scientific reports

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# Elephant habituation to drones as a behavioural observation tool

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**Unmanned Aerial Vehicles, known as UAVs or drones, are increasingly important as a tool in wildlife research and conservation. However, it is crucial to quantify as well as qualify the response of target species to drones. We measured the reaction of African savannah elephants (*Loxodonta africana)* to an off-the-shelf quadcopter drone during sequences of repeated trials. In total we conducted 35 trials involving 14 distinct and individually identified elephant groups, exposing them to the drone on up to four separate occasions. Half of trials recorded evidence of disturbed behaviour, but the proportion of disturbed elephants returned to levels comparable to pre-exposure by the end of the exposure period, suggesting some degree of habituation to drones over the course of a single trial. Additionally, repeated trials had significantly fewer instances of disturbed behaviour compared to initial trials, suggesting long-term habituation as well. Nonetheless, some small-scale changes in activity patterns were observed even after repeated trials. Our results suggest that elephants can habituate to drones, especially when they are flown according to guidelines which minimise disturbance. This indicates that drones can be used as a minimally invasive technology to monitor elephant behaviour provided that baseline activity patterns are recorded and quantified prior to drone exposure.**

**Keywords** Aerial monitoring, Anthropogenic disturbance, Drones, Elephant, Habituation, Unmanned aerial vehicles

The use of Unmanned Aerial Vehicles (UAVs; hereafter referred to as drones) in wildlife research has increased dramatically in recent years[1,2]. Drones present significant advantages over traditional data collection methods that use foot patrols, vehicles or manned aircraft in terms of both efficiency and the quality of data that can be acquired. Advantages include a vastly increased field of view compared to observations at ground level and the ability to quantify nuanced animal behaviour and detailed spatial information over an extended period of time, often in areas inaccessible by other means[3–7]. The costs often associated with other techniques (e.g. fuel and maintenance costs for manned light aircraft) are reduced[4,8], while wildlife observations can be recorded less intrusively[1,3,8,9].

Despite these benefits, drones still have the potential to disturb wildlife[2,10,11]. Therefore, it is important to quantify the extent to which drones impact the natural behaviour of a study species before using them to conduct extended research. Previous studies on wildlife responses to drones have identified factors constituting thresholds of disturbance which can vary greatly by taxa, species and characteristics of the animal subjects under observation[2,12–14]. In addition, the attributes of specific drones and the way they are flown can have a significant impact on animal reactions[2]. For example, the disturbance caused by the noise of a drone might alter the behaviour of the study subjects by causing risk-averse responses[15], thereby undermining the validity of observations[16]. Drones may negatively affect the physiology of a number of species, such as bears[17] and sub-Antarctic seabirds[18], both of which were recorded to have an increased heart rate but only limited behavioural responses to drones. Nonetheless, drones have been used as a tool to observe a range of natural behaviours across a number of species, often with minimal or no disturbance[7]. However, to ensure that data collected by drones reflect natural behaviour, and are not an artefact of drone presence, it is important to determine whether the drone itself and its flight pattern affect (either directly or indirectly) the behaviour of the study animals.

African savannah elephants (*Loxodonta africana*) present ideal candidates for drone-based research[19]. Their size makes them easily visible even from high altitudes and allows for individual identification from drone imagery. Elephants often inhabit areas hard to reach by vehicle and/or with limited ground visibility such as

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tropical rainforests and montane forests[20], with drones providing an advantage as an aerial tool for observation. Moreover, elephants live in complex fission–fusion societies[21], and drones can help quantify socio-spatial ties among individuals within groups (e.g. distances between group members, extent of coordinated movements), as well as offer the opportunity to observe multiple social interactions occurring at once[4,7,22].

Some studies have examined the influence of drone approaches and noise on elephant behaviour[23–27]. Of these, some show that elephants may display a negative reaction to drones under certain circumstances[23–26], with the proviso that[24] aimed to deter elephants from crop-raiding rather than examine details of their reaction to drone presence. It is possible that the negative reactions recorded in some studies could be due to similarities between the sound of drone propellers and that of swarming bees[28], which elephants perceive as a threat[29,30]. While disturbance responses can be mitigated by following flying protocols that minimise elephant exposure to the sight and noise of drones[23,25,26], the extent to which elephants are capable of habituation to drones remains to be examined and quantified in detail. Elephants may habituate to novel objects such as vehicles[31–34], so it is important to determine the circumstances under which drones can be used to observe natural behaviour.

Here, we measured reactions to a quadcopter drone when flown as a monitoring tool aiming to minimise potential disturbance, and we analysed whether or not elephants habituate to its presence through a sequence of repeated trials. We hypothesised that elephants would show progressively less intense and/or less frequent risk-averse behaviour patterns over the course of a single trial and with increasing number of trials. Our null hypothesis was that, since the sound of a drone can closely resemble that of swarming bees, elephants might not habituate and would not show a decrease in the intensity and/or frequency of risk-averse behaviours over the course of a single trial and after repeated trials.

## Materials and methods

### Study system

The study was conducted in the Samburu and Buffalo Springs National Reserves (SNR and BSNR, respectively) of northern Kenya (0.3–0.8° N; 37–38° E), which form part of the greater Laikipia-Samburu ecosystem[35]. The reserves lie at an elevation between 800 and 1200 m above sea level, with hills and seasonal watercourses[36]. The environment is semi-arid, with an average yearly rainfall of 350 mm across two wet seasons between November–December and April–May[37]. The Ewaso Nyiro river, which flows semi-perennially and can dry up completely during drought years[36], divides the two reserves, both of which are unfenced.

The elephant population in these two protected areas has been monitored continuously since 1997, and combined with significant tourist presence has resulted in a population which are habituated to vehicles and therefore observed with ease[21,32]. Elephants in SNR and BSNR are individually identified, resulting in a detailed database of elephant life histories and social interactions[36]. The two reserves are home to a population of resident elephants as well as a number of migratory and sporadic elephants who frequent the reserves at different times of year[36]. This knowledge base was essential when it came to targeting specific elephant groups for repeat trials, and allowed us to record reactions against the group's degree of residency.

### Field trials

To determine whether or not elephants habituate to the presence of a drone, we exposed individually-identified elephants in SNR and BSNR to repeated drone flights. We focused on family groups, consisting of cows and calves. These were chosen in preference to bull groups (consisting of adult males only) because family groups have a more stable composition, thus representing better targets for repeat trials. At a minimum, repeat trials always included the individually identified matriarch of each target group, but sometimes included other groups, females or bulls who happened to be present. We selected seven resident family groups and six non-resident family groups within the study population. Resident groups were identified as those spending more than nine months (on average) within the core study area, whereas non-resident groups use the core study area for less than seven months a year on average, usually during the wet season[36]. The selection of resident groups was based on which elephants were present in SNR or BSNR at the start of the study in March 2023, while non-resident groups were chosen opportunistically as they visited the study area throughout the study period. Recreational drone flying is prohibited within the study area, and there are no licensed drone operators within the two reserves besides the authors of this study. Therefore, we can say that resident elephant groups are unlikely to have been exposed to drones prior to this study, the only exception being occasional past drone use by filmmakers. These instances are infrequent and, to the best of our knowledge, no drones were flown in the reserves in the year preceding the start of this study, nor were any resident elephants exposed to other drone uses outside of this study during the study period. The same cannot be said for non-resident groups, for which we cannot exclude the possibility of exposure to drones in other areas. We decided to contrast resident versus non-resident groups as these might exhibit different responses to observer presence during drone exposures. While resident groups regularly encounter research and tourist vehicles, non-resident groups are less accustomed to vehicles and might be more likely to show risk-averse behaviour to anthropogenic disturbance[32,33].

The drone selected for this study was a DJI Matrice 30 T (hereafter M30T; DJI, Shenzhen, China), a quadcopter equipped with three recording cameras (wide angle, zoom and infrared) as well as a laser rangefinder. For our study, this drone offered an excellent balance between physical portability and camera capability, since the optical zoom (up to 16 × optical, 200 × hybrid) allowed for detailed viewing while keeping the drone as high as possible from the elephant group. Other benefits included a high wind resistance of 12 m/s, making it powerful enough to counter the strong winds regularly encountered in the study area, and a wide range of sensor capabilities that extend the potential range of future studies. The size of a drone is often but not always correlated to its sound output, with some large drones having been found to be quieter than smaller ones[16], which is in line with our assessment of the M30T's sound level as negligible when flying at a height of 120 m (see Supplementary Note S1; Fig. S1), the maximum altitude permitted for drone flight by the Kenya Civil Aviation Authority.

We aimed for a minimum of three drone exposures per target family group. This was not always possible, in particular for those elephants which only spent a relatively short period of time within the study area. In consequence, each group (n = 14) was exposed to between one and four drone flights, for a total of 35 trials. Of this total, nine trials were conducted on resident groups, and 26 trials on non-resident groups (see Supplementary Note S2). Intervals between trials ranged from 1 to 355 days, with an average inter-trial interval of 85.5 days. These trials were carried out by (i) a drone team, consisting of at least one licensed drone pilot and observer, tasked with launching and flying the drone; and (ii) a ground team, consisting of one to four field researchers in a vehicle tasked with filming the elephant reactions to the drone. All phases were recorded using a Sony FDR-AX40 or a Sony RX10iii (Sony Group Corporation, Tokyo, Japan) camera, each with 4 K recording capability, and a timer was used to record the start and end of each phase. The drone and ground teams synchronised their activities via two-way radio communication using Motorola XT420 (Motorola Solutions, Chicago, USA) handheld radios.

Once a target elephant group was located, the drone team drove to a suitable launching site while the ground team in another vehicle positioned themselves close to (< 50 m) the target elephants in a spot with an open field of view. The ground team always attempted to get the whole elephant group in view of the camera, but this was not always feasible in the case of large, dispersed groups or particularly dense vegetation. In these instances the ground team focused on the elephants which were beneath the drone and not those which may have been on the periphery, or would reposition the vehicle to get a better view of the target elephants. The average group size of 9.9 elephants meant that this was rarely an issue, as the elephants were usually found in an area small enough to record most or all members of the group in one frame. The drone was always launched at least 500 m away from the elephant group to minimise the possibility of the animals being disturbed by the drone's take off [cf.[14,38,39]]. Further, the drone launch site was always on the downwind side of the elephant group to reduce noise propagation in the direction of the elephants. Before the start of each trial, the identities, number of individuals and composition of each family group were recorded on a spreadsheet.

We divided each trial into five phases to record behavioural responses in the presence and absence of a drone: (i) a pre-exposure phase, before the launch of the drone; (ii) an approach phase, between the drone launch and the time when the drone was directly above the targeted family group; (iii) an exposure phase, throughout which the drone was directly above the targeted group at an altitude of 120 m; (iv) a retreat phase, during which the drone returned to its launch point; and (v) a post-exposure phase after the drone had landed. Each phase was six min long, except for the approach and retreat phases, which varied between one and seven min depending on the distance between the drone launching point and the target group, the drone's speed, and whether or not the elephants were moving. In addition, there were four exposures early in the study which were longer than six min (12, 14, 15 and 15 min respectively) because we were trialling what the most suitable length of exposure should be. Considering our aim to keep phases (i), (iii) and (v) the same duration, and the logistical difficulty of following elephants by vehicle and maintaining line of sight for potentially more than 45 min, we realised that a shorter phase duration would be necessary. Therefore it was decided for (i), (iii) and (v) that six min would be an appropriate length of time to gauge the reactions of the elephants and establish whether the presence of the drone induced any significant change in their behaviour. Trial phases and their durations are summarised in Table 1.

The pre-exposure phase began once the drone team was in position and ready to launch, at the end of which the drone took off, ascended to 120 m and then the pilot flew the drone towards the target elephant group. The exposure phase was started once the drone was positioned overhead the elephant group, which was communicated to the pilot by observation from the ground team. If the elephant group moved during the exposure period the drone would follow them, maintaining a position as close as possible to the approximate centre of the group. This was assessed by the drone pilot, who would keep as many elephants in the camera's frame as possible by using the drone's wide angle lens and visually determine the approximate centre of the group. After the exposure, the drone returned to the launch point and the post-exposure phase was started once the drone had landed. This last phase was not always completed to the full six min (n = 16) if the elephants moved into inaccessible areas or due to operational constraints.

Environmental data such as temperature and wind speed that could affect elephant responses to the drone (e.g. by disrupting sound propagation), was sourced after each flight from a third party application (www.airdata.com) which retrieves flight data from the M30T's computer systems.

## Behaviour scoring

Five sample clips, each of one min duration, were extracted from the ground footage of each trial. Drone footage was not used as it could not be scored without revealing to the coder which stage of the trial was being shown. The clips were lifted in this order: the last minute of pre-exposure, the last minute of approach, the first and last

| Phase | Duration | Drone airborne |
|---|---|---|
| Pre-exposure | 6 min | No |
| Approach | Variable | Yes |
| Exposure | 6 min | Yes |
| Retreat | Variable | Yes |
| Post-exposure | 6 min | No |

**Table 1**. Drone trial phases and durations.

minutes of exposure, and the first minute of post-exposure (Fig. 1). These intervals were expected to be the most indicative of elephant behaviour before, during and after exposure to the drone while creating a manageable workload for analysis. This expectation was founded on the assumption that the introduction of the drone as a stimulus overhead the elephant group would elicit the most disturbance, if any, at the time of its approach and arrival, and that any difference or trends in behaviour in the presence of the drone would be best ascertained from analysing footage at the end of the exposure phase. Similarly, it was decided that the clips from the last minute of pre-exposure would give us the most accurate baseline for elephant behaviour prior to the drone's take off, and that the first minute of post-exposure would allow us to gauge the return, if any, to this baseline, with the retreat phase allowing time for the drone as a stimulus to be removed. We also hypothesised that the withdrawal of the drone would be less likely to induce a change in elephant behaviour than the preceding phases when it was introduced. The post-exposure clip selection was also influenced by the fact that we were unable to complete some post-exposures to the full 6-min length, meaning that there would have been some missing data had we chosen to analyse the last minute of post-exposure instead of the first. There were a small number of clips (n = 18) which were irretrievable due to errors such as cameras not recording or circumstances such as the elephants moving out of sight. This includes four post-exposure clips which were not retrieved from the earlier trials which had longer exposure periods beyond six min in order to retain data integrity.

The resulting one-min clips (n = 157) were randomised and analysed by experienced elephant behavioural researchers who had not been present at the corresponding trials. The audio was removed from these clips so that the coder would not know which phase of the trial was shown. The scorer recorded the number of elephants engaged in each of the following activities every 10 s: feeding, walking, walking while feeding, resting, drinking, wallowing, dusting, social interaction as well as unknown behaviour when the elephant could not be seen clearly. All elephants in the frame were scored in this way, which may have at times included other associating elephants who were present alongside the target group in repeat trials, but the focus of the frame was always centred on the target matriarch and her family as much as possible.

Once the activity scoring was complete, the clips were reviewed a second time to record any instances of behaviour which could be an indicator of a stress response. The scorer recorded the number of elephants exhibiting each of these disturbed behaviour indicators throughout the duration of each clip: running, trunk up, head up, head shake, tail up, tusking, thrashing, gland secretion and bunching. These nine categories of disturbed behaviour indicators range from mild, to moderate, to significant in terms of the level of stress displayed by the elephant. Some indicate alertness, threat display or an attempt to identify the source of disturbance (*Trunk Up, Head Up*), others show signs of irritation, impatience or excitement (*Head Shake, Tail Up, Gland Secretion*), others are indicative of a fear response (*Running, Bunching*), while the rest (*Tusking, Thrashing*) could be considered aggressive[31,40].

## Statistical models

To test the effects of the drone on elephant behaviour we created four generalised linear mixed-effect models with beta-binomial distributions and a *logit* link function. The response variables were constructed as a matrix of successes and failures where successes were the number of elephants exhibiting each behaviour (disturbed, feeding, moving, and resting) and failures were the number of elephants not exhibiting each behaviour. In this framework, the total number of elephants in the group is explicitly included as the denominator of the

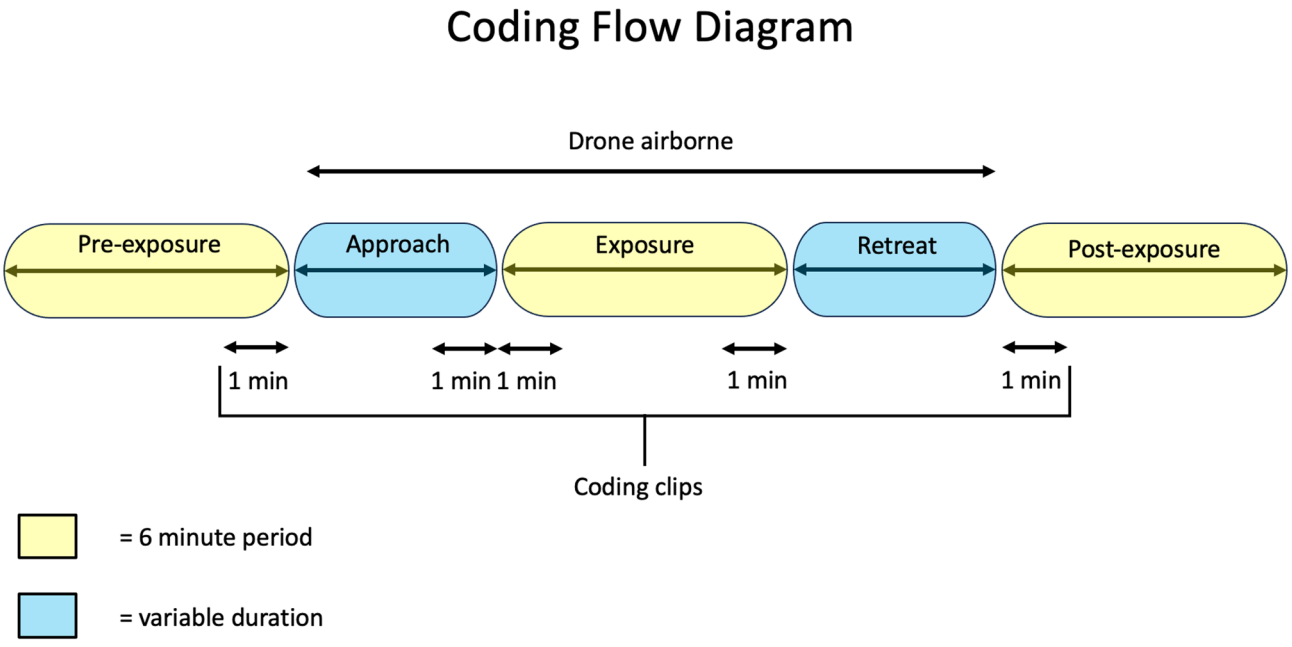


**Fig. 1**. Visualisation of the process by which clips for analysis were taken from the bank of footage.

response, so the probability of a behaviour is inherently conditional on group size and no separate offset term is required[41–43]. With the response variables constructed in this manner, they serve essentially as the proportion of elephants exhibiting each behaviour per group while implicitly accounting for group size as a confounding variable. The number of elephants exhibiting disturbed behaviour was taken from the total for each clip, while the number of elephants resting, walking, and feeding was calculated at each 10 s interval. We included exposure phase and trial type as fixed effects and group ID and flight ID as random effects. We explored including environmental covariates such as temperature and wind speed alongside group ID and flight ID as random effects. However, models with these additional predictors failed to converge, likely due to sample size limitations and the correlation structure among variables. We therefore retained the more parsimonious model structure presented here, which balances interpretability with statistical stability. A limitation of our study is that sample size constraints prevented us from simultaneously modelling environmental covariates and random effects. Future studies with larger datasets will be better able to disentangle environmental influences from group- and flight-level variation.

Exposure phase (*Pre-Exposure, Approach, Exposure 1, Exposure 2, Post-Exposure*) was a categorical variable with *Pre-Exposure* as the reference category, and trial type (*First Trial, Repeated Trial*) was a categorical variable with *First Trial* as the reference category. We only constructed models for resting, walking, and feeding since these were the activities that were most often observed. Models were produced using the *glmmTMB* package[41], model fit was assessed using the *DHARMa* package[44], including explicit tests for temporal autocorrelation in model residuals using the testTemporalAutocorrelation function. No significant autocorrelation was detected (all $p > 0.05$), and graphs and tables were generated using the *ggplot2*[45] and *sjPlot*[46] packages in *R* version 4.4.1[47].

## Ethics

The ethical implications of this study were carefully considered at all times, following[10]. No elephant group was exposed to the drone more than once in a 24 h period, and the drone was to land if any signs of prolonged agitation were observed. Drone flights were conducted with the permission of the managers of Samburu and Buffalo Springs National Reserves, and under the authorisation of the Kenya Civil Aviation Authority, permit reference: KCAA/OPS/2117/ROC/26 Vol. 2(47). This research was conducted with the permission of Kenya's Wildlife Research and Training Institute under the permit number WRTI-0375-011-23, as well as the National Commission for Science, Technology & Innovation under the licence number NACOSTI/P/25/414706.

## Results

Disturbed behaviour, for the purpose of our analysis, was classified as any behaviour which fell outside of diurnal activity budget indicators such as feeding and walking. We observed at least one instance of disturbed behaviour in 18 trials (51.4% of the total). During pre-exposure, we observed disturbed behaviour in an average of 4.35% of elephants per group (SE = 0.019). The percentage was higher on approach and in the first minute of exposure with an average, respectively, of 8.39% (SE = 0.028) and 10.95% (SE = 0.043) of elephants exhibiting disturbed behaviour (Fig. 2). However, the percentage was lower in the last minute of exposure and first minute of post-exposure with an average, respectively, of 1.39% (SE = 0.0086) and 0.68% (SE = 0.0068) of elephants exhibiting disturbed behaviour. The average occurrence of disturbed behaviour in the first trial was 9.46% (SE = 0.026) but was lower throughout every phase of exposure in repeated trials, with an average of 3.23% (SE = 0.012) of elephants exhibiting disturbed behaviour (Fig. 2).

These results were confirmed in the generalised linear mixed-effect models, where elephants exhibited 3.5 times more disturbed behaviour in the first minute of exposure ($\beta = 1.26$, $p = 0.02$) than in pre-exposure, but were 70% less likely to display disturbed behaviour in repeated trials ($\beta = -1.19$, $p = 0.03$) compared to the first (Fig. 3a). Elephants fed 43% less on approach ($\beta = -0.56$, $p = 0.01$), 28% less in the first minute of exposure ($\beta = -0.33$, $p = 0.04$), 30% less in the last minute ($\beta = -0.36$, $p = 0.03$) and 50% less in post-exposure ($\beta = -0.69$, $p < 0.01$) than during pre-exposure (Fig. 3b). Elephants moved 83% more in the first minute ($\beta = 0.61$, $p = 0.01$) and 100% more in the last minute of exposure ($\beta = 0.69$, $p < 0.01$) than during pre-exposure (Fig. 3c). Elephants rested 67% less in the last minute of exposure ($\beta = -1.11$, $p = 0.01$), and were nine times more likely to rest during post-exposure ($\beta = 2.24$, $p < 0.01$) compared to pre-exposure (Fig. 3d). Fixed effects explained 31.7% of the variance in disturbed behaviour, suggesting a strong influence of exposure phase and trial type on disturbed behaviour responses (see Supplementary Note S3). In contrast, fixed effects explained less variance in feeding (4.0%), moving (6.9%), and resting (2.1%), indicating a larger role for individual or group-level variation.

Though we recorded residency status of groups at the time of observation, we found that including group ID as a random effect better accounted for differences in behaviour between groups. Similarly, including flight ID as a random effect better accounted for variations in environmental conditions between flights than temperature or wind speed alone. In this way, the models are constructed such that the only fixed effects are the experimental variables of interest as they relate to the drone as a stimulus, and the random effects include all types of variation that may arise outside of the experimental variables (i.e. inter-group differences and environmental conditions).

When subdividing disturbed behaviour into categories based on intensity of response we recorded no aggressive responses while fear responses were recorded only five times in 157 clips (Fig. 4). Most of the recorded disturbed behaviour falls at the lower end of the disturbance spectrum, corresponding to alertness and irritation.

## Discussion

Drones are becoming an increasingly powerful tool in studies of animal behaviour. In contrast to monitoring by conventional ground-based means, the use of a drone in fundamental studies of behaviour patterns requires research on the effects of the very tool used to make such observations. To date, there are a limited number of studies that investigate the capacity for a target species to habituate (or not) to the presence of a drone[11]. Here

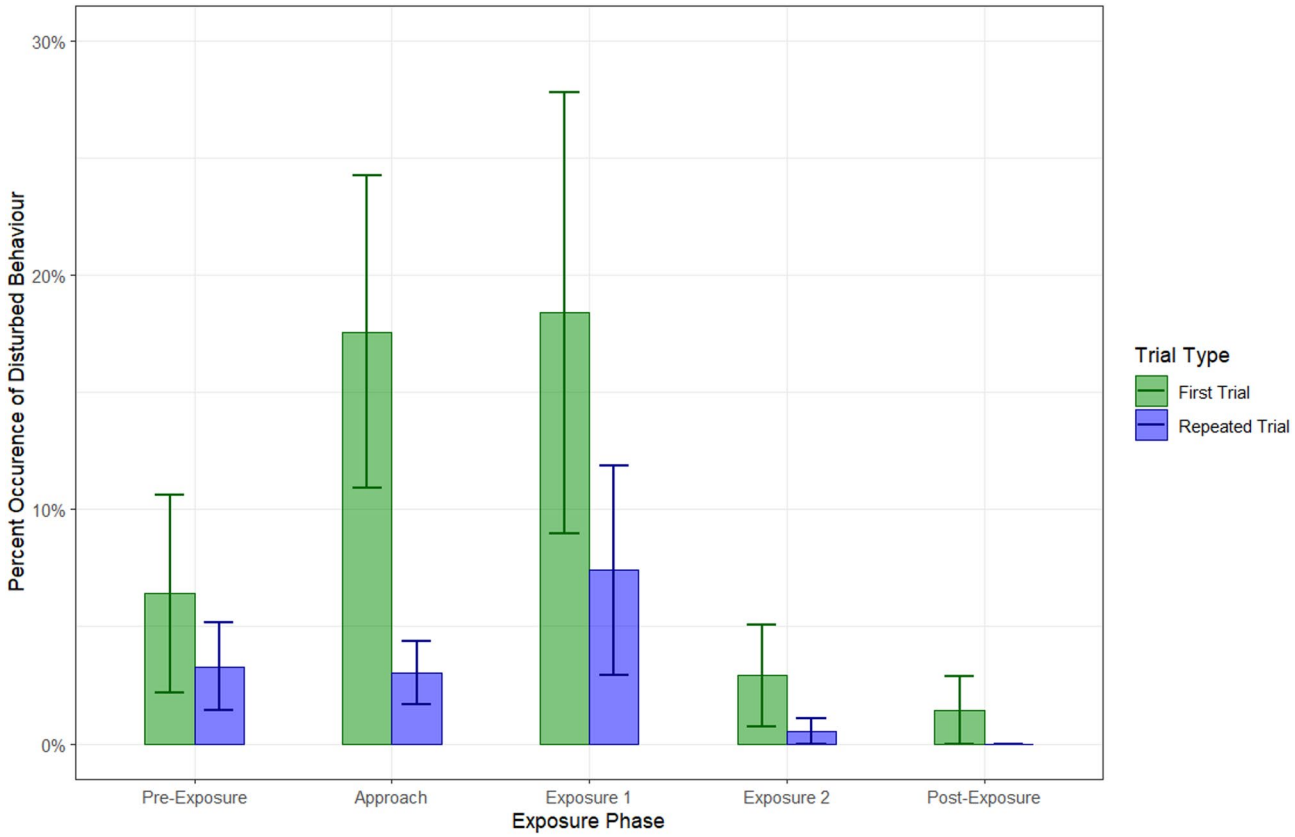


**Fig. 2**. Average percentage of elephants per group exhibiting disturbed behaviour throughout the phases of exposure, and in the first trial compared to repeated trials, with error bars denoting standard error.

we tested whether African elephants habituate to the presence of a drone being flown as a tool for observation via repeated trials of individually-identified family groups, measuring both negative reactions (disturbance) and baseline activities such as walking and feeding. We found that elephants displayed any kind of disturbed behaviour in around half of the drone exposure trials, indicating that drones do not invariably elicit negative or fleeing responses. Moreover, we found that despite an initial increase in the proportion of disturbed elephants in a group during the first minute of exposure, instances of disturbed behaviour returned to levels comparable to pre-exposure in the last minute of exposure and during post-exposure, suggesting that elephants can habituate to some degree to the presence of a drone over the course of a single trial. Additionally, elephants exhibited significantly less disturbed behaviour in repeated trials compared to the first. Taken together, this suggests that elephants can habituate to the presence of drones in both the short and long term. However, elephants significantly altered their baseline activity when exposed to a drone with proportionally fewer elephants feeding during each phase of the trial, more elephants walking in the first and last minutes of exposure, fewer resting in the last minute of exposure, and more resting during post-exposure. Exposure phase and trial type only explained 2–7% of the variation in baseline activity, so much of this variation is likely due to differences in behaviour between groups. Nonetheless, this indicates that behavioural observations from drones must take into account small-scale activity shifts, even if there seem to be no outward signs of disturbance [cf.[48]]. The implications of this could be especially significant if elephants are exposed to drones for much longer periods than the ones in this study.

During just under half of drone exposures no disturbed behaviours were recorded, indicating that flying techniques can significantly reduce the negative effects that a drone may have on elephants. This is in line with[25] who found that specific drone flying protocols lowered likelihoods of elephants exhibiting signs of disturbance. In addition,[27] found that a fixed-wing drone flying at 100 m had no discernible impact on the behaviour of elephants. Conversely, erratic and low altitude flight patterns of drones have been shown to consistently elicit a fleeing response, as when used to deter and chase elephants to prevent human-elephant conflict[24]. For fundamental research of elephant behaviour and in order to minimise disturbance, we recommend flying drones at higher altitudes (120 m or above, if possible) and to launch the drone at a good distance downwind from the elephant group (at least 500 m).

The observed decline in disturbed behaviour among elephants over single and multiple drone trials is comparable to findings from other studies providing evidence (or suggesting the possibility) of habituation to drones across a variety of mammalian and avian species[1,5,49–56]. However, the persistent alterations in baseline activity are comparable to other studies that found no habituation to the presence of drones and recorded sustained responses with no reduction in their frequency or intensity[14,24,39,57,58]. It is thus possible

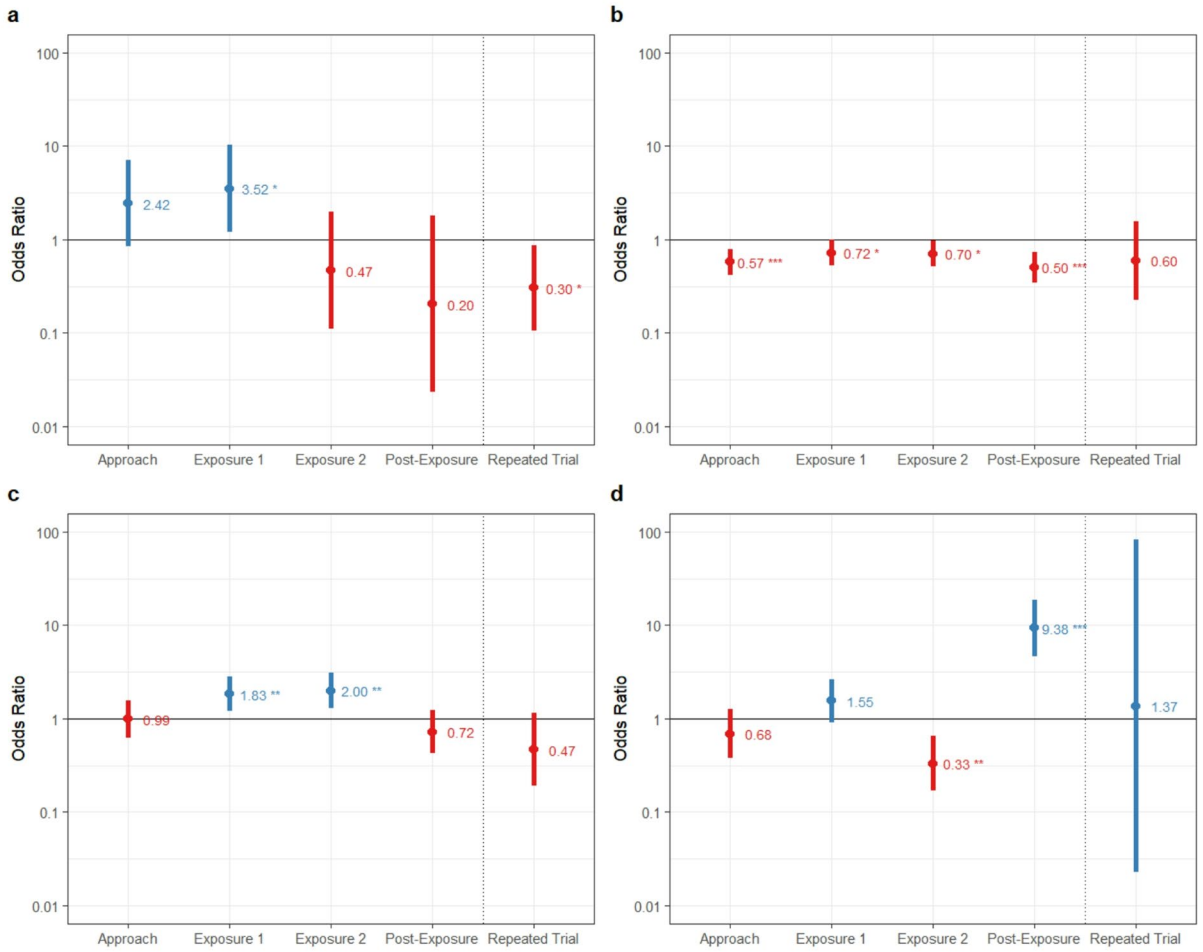


**Fig. 3**. Odds ratios (±95% confidence intervals) for behavioural responses across trial phases in beta-binomial GLMMs. Odds ratios are plotted on a logarithmic scale, with proportion of elephants per group exhibiting disturbed behaviour (**a**), feeding (**b**), moving (**c**), and resting **(d**) throughout the randomised clips. Red points indicate significantly lower odds compared to baseline (Pre-Exposure or First Trial); blue points indicate higher odds. Stars denote significance levels ($p < 0.05$; $p < 0.01$; $p < 0.001$).

that, despite behavioural indicators of habituation, some low-level disturbance caused by drones is persistent even after repeated trials. Such low-level disturbance might only be detected via fine-scale behavioural and/or physiological analyses, the latter of which was not recorded in this study [cf.[17,18,59]]. It also important to consider that animals habituated to human presence may still alter their behaviour and respond in different ways over time[60]. Cross-species comparisons using these techniques might help elucidate the underlying habituation mechanisms driving these trends.

To date, there are very few published studies in which elephants are exposed to drones, and none demonstrating that elephants can habituate to drone observation. However, there are other studies of elephants habituating to stimuli that reveal similar patterns. For example, it has been shown that elephants are capable of habituation to vehicles in places where they are often exposed to them[31–34]. A preliminary study has also shown that captive African elephants can habituate even to threatening auditory stimuli (buzzing bees and banging on pots and pans), indicating that they can develop stimuli-specific responses when exposed to them repeatedly[61]. Additionally, Asian elephants were found to partially habituate to playbacks of some predator vocalisations, which reduced their efficacy as a crop-raiding deterrent[62]. These varied precedents suggest that elephants are capable of habituating to various stimuli, and therefore could be capable of habituation to drones as well.

Even though our results show evidence of habituation in both the short and long-term, it is unclear exactly how long the effect lasts in elephants. The intervals between exposures for some groups during our trials were very large (up to 355 days), which suggests that the effects of habituation could be persistent over a long period of time. This is in line with the ability of captive bears to remain habituated to drones even after a significant interval[51]. Long-term research is needed to examine the persistence of habituation effects.

The observed increase in the proportion of elephants resting during post-exposure was unexpected. While a decrease in feeding and an increase in movement might indicate some disturbance (e.g. elephants becoming more alert and moving away from the drone), resting is not a clear indicator of disturbance effects. Given that resting and listening cannot be readily differentiated by visual observation, it is possible that elephants were

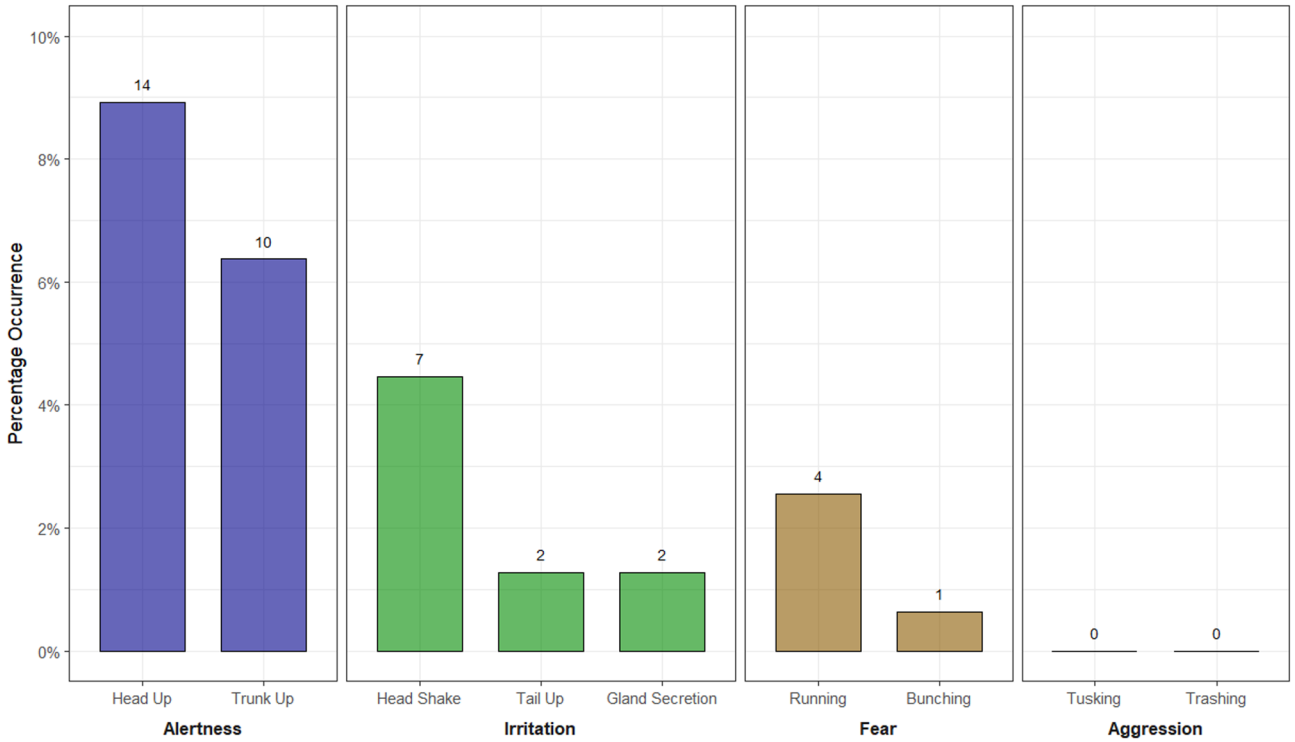


**Fig. 4**. Types of disturbed behaviour per category of disturbance and their recorded frequencies in each clip (n = 157).

listening out and alert during post-exposure in case the drone should return. At the same time, it is possible that this resting behaviour was an effect of habituation and a sign of tolerance for the drone over the course of a trial. However, since resting was the least observed of the activities included in the models (present in only 24% of observations), this shift in behaviour might be limited to specific circumstances or an artefact of the small sample size. Studies of acoustic communication (e.g. whether elephants stop vocalising to better hear the drone) could help understand these patterns.

There are other external factors that could have affected our results. For example, baseline behaviour can be influenced by the presence of vehicles or environmental factors such as the arrival of a musth bull in a cow/calf group[31,63]. On one occasion the arrival of the drone overhead a cow/calf group coincided with that of a bull, which could have affected group activity. In addition, there were a few groups which showed greater signs of disturbance than others during pre-exposure. This was particularly evident in the case of one cow/calf group who were visibly skittish and seemed to be actively avoiding vehicles. The matriarch of this particular group was fitted with a tracking collar, which revealed that the group had arrived in SNR only the day before their first exposure to the drone, after a journey of 45 km across an area with high levels of historical illegal killings of elephants[64]. This trek was completed mostly at night and at high speed, indicating that the members of this family would have been in a heightened state of alert due to a perceived threat of danger[64]. Given these circumstances, it is perhaps unsurprising that the group exhibited nervous behaviour around unfamiliar anthropogenic stimuli. Despite this heightened level of alert, the group still showed signs of decreasing disturbed behaviour during the second half of their first exposure to the drone and across subsequent trials. Studies on other elephant populations could further explore habituation to drones among groups who are less tolerant of human presence.

In summary, our results indicate that elephants in SNR and BSNR demonstrate gradual habituation to drones. The decrease in disturbed behaviour over the course of each drone exposure and repeated flights suggests that drones can be used as an effective tool for behavioural observation. However, changes to activity patterns need to be accounted for by establishing baseline behaviour prior to drone exposure. We recommend that future studies using drones for observing elephant behaviour follow protocols to minimise disturbance and to evaluate fine-scale impact on behaviour over time.

## Data availability

All data and code are available from Dryad digital repository: https://doi.org/10.5061/dryad.c866t1gjb. Point of contact: angus@savetheelephants.org.

Received: 8 May 2025; Accepted: 24 October 2025
Published online: 27 November 2025

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## Acknowledgements

The authors would like to extend their gratitude to Kenya's Wildlife Research and Training Institute and the National Commission for Science, Technology and Innovation for granting the relevant permissions for this study. We are grateful in addition to the management of Samburu and Buffalo Springs National Reserves for granting permission for the field trials. We thank Colossal Biosciences for financial support and are grateful to all staff of Save the Elephants for support throughout the study.

## Author contributions

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## Declarations

## Competing interests

The authors declare no competing interests.

## Additional information

**Supplementary Information** The online version contains supplementary material available at https://doi.org/10.1038/s41598-025-25762-2.

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