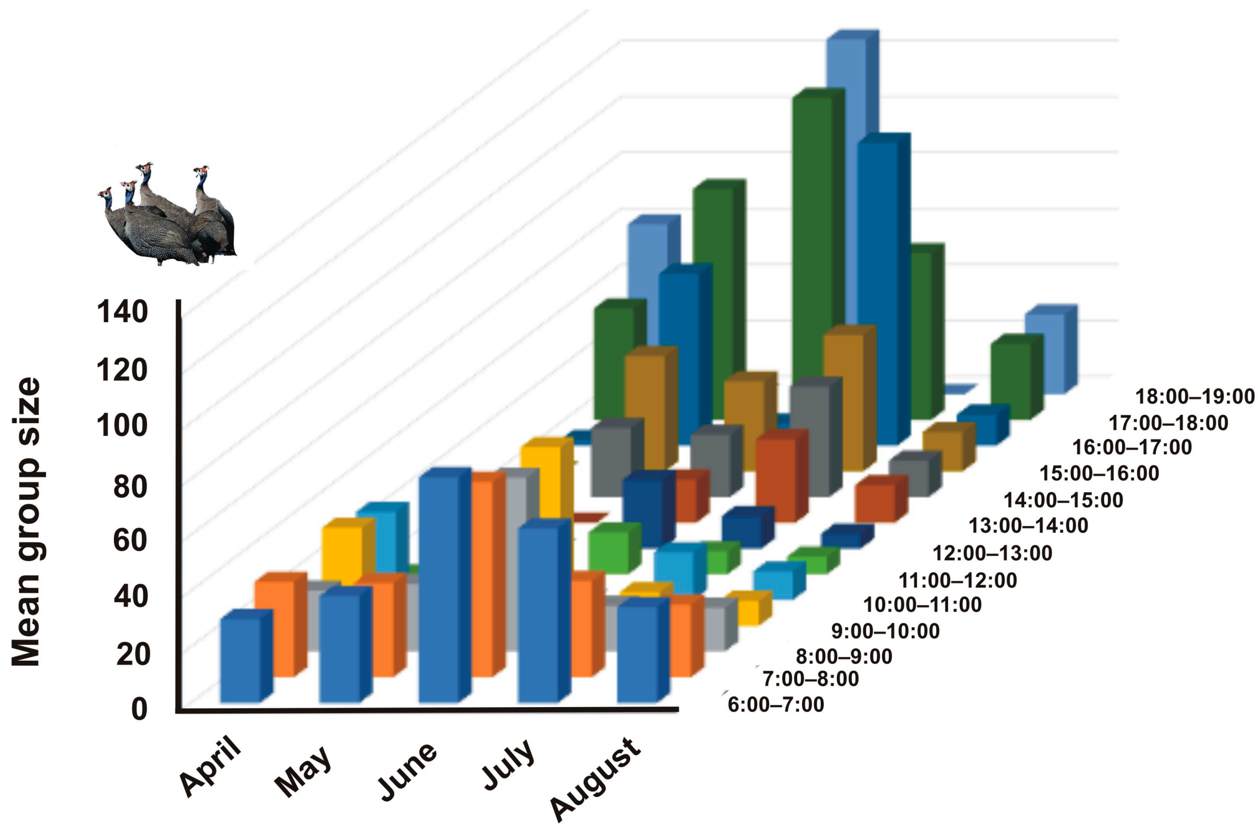

Figure 2. Temporal illustration of group dynamics of the Helmeted Guineafowl population under study across months (1st dimension) and daytime (2nd dimension) during winter (Guineafowl photo credit: John Beckworth, Macaulay Library in the Cornell Lab of Ornithology 192389531).

Table 1. Descriptive statistics and Kruskal–Wallis tests comparing group sizes during different times of the day. The H statistic = 25.41 ($p = 1.23 \times 10^{-5}$). A Dunn's post hoc test is included to show differences between pairs (p-value = 0.008 after Bonferroni correction). IQR: interquartile.

IQR	Sample	Median	Mean Group Size	Time
6	18	6	15.61	7:00
7	39	10	6.35	9:00
20	67	15	12.08	16:00
20	50	15	20.16	18:00
***p*-Value**	**Critical Value**	**Z**	**Mean Rank Difference**	**Pair**
0.0264	27.9644	2.2203	31.6795	7:00 vs. 9:00
0.9669	26.0538	0.04154	−0.5522	7:00 vs. 16:00
0.1063	26.9755	1.6152	−22.23	7:00 vs. 18:00
0.001393	19.766	3.196	−32.2317	9:00 vs. 16:00
4.66×10^{-7}	20.9659	5.0396	−53.9095	9:00 vs. 18:00
0.02052	18.3403	2.3166	−21.6778	16:00 vs. 18:00

3.2. Group Sizes on the Plain and in the Scrub

One or two hours after descending from their roost onto the plain early in the morning, most guineafowl were invariably dispersed in the scrub. The group sizes in both locations were determined simultaneously during camera sweeps. In the afternoons, most birds resorted to the open plain for feeding. Noteworthy, the effect of time of the day on group size was not significant ($z = -0.52$, $p = 0.604$) as opposed to habitat feature ($z = -44.84$, $p < 0.001$), with significantly larger groups being observed in the open (mean size = 41.21, range = 2–200, SD = 37.14, n = 432) than in the scrub (mean size = 14.03, range = 2–60, SD = 11.65, n = 154).

3.3. Social Distance

The mean SoD between group members was minimal when they stood shoulder to shoulder while drinking water (0.071 m). The SoD was even smaller (0.034 m) when guineafowl huddled together after being attacked by a jackal and just before or after roosting. A larger mean SoD (0.835 m) was calculated for birds foraging on the open plain than for those feeding in the scrub (0.279 m). The SoD was significantly higher in birds feeding in the open plain relative to those engaging in all other activities elsewhere in the study area ($p \leq 0.01$; Table 2). Likewise, the mean SoD was significantly higher in the afternoon than in the morning ($p \leq 0.02$) and even in the late afternoon compared with the early afternoon ($p = 0.004$; Table 3).

Table 2. Descriptive statistics and Kruskal–Wallis tests comparing guineafowl social distances across different locations in the study site and when engaging in different activities. H statistic = 31.3662 ($p = 7.1 \times 10^{-5}$). A Dunn's post hoc test is included to show differences between locations/activities (p-value 0.008 after Bonferroni correction). IQR: interquartile. SoD: social distance.

IQR	Sample	Median	Mean SoD	Activity or Location
0.76	249	0.6312	0.835	Plain
0.3029	144	0.4257	0.274	Scrub
0.3367	8	0.4329	0.034	Huddling
0.1598	10	0.4003	0.071	Drinking
***p*-Value**	**Critical Value**	**Z**	**Mean Rank Difference**	**Pair**
1.239×10^{-6}	25.2673	4.8492	62.5149	Plain vs. scrub
0.01278	70.62	2.4899	89.7149	Plain vs. huddling
0.01658	63.4098	2.3959	77.5149	Plain vs. drink
0.4646	72.905	0.7312	27.2	Scrub vs. huddling
0.6557	65.945	0.4458	15	Scrub vs. drink
0.7976	93.2604	0.2564	−12.2	Huddling vs. drink

Table 3. Descriptive statistics and Kruskal–Wallis tests comparing larger guineafowl social distances when feeding actively in the afternoons. H statistic = 24.104 (p = 0.0196). A Dunn's post hoc test is added to show differences between locations/activities (p-value = 0.004 after Bonferroni correction). IQR: interquartile. SoD: social distance.

IQR	Sample	Median	Mean SoD	Time
0.375	20	0.095	0.302	6:00–6:59
0.453	44	0.175	0.233	7:00–7:59
0.621	53	0.184	0.382	8:00–8:59
0.771	21	0.109	0.614	9:00–9:59
1.284	10	0.935	0.653	10:00–10:59
1.082	5	0.316	0.316	11:00–11:59
0.84	9	0.438	0.408	12:00–12:59
0.682	8	0.196	0.546	13:00–13:59
0.855	14	0.635	1.09	14:00–14:59
1.02	42	0.357	0.889	15:00–15:59
0.977	72	2	0.806	16:00–16:59
0.888	80	0.163	0.806	17:00–17:59
0.734	20	0.194	0.439	18:00–18:59
***p*-Value**	**Critical Value**	**Z**	**Mean Rank Difference**	**Pair**
0.0922	107.665	1.684	−53.116	6:00–6:59 vs. 8:00–8:59
0.205	126.767	1.267	−47.052	6:00–6:59 vs. 9:00–9:59
0.0317	155.655	2.148	−97.961	6:00–6:59 vs. 10:00–10:59
0.0092	140.636	2.604	−107.290	6:00–6:59 vs. 14:00–14:59
0.004	111.182	2.913	−94.861	6:00–6:59 vs. 15:00–15:59
0.001	103.860	3.360	−102.210	6:00–6:59 vs. 16:00–16:59
0.0416	102.840	2.038	−61.398	6:00–6:59 vs. 17:00–17:59
0.137	126.767	1.486	−55.194	6:00–6:59 vs. 18:00–18:59
0.381	80	0.876	−20.533	7:00–7:59 vs. 8:00–8:59
0.0347	120.775	2.112	−74.706	7:00–7:59 vs. 14:00–14:59
0.0121	84.674	2.511	−62.278	7:00–7:59 vs. 15:00–15:59
0.001	74.799	3.178	−69.627	7:00–7:59 vs. 16:00–16:59
0.180	73.377	1.341	−28.815	7:00–7:59 vs. 17:00–17:59

3.4. Roosting Behaviour

From March to August 2021, the guineafowl groups on the plain were found to roost communally in a single clump of trees, with most birds roosting in three or four adjacent sweet thorn trees opposite the waterhole (40 m across; from tree to launching pad; see Figure 1). The average roosting group size, which was relatively smaller in March, increased in June and July but then tapered off as smaller units moved to secondary roosts elsewhere during wintertime when the amount of residual tree foliage diminished. Accordingly, the mean group size in April (47.5) was significantly smaller than in June (109.2) and July (91.31), shrinking significantly again in August (53.37) (Table 4).

Table 4. Descriptive statistics and Kruskal–Wallis tests comparing roosting group sizes during winter. H statistic = 21.631 ($p = 6.15 \times 10^{-4}$). A Dunn's post hoc test is added to show differences between months (p-value = 0.003 after Bonferroni correction). IQR: interquartile. SoD: social distance.

IQR	Sample	Median	Mean SoD	Activity or Location
0.76	249	0.631	0.835	Plain
0.303	144	0.426	0.274	Scrub
0.337	8	0.433	0.034	Huddling
0.16	10	0.4	0.071	Drinking
***p*-Value**	**Critical Value**	**Z**	**Mean Rank Difference**	**Pair**
1.24×10^{-6}	25.267	4.849	62.515	Plain vs. scrub
0.0128	70.62	2.49	89.715	Plain vs. huddling

Table 4. *Cont.*

p-Value	Critical Value	Z	Mean Rank Difference	Pair
0.0166	63.41	2.396	77.515	Plain vs. drink
0.465	72.905	0.731	27.2	Scrub vs. huddling
0.656	65.945	0.446	15	Scrub vs. drink
0.798	93.260	0.256	−12.2	Huddling vs. drink
0.706	28.505	0.377	5.479	March–August
0.0517	19.003	1.946	−18.867	April–May
0.001	19.273	3.474	−34.164	April–June
0.006	18.764	2.763	−26.45	April–July
0.597	17.52	0.528	−4.721	April–August
0.083	17.298	1.733	−15.2976	May–June
0.374	16.729	0.889	−7.583	May–July
0.070	15.321	1.81	14.146	May–August
0.375	17.035	0.888	7.714	June–July
2.27×10^{-4}	15.654	3.687	29.444	June–August
0.005	15.023	2.835	21.729	July–August

The birds ascended the trees one by one or in small groups of three to four, but when they descended, they did so in groups of twenty to forty per batch. On average, the time between the first and the last bird to fly into the roosting tree from the launching pad (regular ascending patch) in the late afternoon/evening was 8.23 min. Such duration was significantly shorter in the mornings when the birds were found to leave the trees in 2.44 min (H = 49.059, $p < 0.5$, n = 71). The time needed for the group to enter the trees was not correlated with the number of birds roosting together ($R^2 = 0.095 \times 10^{-3}$; $F_{1,38} = 0.006$; $p = 0.952$), nor was the time needed for birds to descend the trees ($R^2 = 0.035$, $F_{1,26}$, $p = 0.341$: Table S3).

3.5. Vigilance Behaviour

The number of suitable photographs selected to count head-up postures was 190, with 3816 birds appearing in the images (Table 5). The least head-up postures were measured in groups located in scrub (5.39%) or on the open plain (1.10%) as opposed to those drinking water (40.21%) or huddling together (45.01%) before roosting in which the highest counts were recorded ($\chi^2 = 185.655$, $df_{1,3}$, $p < 0.001$). No correlation was found between head-up postures and group size ($r_s = -0.011$, $p = 0.91$, n = 101: Table 5). In a few instances (n = 5), the head-up posture in a group was adopted by the same member identified based on its unique helmet shape, but when an alarm call was emitted, several other birds joined it.

Table 5. Descriptive statistics and study periods during which data were obtained from photographs for head-up counts in groups under different conditions. * = no. of groups; SD: standard deviation.

Group Size			Head–Up		No. Birds	No. Photos *	Date	Activity
SD	Range	Mean	%	Counts				
42.92	2–190	36.6	45.01	917	2037	56	May–August 2021	Huddle
32.9	2–190	16.63	40.21	220	547	33	September 2020–August 2021	Drinking
8.28	2–40	8.31	5.39	13	241	29	August 2020–August 2021	Foraging in scrub
12.42	2–55	13.76	1.1	11	991	72	August 2020–August 2021	Foraging in open
			1161		3816	190		Total

3.6. Vocalisations

While foraging, guineafowl invariably emitted a soft contact whistle, sounding like "so we we we" (at about 40 dB), which served to keep group members together while keeping their heads down [45]. When an intruder was detected at a distance, one or two individuals usually emitted a low-intensity alarm call sounding like a medium-loud "chit" (at between 50 and 60 dB) to signal a potential threat [46], with such an occurrence being recorded on 40 different occasions. Finally, a loud (between 70 and 85 dB) "chit chit chiiir" call was emitted by several birds while adopting a high alert posture, with their heads and necks stretched out to signal the presence of a dangerous intruder [46]. This occurred 35 times overall, not only during raptor and jackal chases but also when a lion pride or a baboon troop with a dominant male approached the guineafowl in the scrub in the early morning.

3.7. Jackal-Targeted Guineafowl Groups

On 26 occasions, jackals were observed to attack guineafowl, but only one kill was reported. Roaming jackals were frequently spotted on the plain, in full view of their preys throughout the day (0.874 jackals/hour recorded on average; Figure 3). Photographs showing unique markings on individual jackals (JHvN, unpublished work) suggested that at least five individuals lived permanently in and around the plain during winter. Overall, we observed at least five different hunting strategies by the jackals, each eliciting a different response from the prey (Table 6). On 20 occasions, jackals were seen strolling past or sitting 10 to 15 m away from feeding guineafowl with their heads down. In one case, a jackal chased a bird, which caused the others to fly up and land sequentially across a 100 m straight line. Jackals were more visible on the plain in the early morning and late afternoon (Figure 3). On four occasions, the guineafowl successfully mobbed the approaching jackal by forming a tight group in front of it and making loud noises. Each time, the jackal turned away and left the scene after approximately ten minutes (Table 6).

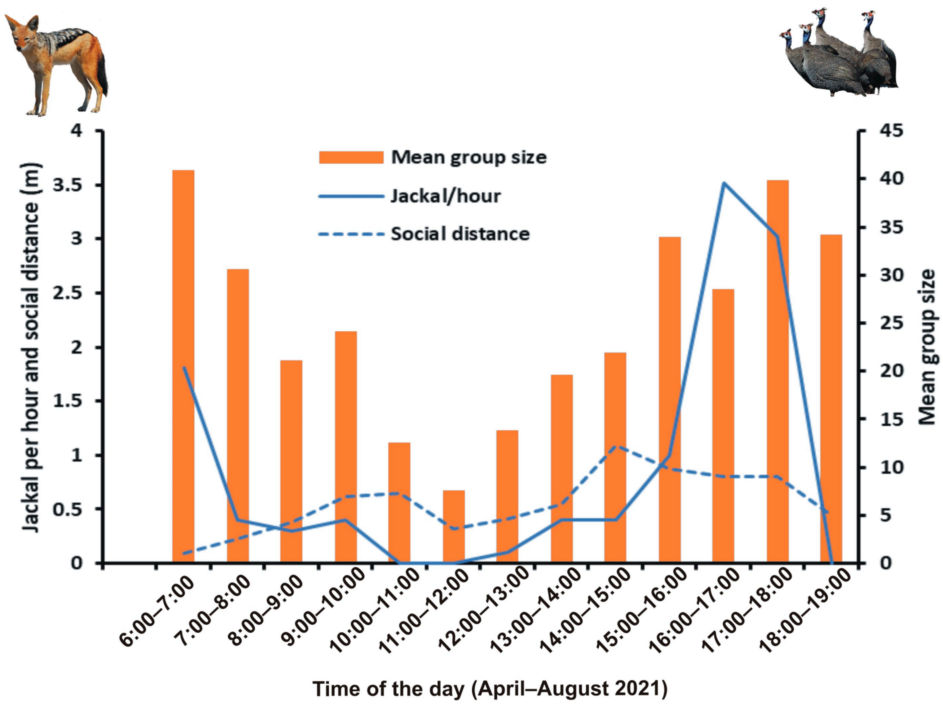

Figure 3. Correlation between mean guineafowl group size, jackal/hour and social distance between group members at Tau from April to August 2021. The jackal picture is available under the Creative Commons CC0 1.0 Universal Public Domain Dedication at https://commons.wikimedia.org/wiki/File:Southern_black-backed_jackal,_CKGR,_Botswana.jpg#file (accessed on 3 January 2024). Pictures not to scale.

Table 6. Hunting strategies of jackal and guineafowl response strategies observed in Madikwe Game Reserve. Obs.: observations.

Prey Response	Predator Attack Strategy	Obs.	Name
After that, some birds flew to the tops of nearby trees, making a loud "chit chit chirr" call. This distracted one predator while another searched for guineafowl hidden in the grass. The birds in the tree attracted the jackals, which allowed the hidden birds in the grass to fly up into the trees.	Jackals approached a group of guineafowl in pairs, chasing them until they flush out in all directions.	3	Bombshell in the scrub
The guineafowl responded by running towards each other first, then altogether 10 to 20 m away, producing a loud "chit chirr" call before continuing to feed.	Lone jackals were seen approaching a group of six to ten guineafowl in a non-threatening manner on the plain, lying 5 to 10 m away from the group. When a bird turned its back to the jackal, the jackal would dash towards it to catch it.	4	Surprise attack
The birds gathered in a dense group, confronting predators by mobbing them and emitting loud calls. The jackals stood motionless for 10 min, appearing confused before walking away as the birds continued foraging.	A pair of jackals dashed into a group, stopping near the birds and waiting to catch one.	4	The challenge
The guineafowl responded by forming a close-knit group of about 20 to 30 birds and running short distances, staying close to the launching pad, just ahead of the jackal for several minutes before flying into the roosting trees.	Groups were chased by a jackal at the launch pad, where they gathered from different directions before roosting.	20	Herding
Like the first response above. Some birds distracted predators by making loud calls, allowing others to escape into trees.	This type of hunting occurred when the groups of guineafowl in the scrub were first disturbed or chased by other animals perceived to be hazardous, such as lions and hyenas. The threatening animals caused the guineafowl to flush out, and the jackal quickly appeared at the scene to pursue the hidden birds in the grass cover.	4	Eavesdropping

3.8. Guineafowl Response to Predatory Bird Attacks

On 14 occasions, raptors were observed to attack guineafowl, with only one kill reported by a Martial Eagle (*Polemaetus bellicosus*). The approaching predators caused the guineafowl group to fly low over the ground (3 to 4 m above ground level) and hide under trees with overhanging branches, remaining there for up to one hour. On five occasions under these conditions, some group members repeatedly moved about 5 m away from the shelter as an exit strategy. In other words, if no further attempts at aerial attacks occurred, the rest of the group also emerged with all individuals commingling to their feeding spot. Of about 100 birds, 30 flew down to the plain when attacked by a raptor, remaining there for about 15 to 20 min before flying back to the trees 40 min after sunset.

Deducing the particular hunting strategy adopted by aerial predators, as performed for the jackals, was not feasible. However, guineafowl were attacked either on the ground or in trees. During the overflight of an unidentified raptor, the group flushed out into cover in all directions. On three occasions, such chases prompted individuals of different groups to gather and emit ear-deafening "chit chit chirr" calls while staying in the same spot.

3.9. Group Size as a Predictor of a Predator Attack

Group size (χ^2 = 27.6, p < 0.001) was a significant predictor of attack type when the model was controlled by the significant effect of month (χ^2 = 22.0, p = 0.005), with February witnessing significantly more predation events. The mean group size during raptor attacks was 34.86 (range = 5–90, SD = 24.55, n = 14); during jackal attacks, it was 39.73 (range = 2–200, SD = 40.14, n = 81), and in the absence of predators it was 15.78 (range = 2–150, SD = 30.49, n = 817). Thus, jackal attacks increased significantly with larger guineafowl groups (Figure 4), while no significant effect of the time of day was found.

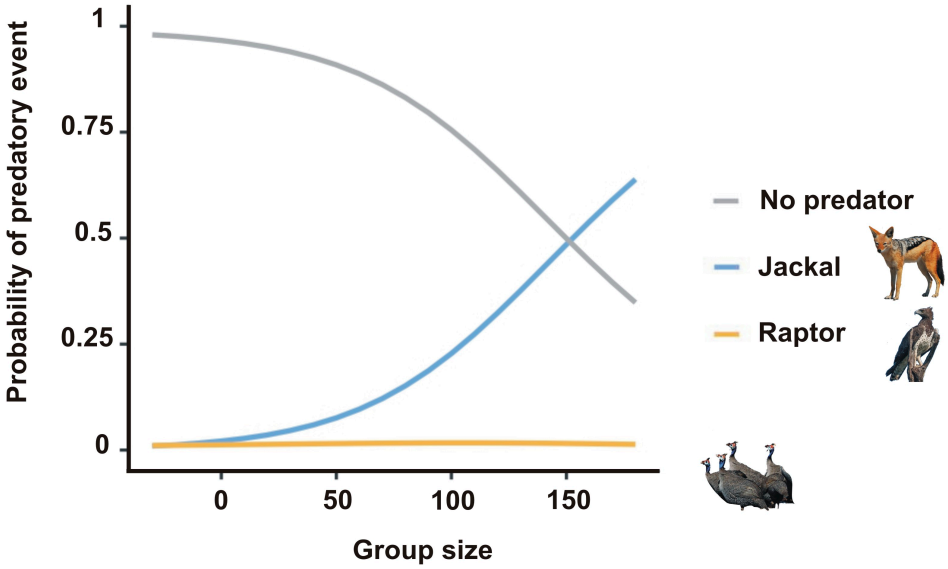

Figure 4. Plot representing a predatory event as a function of guineafowl group size according to a multinomial model corrected by time of day and date. The Martial Eagle picture was taken by Charles J. Sharp (Sharp Photography, sharpphotography.co.uk) and is available under the Creative Commons CC BY-SA 4.0 at https://en.wikipedia.org/wiki/Martial_eagle#/media/File:Martial_eagle_(Polemaetus_bellicosus).jpg (accessed on 3 January 2024). Pictures not to scale.

3.10. Estimated Avoidance Time

The average size of the group attacked was 43.62 birds (range = 2–200, SD = 41.06, n = 43). The mean avoidance (i.e., to keep in hiding under cover after an attack) [47] time for jackals (15.13 min; range = 1–60 min, n = 19) and predatory birds (14.66 min; range = 1–45 min, n = 16) after an attack was not statistically different (H = 0.32811, p = 0.56, n = 35). The estimated daily feeding time that guineafowl lost because of jackal and predatory bird harassment was 30.90 min and 16.49 min, respectively. The number of jackal sightings on the plain far outnumbered that of the predatory birds, 113 vs. 14.

4. Discussion

In this study, we investigated the possible role of predator pressure on group formation in the Helmeted Guineafowl. We found different responses to aerial (raptors) and terrestrial predators (jackals), with the former invariably eliciting fear as opposed to the latter, which were sometimes either tolerated or confronted by adopting different strategies. Grouping behaviour in Helmeted Guineafowl serves various vital functions such as search for food and cooperative breeding [35]. However, its role as an anti-predator strategy has never been studied so far. These birds lived under constant threat from predators, especially black-backed jackals. In Borakalalo Game Reserve (North West province, South Africa), guineafowl groups are known to be attacked by these canids, especially in February when juvenile birds join the group. Jackals also stalked guineafowl in Krugersdorp Game Reserve (Gauteng province, South Africa) during winter and, in one case, were seen to kill one (JHvN, unpublished work).

Territorial jackals were often found to roam across the favourable foraging grounds for guineafowl, resulting in a permanent spatiotemporal predator–prey overlap. In such conditions, it is conceivable that prey species develop specific defensive strategies to survive if trade-offs are likely to occur in a predator-riddled environment [48,49]. Raptors did not keep guineafowl away from their favourite grounds, as also observed in Krugersdorp Game Reserve, where they kept coming back to old vegetable gardens (a favourable 6 ha feeding spot) despite the kills [50], thus showing a strong site fidelity.

4.1. Habitat Use

Madikwe plain is a favourable feeding ground for guineafowl thanks to the nutrients released by elephant and antelope dung and droppings. Guineafowl daily presence during winter suggests that the surrounding bushes do not offer enough nourishment. Not only do these droppings contain seeds that are picked out to consume, but they are also overturned by guineafowl searching for invertebrates underneath [51]. In addition, the manure fertilises the soil, which becomes a lust land with grass seeds for the birds to feed on during the rainy season.

We believe that guineafowl have the skills to counteract predation in and around the plains, which enables them to remain in a lethal space (open plain). Averting terrestrial and aerial predators is possible through behavioural compensation and specific landscape features such as nearby bushes with overhanging branches, foliage and grass cover to conceal during attacks. Nevertheless, both in Madikwe and Krugersdorp Game Reserve [50] guineafowl seemingly endure the current kill rate as they continue to visit the same spots where predation occurred. Ostensibly, this high site fidelity is subject to the net sum of kills being equal to or lower than the group reproductive output, otherwise the birds would roam over larger areas [52].

4.2. Roosting

Roosting is a critical time for guineafowl, as predators can quickly attack when they gather in large groups on a launching pad before flying up to roost in trees, which represents a safety strategy to avoid predators during winter as opposed to the breeding season when they roost in small groups or individually on the ground. Nevertheless, in late winter afternoons/early evenings, guineafowl fly up to trees in small groups of two to three birds. In the morning, they fly down in groups of up to 30 individuals, which seems to contradict the anti-predator strategy enacted when flying into their roosts a few hours before. Despite this risk, they gather in larger groups on the ground, presumably taking advantage of the many-eyes (as suggested by the head-up posture) and dilution effects; cf. [53].

4.3. Terrestrial Predation

Although jackals have been mainly described as scavengers, they are also active hunters [54]. We found a correlation between their presence and guineafowl group size, suggesting that the larger it is, the more attracted these canids are to these birds. Even though this positive relationship followed an exponential trend, it did not reach an asymptote, suggesting that group size was not large enough to attract jackal attention consistently throughout the recording period. Arguably, a trade-off between chances of success and prey group size might occur because of the ensuing chaos and confusion effect as well as the probability of prey to fight back cf. [55]. Still, the data available do not allow us to assume this was the case here confidently. Moreover, based on our observations, jackals were not perceived as hazardous predators, which accounts for the guineafowl tolerating their continuous presence 5 to 10 m away while foraging. However, the birds kept contact with each other with their soft "so wee wee wee" calls or clicks, which were likely to increase in volume and urgency whenever a jackal made a sudden dash towards them. This behaviour allowed guineafowl to evade the attack and continue foraging a few meters away, pointing to the importance of exploiting productive patches without having the urge to move away from their predators [56].

The jackals preferentially approached guineafowl when they occurred in larger groups, usually before roosting or sunning in the morning. In the current study, the birds could be seen to become increasingly agitated before flushing under cover when facing jackals hunting in pairs. On such occasions, however, the guineafowl sometimes formed tight groups of five to ten birds, mobbing the jackals with loud cackle calls, in response to which the predators moved away, as also seen in other studies on this species [30]. The knock-on effect of the loud calls often alerted other groups, much to the disadvantage of the jackals involved, which tended to stand still in bewilderment for up to 10 m before walking away. The poor skills that jackals possess to catch wild birds are also evident from the relatively low occurrence (3.1%) of their remains in their stomachs [57–59]. However, such constant harassment of guineafowl groups curtailed their feeding time by about 29.79 min daily; therefore, the extent of predation to which such birds are exposed could be critical for their survival, especially during dry years marked by poor recruitment in food-depleted habitats [6,60]. Group harassment is a long-term strategy aimed at weakening the birds over time [7], possibly because the jackals persist despite the low hunting success. It is also arguable that guineafowl have not yet evolved proper defensive mechanisms against an opportunistic predator. The same consideration applies to baboons, which were mainly tolerated by the birds even at short distances even if, on at least one occasion, they were seen to prey upon a guineafowl in Krugersdorp Game Reserve [45]. Not surprisingly, the two species share the same feeding patch in other South African reserves in winter [61]. On the contrary, the bold response to approaching lion prides indicates that these large carnivores are adept at hunting guineafowl, as witnessed on one occasion before the onset of this study.

4.4. Aerial Predation

Attacks by raptors were primarily stealth and rare, and their presence was not explained by prey group size. However, the guineafowl did not tolerate these attacks as they did with the jackals and invariably fled away, being particularly wary of predators when ascending their roost. Unlike other birds, such as the Brown-Headed Cowbird (*Molothrus ater*), the guineafowl did not enter their roosting trees in a circadian rhythm; instead, they stayed out on the plain until the light was dim [62]. Furthermore, they ascended the trees in small groups of two to three birds at a time, which could represent a strategy to evade the attention of predators after huddling at the launching pad for 20–30 min without feeding, suggesting maximal vigilance.

When a raptor alerted an individual or group, other individuals were encouraged to take evasive action together, such as flying off low over the ground in the same direction for cover and huddling under the shade of trees with overhanging branches. This explains why raptors mostly attacked groups larger than the year-round mean group sizes (34.07 vs. 14.26), similar to jackals. Comparatively speaking, larger groups have also been observed to be attacked in other predator–prey systems [7] since this strategy maximises the chances of success for the predator.

Evading raptors also prevented the guineafowl from foraging, yet to a lesser extent than in the case of jackals (16.49 min per day vs. 30.90 min per day, respectively). The aggregation of smaller groups moving in one direction in response to raptor attacks seem congruent with the self-organisation theory [63]. It is likely that most guineafowl did not see the predator but still reacted to the flee alarm signals issued by their neighbours and the fluttering of other avian species in nearby trees as warnings. This coordinated movement reduced the cognitive cost of tracking down predator locations as well as the risk of being caught. The evasive action was coordinated without centralised decision-making (i.e., one or two dominant birds leading the others away from danger) since groups joined and flew immediately to reach cover.

4.5. Surveillance

Guineafowl were exposed to predators while drinking water, standing shoulder to shoulder to minimise risk. They alternated with each other while some individuals maintained the neck stretched and head-up postures to scan the area for predators. Interestingly, the birds also performed a head-up movement to swallow water, which seems functional for surveillance too. Comparatively, spurfowl (*Pternistis* spp.)—medium-sized galliforms often coexisting with guineafowl in the same habitat—do not hold their heads up when swallowing water at drinking points but withdraw their necks with their beak remaining parallel with their crouching body (JHvN, personal observation). Moreover, they often visit drinking points singularly, possibly because single birds attract fewer predators than groups.

As opposed to drinking, the percentage of head-up postures was less frequent in the scrub and on the open plain than at the waterhole. In the scrub, where visual contact is limited, guineafowl foraged relatively close to each other, relying on continuous soft "so wee wee wee" contact calls emitted by group members. Hence, the head-up posture is seemingly less critical when the birds are in close contact under cover. Interestingly, the Crested Guineafowl (*Guttera edouardi*) also emits these contact calls in social groups [46].

The plausible explanation for the low head-up rates in the afternoons when guineafowl forage out in the open is that, by keeping their heads down, they increase food intake and, hence, metabolic rate when roosting in trees during cold winter nights (cf. [64]). Instead of the head-up posture, guineafowl rely on a louder "chit chit chit" call to warn their neighbours when a threat is detected. The larger SoD that these galliforms keep in a large group when out in the open—granting them enough space to take flight and avoid collisions with their neighbours when escaping—possibly discourages sudden attacks by jackals. However, when they huddle before roosting or sunning, they form a more compact group (i.e., shorter SoD), making them more vulnerable but allowing for better predator detection. The birds also stand shoulder to shoulder when drinking water and maintain a short social distance when idling from 11:00 to 12:00, allowing effective group communication when a predator approaches.

4.6. Study Limitations

Even though the study site offered several logistical advantages for carrying out this investigation, we should acknowledge that we focused on a single spatially restricted area over a single study season, which was also limiting in terms of sample size. Moreover, the inclusion of mark and recapture sessions in the study design would have allowed the banding of birds from various groups with differently coloured rings, thus assisting in identifying them. At the same time, this would have allowed us to measure the body conditions in individuals from groups of different sizes, thus answering the question of whether the larger aggregates with more individuals scanning for predators correspond to a higher individual feeding time (which could, compensate for the higher risk of attacks). It is worth noting, however, that this work was performed during the COVID-19 pandemic, which severely limited researcher activities (especially in terms of fieldwork and related trips) but also reduced human disturbance to a minimum, thus ensuring that prey responses were uniquely elicited by natural disturbances (i.e., predators).

5. Conclusions

Grouping behaviour may have many functions in guineafowl, and our findings suggest that grouping helps the birds to avoid predation. This conclusion is based on the following results: (1) guineafowl change their group structure during sunning when the birds huddle under attack and when they gather to roost. Predator pressure increases with the number of birds in a group yet ostensibly, the many-eye effect counterbalances the higher risk of attacks since when huddling together or sunning, most individuals hold their heads up to look for predators while emitting soft contact calls. (2) The limited individual investment for predator surveillance and avoidance allows guineafowl to remain on feeding patches even in the presence of jackals, whose threat level is perceived as tolerable (as supported by the low killing rate). (3) The high attack rate on larger groups ascending roost trees is mitigated by the many-eyes advantage for predator detection. (4) Groups serve as communication centres for their members, which, with their physical signs (e.g., head-up posture) and calls, not only warn about predation presence but also assist in maintaining group cohesion when fleeing towards the canopy of a tree [36]. (5) Finally, guineafowl use grouping to confront predators by mobbing them with ear-deafening cackles.

Supplementary Materials: The following supporting information can be downloaded at https://www.mdpi.com/article/10.3390/birds5040047/s1: Table S1: Sub-sampling from the 586 group recordings obtained from August 2020 to August 2021 regarding the different themes addressed in this study. SoD: social distance; Table S2: Sampling dates and times at Tau Waterhole (Madikwe Game Reserve). The low sampling time in December 2020 is ascribed to the absence of guineafowl from the study site because of breeding. Login time was 5 min, while "additional time" refers to the extra time added to monitor predator–prey interaction; Table S3: Time difference (min) between the first and last bird that flew into trees to roost (42 observations) and again when the first and last bird descended from the trees (29 observations) in the mornings from 18 May to 14 September 2021. Some fly-down data are missing because of adverse meteorological conditions that impaired recording. The raw data used in this study are available upon request from the corresponding author.

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