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The Use of Open Vegetation by Red Deer (*Cervus elaphus*) and Fallow Deer (*Dama dama*) Determined by Object Detection Models

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Abstract: Studies of habitat-related behaviour of mammals are time-consuming. This study aims to develop a model for monitoring the behaviour of mammals in different habitat types using drones mounted with thermal cameras in combination with a YOLO object detection model. Red deer (*Cervus elaphus*) and fallow deer (*Dama dama*) were used as model species. The data were collected in the nature reserve, Hanstholm, Northern Denmark. The aim is to develop an AI model capable of distinguishing between four behaviours, "foraging", "locomoting", "lying" and "standing", allowing for insights into the rumination and foraging cycle of the two species. At the same time, the behaviour was linked to habitat types by geocoding individuals. The method developed in this study proved to be time-efficient and provided information about how the two deer species used vegetation types and interspecific interaction between the two species. Technical challenges were to follow individuals and the possibility of missing cyclical behaviour. It was found that the degree to which the ungulates actively foraged was significantly different between the two species and that they were clearly geographically separated within the study area.

Keywords: machine learning; artificial intelligence; drone; UAV; behaviour; YOLO

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1. Introduction

Recent advancements in both the field of machine learning and drone technology have increased the repertoire of methods for biologists studying population dynamics and sizes as well as behaviour [1–3]. Many of these methods have proved to be better than conventional monitoring and behaviour assessment methods, such as wildlife surveillance and transect counts, and at the same time, less time-consuming [3–7]. Machine learning algorithms can automatically execute behaviour or species identification after being trained. The algorithms can be evaluated, meaning that their errors are transparent and interpretable, providing researchers the opportunity to decide which behaviour classes, nodes or species the model can distinguish between and decide if the model can be used for further analysis or must be improved [8]. When the drone is equipped with onboard chips that process a live video with object detection models, the drone can be pre-programmed to fly specific routes and to stop and record when encountering animals [9]. These advantages make the new technologies superior to conventional methods, but they still have many challenges. Many of these challenges are comparable to those of conventional methods, such as the likelihood of recounting individuals. Also, the potential disturbance of animals caused by the presence of researchers in the field may bias results [3]. Object detection models, which predict

object classes, and pose tracking models, which predict the position of morphological points, must be trained and evaluated on a diverse material to ensure high robustness as well as precision and recall of predictions [10]. There is a need for thorough collection of training material representative of the diversity of a study area to ensure equally accurate predictions throughout the study area [10]. Infrared cameras are often used since they make the spotting of individuals easier and since nocturnal species cannot be monitored with RGB cameras. But they have low resolution, which limits the distance from which video material can be recorded and the precision with which the model can distinguish between behaviours, sexes, ages and species. Tracking of individuals is especially challenging in herd species since they often move in front of each other within the frame, resulting in models losing track of individuals. This challenge can be avoided by simply not tracking the individuals and instead perceiving the groups as units, consequently resulting in much lower sample sizes [3]. The development of better algorithms for object detection, as well as algorithms specialised in animal identification, is in rapid progress, and the Yolov8 algorithm, which is used in this study, is commonly used in wildlife biology [11]. Its usability is partially due to its high efficiency in real-time performance and accuracy in many applications and partially due to its relative ease of use [11]. YOLO has been used in many applications in wildlife biology, such as in the estimation of the number of breeding pairs of the Antarctic shag (*Leucocarbo atriceps*) by detecting nests [12] or in the classification of baboon and ungulate behaviour [3,13]. Other studies have further developed this algorithm to specifically be designed for wildlife classification and with an improved Kalman filter for better multi-object tracking [14].

Accurate temporal and geographical representation is especially important in studies of daily migration patterns and is possibly attainable with drones and thermal cameras. This would, depending on the size of the study area, require multiple drones simultaneously surveying the entire area if the daily migration patterns change each day. One drone could possibly accomplish accurate temporal and geographical representation if the daily migration patterns are stable since the whole study area could be represented at all time intervals over multiple days of data collection. In Denmark, red deer are known to have relatively stable daily migration patterns, where individuals typically spend the daytime in forests or scrubs and the nighttime, where human disturbance is lower, in open vegetation types or fields [15]. Fallow deer generally spend the day resting and ruminating while lying and move to open areas for foraging during the night [16]. This study aims to demonstrate the applicability of the combination of drone-mounted thermal cameras and object detection models for studies of behaviour in deer by investigating the following:

1. The distribution of populations of red and fallow deer within Hanstholm Nature Reserve;
2. Their preference for different natural vegetation types and habitat-related behaviour;
3. The daily migration patterns of populations of red deer and fallow deer within Hanstholm Nature Reserve.

2. Materials and Methods

2.1. Study Area

This study was conducted in Hanstholm Nature Reserve, located in the northwestern part of the Danish peninsula, Jutland. This area is a moor consisting of patches of open vegetation types such as humid dune slacks and grey dunes, as well as some forest and scrubs. Material was collected on the four nights, 14−15 October, 15−16 October, 16−17 October and 17−18 October, of 2024 within three temporal intervals: 4:09 a.m. to 6:58 a.m., 6:30 p.m. to 8:35 p.m. and 11:26 p.m. to 1:34 a.m. Two take-off points were chosen from which a radius of approximately two kilometres was covered (see Figure 1). They were chosen to

maximise the area coverage of the drone, hence a point in the northern part and one in the central part of the study area.

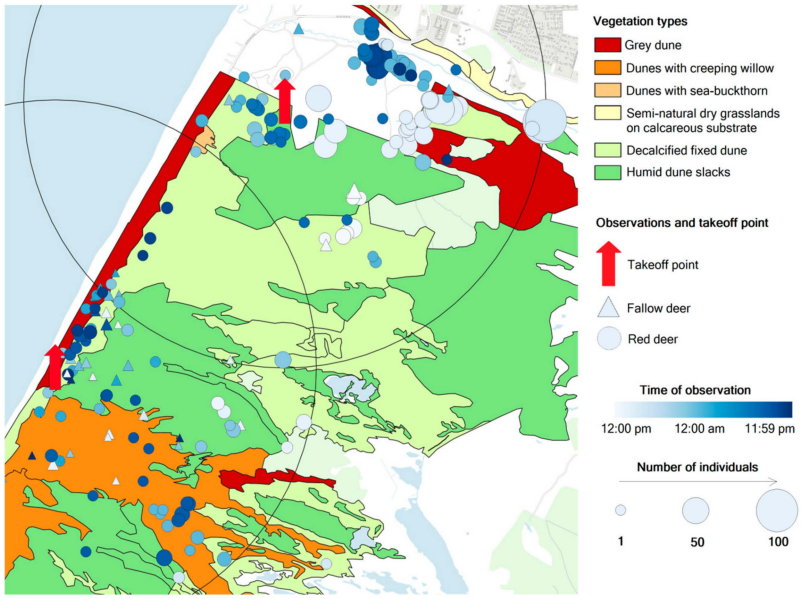


Figure 1. Map of the study area within Hanstholm Nature Reserve. Take-off points are indicated with red arrows, and the approximate range of data collection is indicated by the circular arcs (radius = 2 km). Triangles indicate observations of fallow deer, and circles indicate observations of red deer. The size of these symbols indicates the number of individuals observed, and the intensity of the blue fill colour of these symbols indicates the time of observation. Vegetation types are indicated by colours ranging from red to green.

The ranges from each take-off point were covered in all three temporal intervals multiple times to ensure sufficient and equal temporal coverage of the take-off point ranges. Data collection was cancelled when weather conditions entailed low visibility or when wind speeds were too high for safe flight. The average temperature throughout the collection period was 9.9 °C, and the maximum wind gust was 18.8 m/s. The area of the covered study area was approximately 11.42 km^2.

2.2. Collection of Material and Data

In this study, video material was collected with a DJI Matrice 300 RTK (M300 UAS) (SZ DJI Technology Co., Nanshan, Shenzhen, China) drone equipped with a high-resolution thermal camera, Zenmuse H20N (SZ DJI Technology Co., Nanshan, Shenzhen, China). The Zenmuse H20N is equipped with two thermal cameras and an RGB camera, enabling a thermal resolution of 640 × 512 and up to 8× optical zoom. The video was recorded with 30 FPS and was later compressed for data analysis. The drone is equipped with a laser rangefinder facilitating automatic coordinate estimation through a pinpoint marker function. The drone was piloted manually and within a restricted zone for which a permit was acquired. The altitude was always restricted to between 70 and 120 m (except during take-off and landing) to ensure minimal disturbance of the animals during the collection of material. Observations where animals clearly noticed the presence of the drone were removed from the statistical analysis. Flights were conducted in accordance with the scouring drone method developed by Povlsen et al. [17]. This entails that animals generally were spotted at higher flight altitudes around the take-off points, after which the distance to the spotted animals was reduced and the altitude slightly lowered before initiation of recording. Each group was recorded for one minute. Initially, the zoom was adjusted to include the whole group within the frame to enable the counting of group size. In

cases where sufficient resolution for behaviour classification was not possible when all individuals of the group were located within the frame, the zoom was adjusted so that only a smaller subset of the group was within the frame. The frame was then moved around the group every minute to ensure representation of all individuals. After a group was recorded, the altitude was increased and the area was explored from the new location. If other groups were spotted from the new location, the process of reduction in distance and lowering of altitude would begin again. If no other groups were visible, the drone was brought back to the take-off spot from which the area would be explored again.

2.3. Species Identification

Both red and fallow deer were present within the study area throughout the collection period. Species were identified manually from morphological and behavioural differences, as described by Fugl et al. [3]. This includes identification based on differences in limb movement speed in locomoting individuals, where red deer move more slowly, as well as morphological differences such as the elongated faces of red deer or the visible white markings around the neck or backside of fallow deer, which are visible on thermal imagery [3].

2.4. Behaviour Classification

Behaviour was classified with an object detection model [18]. Annotation was performed with Roboflow (version 1.0), which provided the training material for the object detection algorithm YOLOv8 (You Only Look Once) by Ultralytics (Los Angeles, CA, USA) [18,19]. The behavioural classes were limited to "foraging", "interacting", "locomoting", "lying", "standing" and "other" and are defined in the ethogram (see Table 1). Behaviour was differentiated into these classes since, by examination of the collected video material, it was concluded, that these were general enough that most observations could be classified as one of these, and since the consequently relatively low resolution of behaviour was expected to be sufficient to acquire valuable biological information. The training material consisted of 10 recordings that were compressed to between 1 frame per 30 frames and 1 frame per 5 frames. This resulted in 3447 frames with a total of 6128 annotations. Video material for model training was collected in Lyngby Hede, Thy, Denmark, which has similar vegetation to that of the study area. Video material for training the object detection model was collected at a separate site to ensure that the precision of predictions was not biased by the model being trained on the same video material used for statistical analysis. The videos were intentionally selected to ensure a similar representation of all behaviour classes from multiple viewing angles.

Table 1. Ethogram for deer behaviour.

Behaviour	Description
Foraging	Head of animal placed lower than shoulders
Interacting	Head of one animal touching the body of another animal
Locomoting	Animals moving
Lying	Animals lying and limbs are not visible
Standing	Animals standing upright and not moving
Other	Other behaviours, transitioning from one behaviour to another or behaviour determination inconclusive

The 6128 annotations were split into datasets for training, validating and testing. The training dataset received 4488 frames (~73%), the validating dataset received 1151 (~19%) frames and the testing dataset received 489 (~8%) frames. The mode of the Yolov8 algorithm was set to "detection" for the training. The trained model was evaluated on precision, recall

and mAP50 (mean average precision with a union threshold of 0.5) of predictions of each behaviour class.

2.5. Data Analysis and Definition of Variables

Each recording was compressed to 1/30 of the original length, resulting in each second being represented by one frame. The temporal resolution of behaviour was therefore 1 s. This length was a compromise between having sufficient temporal resolution and assuring reasonable computation time. Four behaviours were predicted with sufficient precision for use in behaviour analysis. These were the behaviours: "foraging", "locomoting", "standing" and "lying". Validation metrics of behaviours are presented in Section 3.1 Model Performance Metrics. For each group, the total number of predictions of each behaviour was divided by the total number of predictions of any behaviour, resulting in the proportions of time spent on each behaviour for each group. Their proportions are expressed as follows:

$$\text{Proportion of time spent on specific behaviour} = \text{Total time specific behaviour predicted} / \text{Total time any behaviour predicted} \quad (1)$$

These proportions were the primary dependent variables used in the statistical analysis, together with the number of individuals within each group, which was counted manually from thermal footage.

2.5.1. Vegetation Type and State

The groups were, by their coordinates, assigned a vegetation type from the Danish Environmental Agency. This agency also records information on the state of vegetation separated into structural state indicators and indicator species. This information was also used in the statistical analysis. These assignments were executed in QGIS version 3.40 (QGIS.org, 2024, QGIS Geographic Information System, QGIS Association (available online: http://www.qgis.org, accessed on 2 December 2024)).

2.5.2. Statistical Analysis

The behaviour classes foraging, locomoting, lying and standing, as well as vegetation variables, were tested for normality with the Shapiro–Wilk test [20] within each group, and the homogeneity of variance between each group was tested with the Bartlett test [21]. The only normally distributed variable was the proportion of time spent standing, and this was only the case when comparing vegetation types within observations of fallow deer. For this case, ANOVA was used to compare vegetation types. All other comparisons were performed with nonparametric tests. The Mann–Whitney U test was used for pairwise comparisons, and the Kruskal–Wallis test was used for comparisons of multiple groups. Mann–Whitney U test was used for nonparametric post hoc analysis, and Tukey's test was used for parametric post hoc analysis. The Mann–Whitney U test was used since it is unknown whether the individuals observed are the same across observation periods. The samples should therefore be considered independent. Behavioural instability was also investigated in this study. Therefore, MAD (mean absolute deviation) kurtosis and skewness were calculated for each behaviour proportion within each species and vegetation type. Correlations were tested with Spearman's rank correlation test [22]. All comparisons and correlation tests were performed in RStudio ("The R Project for Statistical Computing", v. 4.3.2, available online: https://www.r-project.org (accessed on 18 December 2024)).

3. Results

3.1. Model Performance Metrics

The final model predicts the four behaviours, "foraging", "locomoting", "lying" and "standing", with high precision and low confusion, enabling the analysis of forage behaviour and migration in the present vegetation types. These behaviours were predicted with sufficient precision, that being mAP50 metric exceeding 0.7 (see Table 2).

Table 2. Performance metrics of the final model that was used for behaviour classification. The column "Class" is the behaviour class, the column "Images" is the number of images containing instances of the behaviour class in the validation dataset, the column "Instances" is the total number of instances of the behaviour class in all the images, the column "mAP50" is the mean average precision with union threshold equal to 0.5 and the column "mAP50–95" is the mean average precision across multiple union thresholds up to 0.95.

Class	Images	Instances	mAP50	mAP50−95
All	730	1430	0.664	0.516
Foraging	225	489	0.841	0.686
Interacting	6	6	0.259	0.183
Locomoting	134	273	0.747	0.616
Lying	72	132	0.821	0.624
Other	77	118	0.528	0.340
Standing	227	412	0.787	0.649

Fine-tuning was performed by adding additional images with the behaviour "locomoting" and "standing" since the model was not predicting "locomoting" with sufficient precision and since it often mistook "standing" for "locomoting". However, after the addition of approximately 100 images containing these behaviours, the precision of "locomoting" exceeded 0.7, and false predictions of "standing" when "locomoting" were decreased (see Figure 2).

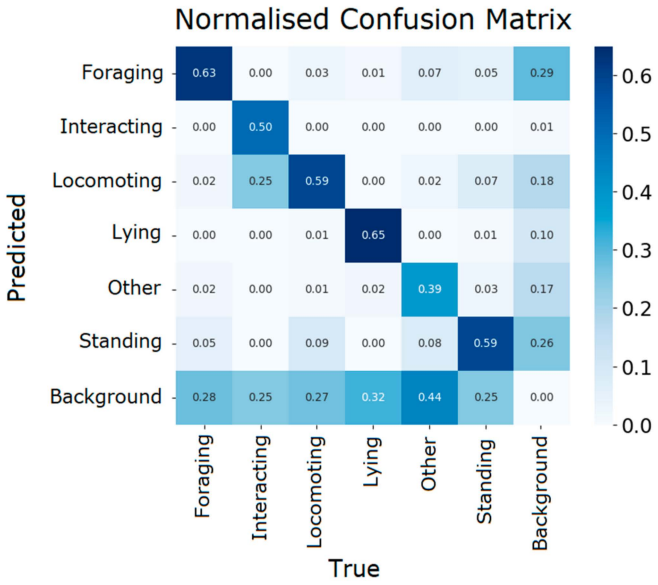


Figure 2. Confusion matrix produced by the validation of the model on approximately 1100 images. All classes are slightly confused with the background but not very confused with each other.

The precision–recall curve in Figure 3 shows that the model can retain high precision and recall simultaneously for the relevant behaviour classes "foraging", "locomoting", "lying" and "standing". Predictions of "other" and "interacting" were not used in statistical

analysis because of insufficient precision and recall. High precision and recall are important characteristics of the model's predictions since both falsely identifying the specific behaviour as another behaviour as well as falsely identifying another behaviour as the specific behaviour has implications for the validity of the data.

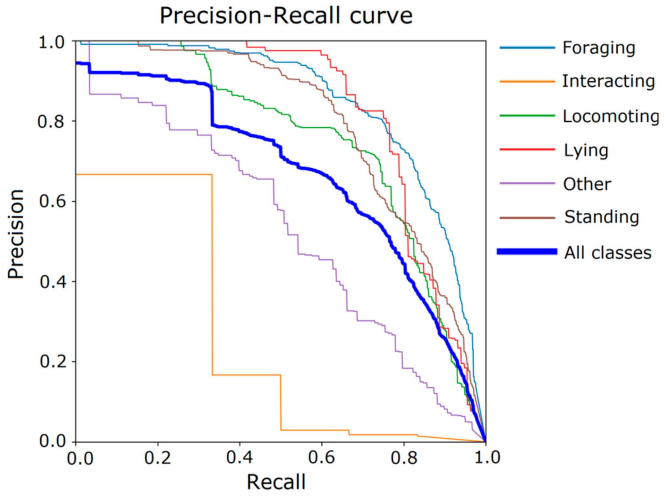


Figure 3. Precision–recall curve of the final model. All relevant behaviour classes retain high precision when the threshold is adjusted to increase recall until a drop at a recall of 0.6. Predictions of "other" and "interacting" were not used in statistical analysis because of insufficient precision and recall.

The models' performance was also evaluated visually by inspection of predictions. A random sample of such predictions can be seen in Figure 4.

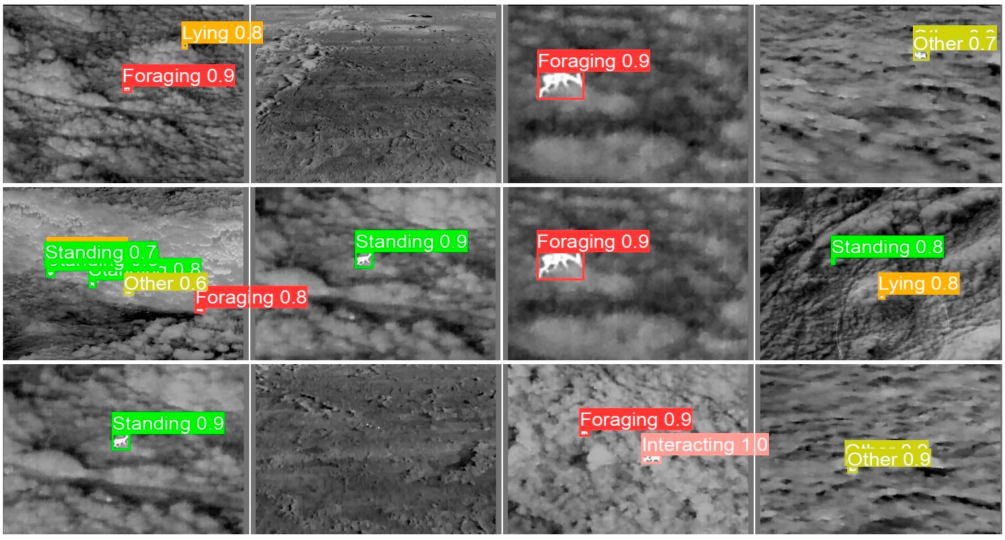


Figure 4. Random sample of predictions produced by the model and used in the evaluation. Each class is indicated by the colour of the bounding boxes and in text alongside the class probability.

High precision is important in predictions of behaviour classes since falsely identifying background as a behaviour class introduces an error that could potentially be background dependent. This could introduce vegetation type-specific differences in predictions, which would bias the results. Similar precision across behaviour classes and low confusion between behaviour classes is at least as important since uneven confusion would entail varying false discovery rates of behaviour classes. Misclassification would not be random but biased towards specific behaviour classes. In this study, the mAP50 ranged from 0.747 in predictions of "locomoting" to 0.841 in predictions of "foraging", and the highest false

recall rate was in predictions of "locomoting" that actually were "interacting" at around 0.25. All other false recall rates between behaviour classes were close to zero, indicating low confusion between behaviour classes and low bias towards specific behaviour classes.

3.2. Distribution of Red and Fallow Deer Within Study Area

The vegetation types that were present within the range of data collection were grey dunes, decalcified fixed dunes, humid dune slacks, dunes with creeping willow, dunes with sea-buckthorn and semi-natural dry grasslands on calcareous substrates. However, deer were only observed in the four first-mentioned vegetation types, as seen in Table 3. In the northern area of the reserve, no data on vegetation types were present, consequently resulting in observations with no vegetation data, as seen in Table 3.

Table 3. Number of groups of red and fallow deer observed in the four vegetation types and in areas with no vegetation type data (*n*), the total area coverage of vegetation types (km^2), as well as the density of observations of individuals of red and fallow deer within each vegetation type (individuals/km^2). "N/A" indicates areas with no vegetation data.

Vegetation Type	Red Deer (*n*)	Fallow Deer (*n*)	Total Area (km^2)	Density of Red Deer (Individuals/km^2)	Fallow Deer Density (Individuals/km^2)
Grey dune	11	3	0.7	55.5	5.4
Decalcified fixed dune	46	12	3.2	85.2	6.6
Humid dune slacks	30	15	3.6	92.7	8.2
Dunes with creeping willow	16	7	1.7	22.4	5.6
Dunes with sea-buckthorn	0	0	0.1	0	0
Semi-natural dry grasslands on calcareous substrates	0	0	0.2	0	0
N/A	51	1	2.0	271.0	1.0
Total	154	39	11.4		

Red deer were observed in locations with significantly higher latitudes than fallow deer ($p < 0.001$, Mann–Whitney U test), as shown in Figure 5. This indicates a clear geographical separation between the two species within the study area. The latitude of observations was also significantly different between vegetation types, where observations within decalcified fixed dunes had significantly higher latitudes than observations within dunes with creeping willow and humid dune slacks ($p < 0.01$, Dunn's test). This indicates a geographical separation of the two vegetation types, where observations within decalcified fixed dunes are more northern than those of dunes with creeping willow. The latitude of observations of deer within decalcified fixed dunes and grey dunes did not differ significantly, indicating that these vegetation types were evenly distributed throughout the area of data collection.

There was no significant difference in the time of observation of red deer between any vegetation types. However, the boxplot of dunes with creeping willow in Figure 6 is located above 12:00 pm, meaning that no red deer were observed in this vegetation type before noon, whereas all other vegetation types had observations of red deer throughout the hours of data collection.

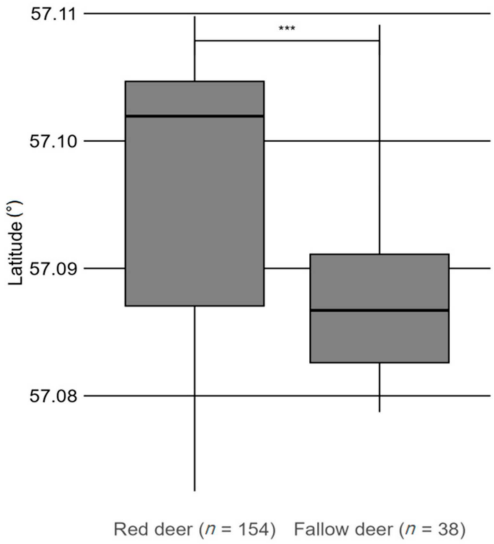


Figure 5. Boxplots showing the latitude (°) of observations of red deer (**left**) and fallow deer (**right**). Latitude of observations was significantly higher in the population of red deer than in the population of fallow deer, indicated by "***" ($p < 0.001$, Mann–Whitney U test).

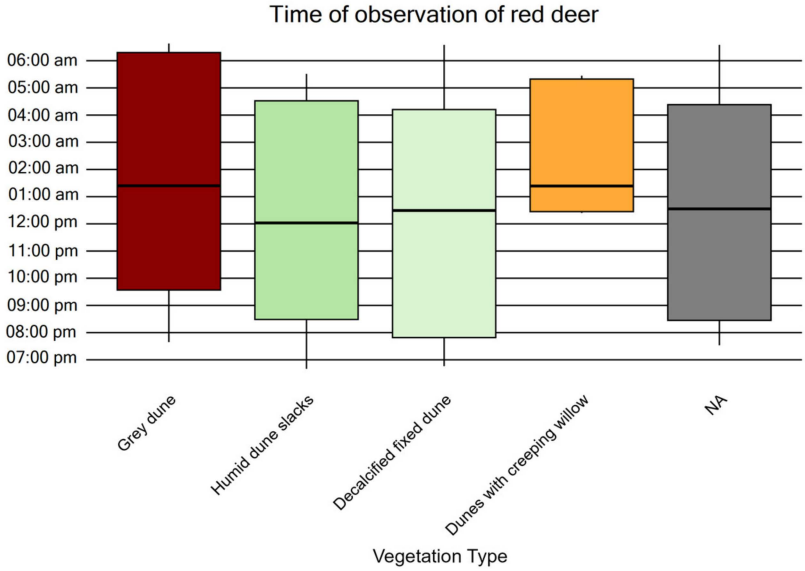


Figure 6. Boxplots of the time of observation of red deer within the vegetation types. There was no significant difference in time of observation between any two vegetation types ($p > 0.05$, Kruskal–Wallis test).

There was no significant difference in the time of observation of fallow deer between any vegetation types (see Figure 7). However, after noon, most groups of fallow deer were observed in grey dunes and humid dune slacks. Before noon, fallow deer were observed in humid dune slacks, decalcified fixed dune and dunes with creeping willows

There was a significant difference in the time of observation of the two deer species within "dunes with creeping willow" ($p < 0.05$, Mann–Whitney U test), indicating that fallow deer were observed earlier than red deer in this vegetation type. There was no significant difference in the time of observation of the two deer species within any other vegetation type.

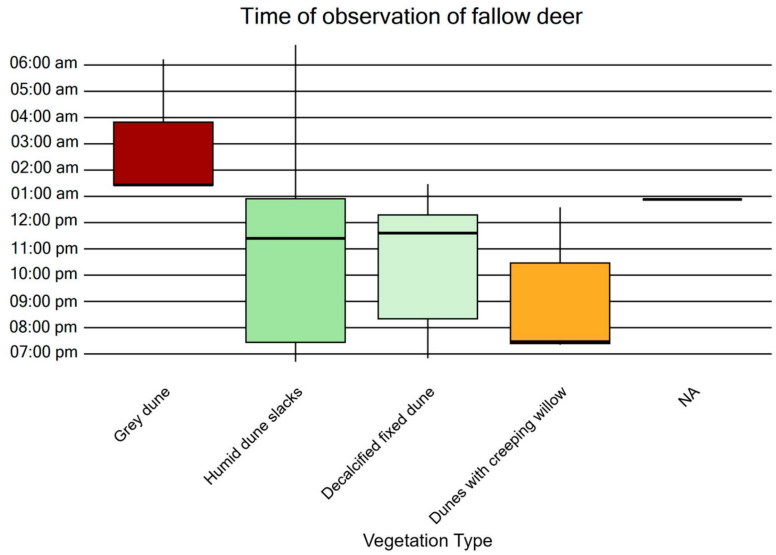


Figure 7. Boxplots of the time of observation of fallow deer within the vegetation types. There was no significant difference in time of observation between any two vegetation types ($p > 0.05$, Kruskal–Wallis test).

3.3. Behaviour Proportions in Vegetation Types and Within Species

Within the vegetation types that red deer were observed, there was no difference in the proportion of time spent foraging. They were moving a significantly larger proportion of time in humid dune slacks than in dunes with creeping willow ($p < 0.05$, Mann–Whitney U test) but were generally not locomoting much in the hours of data collection, as seen in Figure 8. Red deer were observed lying for a significantly smaller proportion of time in humid dune slacks compared to decalcified fixed dunes ($p < 0.05$, Mann–Whitney U test), indicating a preference for resting in decalcified fixed dunes or just at the locations where this vegetation type was present. Red deer were observed standing for a significantly larger proportion of time in humid dune slacks than in dunes with creeping willow. Fallow deer similarly did not seem to have a preference for any vegetation type for foraging when the proportion of time spent foraging is exclusively considered ($p > 0.05$, Kruskal–Wallis test). No behaviour class differed significantly between any two vegetation types for fallow deer ($p > 0.05$, Kruskal–Wallis test and ANOVA). The comparisons of behaviour proportions between the two species within vegetation types can be seen in Figure 8.

3.4. Behavioural Instability

Fallow deer had a higher MAD in the behaviours "foraging" and "lying" in the vegetation type "grey dune" compared to the other vegetation types. MAD in behaviours was similar between red deer and fallow in all other vegetation types. All values of MAD can be seen in Figure 9.

The kurtosis is subtracted 3, resulting in the value "0" being mesokurtic distribution around the mean. The distribution of the behaviour "foraging" was platykurtic in both deer species, except in the population of fallow deer within humid dune slacks, indicating few extreme values. The distribution of the behaviour "locomoting" was leptokurtic in the red deer population, indicating a greater likelihood of extreme values of "locomoting", while the distribution of the same behaviour in the fallow deer population was platykurtic, indicating fewer extreme values. "Locomoting" was therefore more stable in the population of fallow deer than in the population of red deer. The behaviour "lying" was platykurtic within populations of red deer in the vegetation type "decalcified fixed dune", whereas it was leptokurtic in fallow deer. "Standing" was leptokurtic in the population of red deer in

"dunes with creeping willow" and platykurtic in the population of fallow deer. All values of kurtosis can be seen in Figure 10.

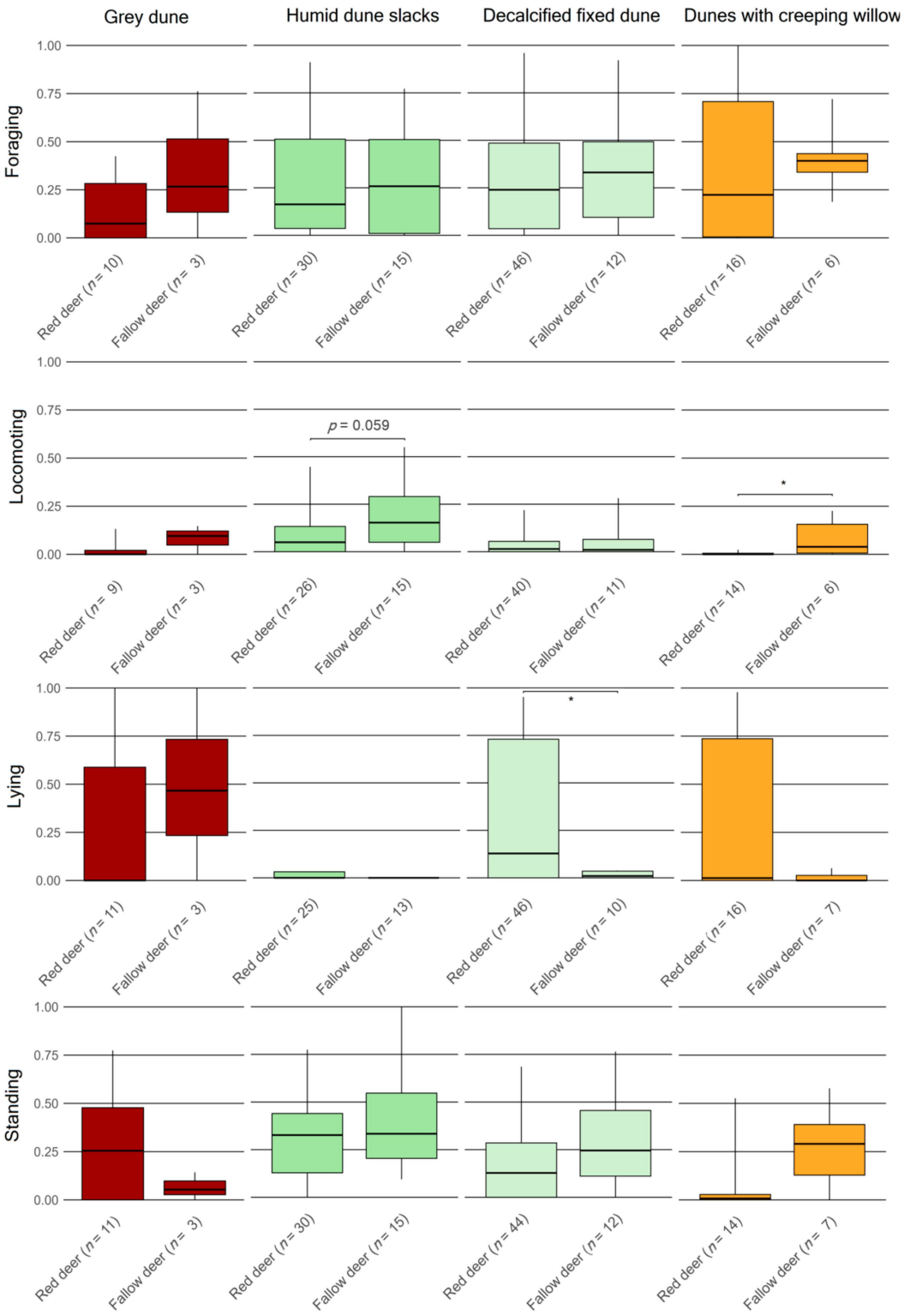


Figure 8. Boxplots of proportion of time spent on the four behaviours visualised as rows and separated in vegetation types visualised as columns and colours. For each combination of behaviour and vegetation type, red deer is the left plot, and fallow deer is the right plot. Only comparisons between the two species are visualised in this plot. Sample size is indicated for each sample, and *p*-values are written for each close-to-significant comparison. Significant difference after Bonferroni correction is indicated with "*" ($p < 0.05$).

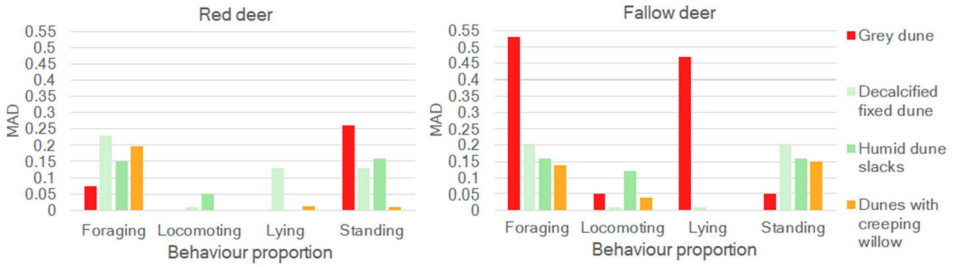


Figure 9. Mean absolute deviation (MAD) of the four behaviour classes "foraging", "locomoting", "lying" and "standing" within the population of red deer (**left**) and fallow deer (**right**) in different vegetation types. Red bars are "grey dune", light green bars are "decalcified fixed dune", darker green bars are "humid dune slacks" and orange bars are "dunes with creeping willow".



Figure 10. Kurtosis of the four behaviour classes "foraging", "locomoting", "lying" and "standing" within the population of red deer (**left**) and fallow deer (**right**) in different vegetation types. Red bars are "grey dune", light green bars are "decalcified fixed dune", darker green bars are "humid dune slacks" and orange bars are "dunes with creeping willow".

Almost all distributions were positively skewed, indicating that most of the observations were located around the mean, but extreme observations had high values of behaviour proportions. This was not the case for any behaviour proportion in the population of fallow deer within grey dunes, where skewness is close to 0, indicating equal amounts of low and high extreme values of behaviour proportions. All values of skewness can be seen in Figure 11.

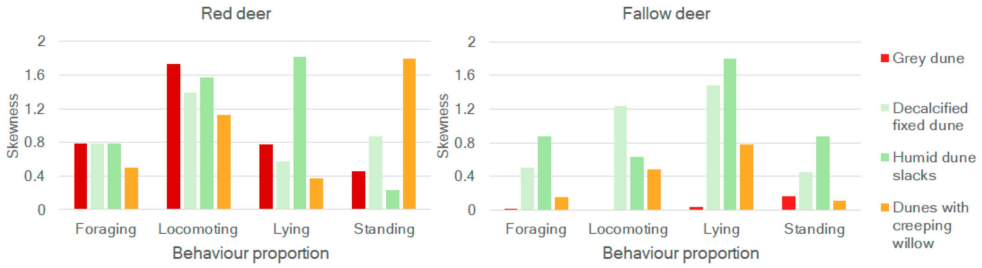


Figure 11. Skewness of the four behaviour classes "foraging", "locomoting", "lying" and "standing" within the population of red deer (**left**) and fallow deer (**right**) in different vegetation types. Red bars are "grey dune", light green bars are "decalcified fixed dune", darker green bars are "humid dune slacks" and orange bars are "dunes with creeping willow".

3.5. Correlations of Vegetative State Data with Behaviour Proportions

Neither state index nor species index correlated with any behaviour proportion in the red deer population. The time spent lying and the vegetation index within the fallow deer population were marginally negatively correlated ($p = 0.073$, $\rho = -0.30$, Spearman's rank correlation test). A significant correlation was found between the structure index and the proportion of time spent locomoting in the red deer population ($p < 0.01$, $\rho = -0.30$, Spearman's rank correlation test).

4. Discussion

4.1. Methodological Considerations

To assess whether the lack of tracking has detrimental effects on the value of the results produced, a comparison between a tracking and non-tracking approach would be necessary. However, successful tracking of individuals instead of consideration of groups as the unit of observation in behaviour studies will benefit the statistical analysis with a much larger sample size and increase the quality and validity of the results. This is because tracking individuals will secure a true representation of the behaviour of individuals where each individual has the same weight in the statistical analysis. When not tracked, individuals in larger groups are less represented in the analysis than individuals in smaller groups; consequently, the behaviour of smaller groups will be overrepresented compared to that of larger groups. This may have implications for the biological accuracy of the results, which stresses the need for the development of a model that is capable of tracking individuals. Achieving high precision in behaviour studies is generally hard compared to species detection, especially with imagery of low resolution, and not many such studies have been performed. For this reason, a less-than-ideal mAP50 threshold of 0.7 was implemented similarly to the study by Fugl et al. 2024 [3]. Species differentiation was performed manually in this study, but future studies should aim to perform species identification with either object detection models or pose estimation models. However, this would require more simultaneous RGB and thermal footage not collected in this study. Using a single drone for data collection is probably sufficient when the collection period is extended to multiple days to ensure equal temporal coverage in the entire area of data collection. To minimise the size of temporal holes of data collection, two drones would be preferred since one drone could collect material while the other's batteries would charge. This would both increase the amount of material and minimise the chance of missing cyclical behaviours, such as rumination and foraging. Additionally, the confusion of the behaviour classes with the background was not equal between behaviour classes, which resulted in error. Future studies should aim to decrease the confusion by adding instances of the most confused behaviour classes. This would equalise the confusion across behaviour types. Finally, it must be mentioned that the movement and distribution, as well as rumination and forage behaviour of both deer species, is expected to change seasonally, which limits the generality of the conclusions of this study since data were only collected over four consecutive nights in October. Future studies should aim to include multiple seasons and preferably multiple data collection periods per season.

4.2. Distribution of Red and Fallow Deer Within Hanstholm Nature Reserve and Their Use of Natural Vegetation

The two deer species were, during the study period, separated in latitude within the area of data collection. Groups of red deer were observed in higher numbers in the northern part of the nature reserve, and groups of fallow deer were observed in higher numbers in the central part of the nature reserve. The vegetation types decalcified fixed dunes and dunes with creeping willow were also geographically separated, where observations within decalcified fixed dunes had higher latitudes than observations within dunes with creeping willow. The separation in latitude and simultaneously in vegetation types is also indicated by the higher relative density of fallow deer in dunes with creeping willow compared to red deer. The geographical separation of the two deer species indicates that red deer prefer decalcified fixed dunes and fallow deer prefer dunes with creeping willow for foraging. However, there was no significant difference in the proportion of time spent foraging between the two species within any of the vegetation types, as seen in Figure 8, indicating that when present, both species use similar vegetation types for foraging. This is

further supported by the analysis of behavioural instability. The MAD of the proportion of time spent foraging was similar between the two species within all vegetation types except grey dunes, within which the sample size of fallow deer was only three. This indicates a similar size of variation in the forage behaviour of groups of both species. The variation was also characterised by a few extreme values in both species since the distributions of the proportion of time spent foraging in both species were platykurtic within most vegetation types. The extreme values of the behaviour proportion were, for both species, mostly higher than the mean in all vegetation types, as seen by the values of skewness. This indicates that the two species of deer spend similar amounts of time foraging in the present vegetation types. Geographical separation between species of deer that coexist within the same area could be a consequence of an evolutionary process where past competition has driven physiological and behavioural differences between species, minimising the interspecific competitive interactions seen today [23]. Dunes with creeping willow often emerge by the invasion of creeping willow in humid dune slacks [24,25]. The vegetation besides creeping willow therefore depends on the hydrology, though creeping willow mostly invades less humid dune slacks. Some common plants in humid dune slacks where humidity is high are the common reed (*Phragmites australis*) and the sedge *Bolboschoenus maritimus*, whereas species of grasses and sedges usually found in meadows and pastures are more commonly found in dune slacks where hydrology is lower, and where creeping willow is more likely to invade [25]. It would therefore be expected that the dunes with creeping willow are rich in grass and sedge species, which are both commonly foraged by both deer species [16,26]. Red deer, being intermediate feeders, would more likely forage on scrubs like creeping willow than fallow deer, which are a more grazing-dominant species. But both species are known to browse on scrubs and woody plants throughout the year, and fallow deer prefer residence and potentially foraging in dunes with creeping willow, which is likely linked to the present vegetation, including creeping willow. Decalcified fixed dunes, which seemed to be preferred for residence and likely for foraging by red deer, are a later successional state than humid dune slacks, which are threatened by lowering of water tables, and dunes with creeping willow, which often arise as an invasion of creeping willows on humid dune slacks [24,25]. The two species were observed in dunes with creeping willow at different times of the night. Red deer were only observed after noon and fallow deer only before noon. This could indicate that the two species actively minimise their interspecific interactions by residing in this vegetation type at different times.

Both species seemed to spend more time moving around "locomoting" in humid dune slacks compared to the other vegetation types, though this was not significant. The characteristics of the distributions of time spent locomoting were slightly different between the two species in this vegetation type. Both species had low MAD in this behaviour and were positively skewed, but the distribution within red deer was leptokurtic, hence more extreme values, and the distribution within fallow deer was platykurtic, hence less extreme values. Together with the fact that both species spent similar amounts of time foraging in humid dune slacks compared to the other vegetation types, it could indicate that the two species are more actively foraging in this vegetation type, either because food is sparse or patchy, and that this active forage behaviour was more stable in fallow deer as indicated by the platykurtic distribution of the proportion of time spent locomoting. Humid dune slacks are very rich in plant species and in habitats ranging from dune lakes to humid grass and reed patches, possibly explaining the need for active foraging [25]. In dunes with creeping willow, fallow deer were locomoting a significantly larger proportion of time than red deer. This is indicative of more active forage behaviour in fallow deer than red deer in this vegetation type, possibly explained by red deer more commonly browsing on scrubs and bushes, like creeping willow, than fallow deer, and availability of creeping willow,

thereby decreasing the degree to which active foraging is necessary for red deer [25]. The characteristics of the distributions of proportion of time spent locomoting within dunes with creeping willow were also similar between the species, but distribution within the red deer population was more positively skewed, indicating that some red deer were actively foraging in a degree more similar to fallow deer.

Fallow deer were generally not lying much, but more in grey dunes than in the other vegetation types, though not significantly more, probably because of the low sample size (n = 3) of observations of fallow deer in this vegetation type. Red deer spent similar amounts of time lying in all vegetation types except humid dune slacks, where they spent less time lying compared to the other vegetation types and significantly less time lying than in decalcified fixed dunes. Both red and fallow deer are crepuscular species, and their activity is affected by many factors such as food availability, predation risk, mating activity, intra- and interspecific interactions and human disturbances [16,26]. Lying is an indicator of rumination, and both species are known to cycle between feeding and lying down for rumination. The low proportions of time spent lying in groups of fallow deer is indicative of maximisation of foraging at the cost of less rumination time. This could be caused by interspecific interactions with red deer, who are in much higher numbers, forcing the fallow deer to spend more time actively foraging to secure sufficient feed intake. Fallow deer were generally not observed much after noon within the area of data collection, as seen in Figure 7. This indicates that fallow deer migrate back to the forests earlier than red deer.

The only vegetation state indicator that any behaviour correlated significantly with was the structure index, and it was only in the red deer population. The correlation was weakly negative, indicating that a high structure index results in less time spent locomoting by groups of red deer. Structure index is estimated by evaluation of vegetative characteristics related to the health of the vegetation type, such as the number of invasive species, the proportion of area covered by grasses and herbs in different heights and the proportion of area covered by dwarf shrubs and woody plants [27]. The value of these characteristics relates to the state of the specific vegetation types and does not tell anything by themselves since what is considered healthy values depends on the vegetation type. The weak correlation therefore indicates that red deer forage less actively when the structural health of the vegetation type is high, probably because of a preference for the plant species emerging when the vegetation is not affected by invasive species and a preference for the ratio between grasses and herbs.

5. Conclusions

In this study, it was demonstrated that thermal camera-mounted drones and object detection models are time-efficient and valuable tools for biologists and conservationists that can provide information on behaviour of deer in different vegetation types despite the method's early developmental stage and technical challenges that need to be solved. This study indicates that red deer and fallow deer chose to forage in different vegetation types, but this needs further seasonal confirmation. The two species showed different foraging strategies and possible different impacts on vegetation types. Fallow deer were found in vegetation types of earlier successional stages than red deer. In future studies, it is important to investigate how the two species affect the vegetation and vice versa to gain knowledge of how the vegetation types affect the foraging behaviour and population size of the species.

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