Logging roads as surrogates for elephant trails: Facilitating social signaling by small forest ungulates despite increasing risks

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Abstract
With global elephant populations in decline, a grave consideration is the loss of their ecological engineering effects that benefit other species, such as the maintenance of extensive trails through tropical forests. Anthropogenic roads can serve as surrogates for elephant trails despite exposing users to higher risk from bushmeat harvest. We explored the use of forest management roads by Weyns’s duiker (Cephalophus weynsi) in Kibale Forest, Uganda. Faecal latrines were located on the road, clustered, and frequently revisited and replaced, with no latrines found in the surrounding forest or trails. Latrines occurred most frequently at road/trail intersections, at the road center, and where canopy and ground vegetation cover were lowest. Latrine decay in the forest was significantly higher than on the road and an exclusion treatment indicated coprophagous beetles as the primary agents of dung removal. Our findings demonstrate the dependence of a forest ungulate on roads for social signaling through dung, which is a behavior common to cryptic forest mammals that coevolved with trail-forging megaherbivores. While logging roads pose multiple threats to forest biodiversity, the catastrophic decline of elephant populations means that forest managers must consider weighing these costs against the benefits of conserving at least some roads as surrogates for elephant trails.

KEYWORDS
Cephalophus weynsi, chemical signaling, coprophagous beetles, duikers, forest conservation, latrine placement, megaherbivore extinction

1 | INTRODUCTION

The construction of road networks through tropical forests causes significant disturbance through edge effects, barriers to movement, and mortality of forest wildlife by vehicles, as well as facilitating biological invasions (Goosem, 2007; Laporte, Stabach, Grosch, Lin, & Goetz, 2007; W. F. Laurance, Goosem, & Laurance, 2009). Additionally, roads facilitate access for forest exploitation by loggers, poachers, or hunters, and industrial activities (W. F. Laurance & Arrea, 2017; W. F. Laurance et al., 2009; Putz, Blate, Redford, Fimbel, & Robinson, 2001). This is particularly problematic because most tropical forests occur in developing countries where conservation management and natural resource policy may be underdeveloped and/or poorly enforced (Smith, Muir, Walpole, Balmford, & Leader-Williams, 2003; Sunderland et al., 2005). For example, in the tropical forests of central Africa, elephant (Loxodonta cyclotis and L. africana)
populations are in decline due to exploitation for the illegal ivory and bushmeat trades (Maisels et al., 2013; Ripple et al., 2016; Wittenmyer et al., 2014).

As the widest-ranging megaherbivore in the tropical forest environment (Blake & Inkamba-Nkulu, 2004), elephants are crucial ecosystem engineers, capable of creating natural clearings of considerable size (G. Haynes, 2012; Laws, 1970). The physical damage that they cause to vegetation, by feeding on and moving through it daily, can occur in dense forests within which they maintain a network of trails (Kortlandt, 1984; Vanleeuwe & Gautier-Hion, 1998). These trails are used by other wildlife species and have cascading effects on the entire forest ecosystem (Blake & Inkamba-Nkulu, 2004; Pringle, 2008). Thus, while the long-term effects of the drastic decline - and impending extinction - of elephants as keystone species remain poorly understood (Blake & Hedges, 2004; Breuer, Maisels, & Fishlock, 2016; G. Haynes, 2012; Poulsen et al., 2017), it seems obvious that one of those effects will be the disappearance of substantial and long-standing trail networks from the tropical forests of Africa and Asia.

The dense undergrowth of primary forests impedes visibility, locomotion, and intraspecific interaction for many forest animals (Pardini, De Souza, Braga-Neto, & Metzger, 2005; Pires, Koeler Lira, Fernandez, Schittini, & Oliveira, 2002). Their socio-behavioral ecology has, however, coevolved with the forest clearings and trails made by megaherbivores (Edwards, Tobias, Sheil, Meijaard, & Laurance, 2014), which are used by the ground-dwelling animal assemblage to frequent water sources, establish territorial borders, and interact with conspecifics (Blake & Hedges, 2004; Vanleeuwe & Gautier-Hion, 1998). Although these trails are beneficial, using them incurs a predation risk that imposes a selective pressure toward crypsis and extended or indirect communication, such as chemical signaling (Brashares & Arcese, 1999; Gosling, 1982) and they provide both visual and olfactory cues, which may be easier to detect by intended receivers. Placement of these latrines depends on their purpose and influences their efficacy for signaling (Brashares & Arcese, 1999; Roper et al., 1993; Wronski, Apio, Plath, & Ziege, 2013). Maximizing detectability to conspecifics is essential and some species preferentially place dung on particular substrates for visual and olfactory amplification (Hayward & Hayward, 2010) and at frequented locations such as waterholes, along territorial borders, trails and abandoned roads, as well as at their intersections (Brown & Macdonald, 1985; Gorman & Trowbridge, 1989). However, there are expected trade-offs of visibility, durability, and security of dung deposits, which vary depending on the conditions of the microhabitat selected.

We predicted that logging roads with low vehicle and pedestrian traffic are functional surrogates for elephant trails through the forest. We tested this prediction for Weyns’s duiker (Cephalophus weynsi), a small antelope endemic to the moist, lowland forests of Central Africa. Despite a lack of range-wide demographic data and the burgeoning bushmeat trade, this species is considered of least concern (IUCN, 2016); however, it serves as a proxy for all threatened small ungulates in this landscape. These duikers defecate at latrines, which is indicative of territorial signaling among solitary and cryptic conspecifics in their densely vegetated habitat. We expected duiker latrines to be placed in sites that are most likely to be frequented by conspecifics, such as along roads and at trail intersections. We also expected latrines to be placed at microhabitats in which dung beetles are less likely to forage, such as open areas where moist dung desiccates rapidly during the day.

2 | METHODS

2.1 | Study area and species

This study was conducted at the Makerere University Biological Field Station, Kanyawara district, Kibale Forest National Park (KFNP), an intermediate altitude (1,530 m), moist evergreen forest in western Uganda (0°13′N–0°41′N and 30°19′E–30°32′E, Figure 1). Mean annual rainfall at Kanyawara is 1,740 mm per annum, with a dry season falling between May and August, and annual mean temperature ranging around 23.1°C. KFNP consists of a variety of ecosystems and vegetation types including mature, midaltitude, moist semideciduous and evergreen forest (57%), colonizing forest (19%), grassland (15%), woodland (4%), and lakes and wetlands (2%), as well as plantations of exotic tree species (e.g., Cupressus lusitanica, Pinus spp. and Eucalyptus spp.) (1%) (Chapman & Chapman, 1997). The focal study area (Figure 1) consisted of a road (~4 m wide), which was originally constructed as a logging road and is now used by wildlife managers and researchers, that extends for 6.5 km from the field station to a swamp. This road through dense, closed-canopy forest is used by human pedestrians, research vehicles (once or twice per week), and large wild primates.
during daytime, and elephants and small ungulates mainly at night.

2.2 Data collection

The forest road and 500 m of all intersecting wildlife trails, as well as 200 m line transects perpendicular to the road into the surrounding forest every 500 m were monitored daily over a 10-day period (August 2015) for faecal deposits by Weyns’s duiker (Cephalophus weynsi), which is common in the area. All dung deposits were flag-marked and GPS-tagged for subsequent nearest-neighbor analysis in QGIS (QGIS Development Team, 2015). Overall trail width and distance to the nearest trail edge were measured at each site, as well as the distance from the nearest trail intersection. Ground and canopy vegetation cover were recorded using a 0.25 m² quadrat and photographed at a standard height (1.5 m) and optical magnification (50 mm) for three locations per deposition: the faecal deposition site, 5 m further along the trail (alternating forward and reverse per site) and 5 m into the forest perpendicular to the trail (alternating left and right per site). Vegetative cover (%) was subsequently determined from these images using Fiji software (Schindelin et al., 2012). Each newly discovered deposit was weighed and divided into five experimental samples of which two were placed inside cages of plastic mesh (mesh diameter 0.22 mm) to exclude dung beetles, with the experimental samples being: (a) “road-uncaged,” left on road with no exclusion; (b) “road-caged,” left on road in an exclusion cage; (c) “forest-uncaged,” placed in the forest with no exclusion; (d) “forest-caged,” placed in the forest in an exclusion cage; and (e) “removed,” removed to the laboratory. Each experimental sample was reweighed daily to assess the relative wet mass (g) loss for caged versus uncaged deposits both on the road and in the forest. The removed samples (treatment 5) were dried on silica pellets in an oven (60°C) overnight and used to develop a wet/dry mass conversion for an average duiker faecal pellet mass.

2.3 Statistical analyses

All statistical analyses were run using R statistical software (R Core Team, 2017). The relationship between frequency of latrines by distance to the nearest neighbor (m), distance to the nearest intersection (m), and standardized distance from the road center (m) was plotted. To determine if the distribution of these latrines along these three gradients was nonrandom, nonparametric (Spearman’s Rank-Order) correlation tests were implemented. Overall significance of canopy and ground cover (%) by potential latrine deposition site (i.e., forest, road and site), as well as daily proportion of dry mass lost (%) per treatment (i.e., forest caged, forest uncaged, road caged and road uncaged) was determined using one-way analysis of variance (ANOVA) implemented in the car package (Fox et al., 2018). Data were visualized using GraphPad Prism version 5.00 for Windows, GraphPad Software, La Jolla, CA (www.graphpad.com).

3 RESULTS

During the 10-day observation period, a total of 90 faecal latrines were observed on the road. The road was intersected by 37 game trails and no latrines were ever found within 500 m of the road along these trails, nor were any found in the surrounding forest. Latrine sites (Figure 1) were densely clustered, with 78% of all sites occurring within 10 m of one
another ($\rho_S = -0.63$ [95% CI: -0.91; -0.23], $p < .01$, Figure 2a). Latrines occurred nearer to game trail intersections, with 71% of all deposits occurring within 10 m of the nearest intersection ($\rho_S = -0.73$ [95% CI: -0.92; -0.28], $p < .01$, Figure 2b). Clearing (road) width at latrine sites was $4.32 \pm 0.6$ m (mean ± SE) and latrines were concentrated in the middle of the road, with 31% of all deposits within 0.2 m, 58% and 83% within 0.6 and 1.0 m from the road centerline, respectively ($\rho_S = -0.63$ [95% CI: -0.89; -0.04], $p < .05$, Figure 2c). There was a significant effect of canopy cover (%) on latrine site ($F_{[2,1,412]} = 131.98; p < .01$, Figure 2d). Post-hoc comparisons indicated that the mean canopy cover over latrine sites (41 ± 21%) was significantly lower than at random nonlatrine sites along the road (51 ± 23%, mean difference = 10.3 [95% CI: 6.9; 13.6], $p < .001$) and in the forest (64 ± 22%, mean difference = 23.0 [95% CI: 19.7; 26.4], $p < .001$), and canopy cover over the road was obviously lower than in the forest (mean difference = 12.8 [95% CI: 9.4; 16.1], $p < .001$). There was also a significant effect of ground cover (%) of herbaceous vegetation on latrine site ($F_{[2,1,413]} = 459.32; p < .01$, Figure 2e). Post-hoc comparisons ($p < .05$) indicated that the mean ground cover at a latrine site (37 ± 18%) was significantly lower than at random nonlatrine sites along the road (55 ± 22%, mean difference = 17.7 [95% CI: 14.2, 21.2], $p < .001$) and in the forest (81 ± 27.4, mean difference = 44.4 [95% CI: 40.9; 47.9], $p < .001$), as well as the road being significantly lower than the forest (mean difference = 26.7 [95% CI: 23.2; 30.2], $p < .001$). Finally, there was a significant effect ($F_{[3,264]} = 101.93; p < .01$) of treatment on average daily dry mass loss (%) (Figure 2f), where average daily dry mass loss in the “forest-uncaged” treatment (19.3 ± 14.9%) was significantly higher than that of the “road-caged” (1.5 ± 1.3%, mean difference = 17.8 [95% CI: 14.2, 21.4] $p < .001$), “road-uncaged” (4.1 ± 6.89%, mean difference = 15.2 [95% CI: 11.5, 19.0], $p < .001$), and “forest-caged” (4.4 ± 14.9%, mean difference = 14.9 [95% CI: 11.3, 18.5], $p < .001$) treatments.

4 | DISCUSSION

As expected, the duikers in our study area were found to defecate in clusters (latrines) and those on the road were generally located near intersections, with the majority occurring within 10 m of both the nearest neighboring latrine (Figure 2a) and the nearest trail intersection (Figure 2b). Such placement has been recorded for carnivores (Brown & Macdonald, 1985; Gorman & Trowbridge, 1989) but has been poorly studied in herbivores. Despite daily attempts to locate latrines in the primary forest by walking line transects, none were found on the forest floor or on intersecting trails made by small animals. Furthermore, duikers placed latrines preferentially along the center of the road as the number of latrines decreased proportionally toward its edge (Figure 2c).

In addition, latrines were most frequent where the road had less surrounding ground and canopy cover (Figure 2d,e). Taken together, these findings suggest that Weyns’s duiker latrine placement in KFNP is nonrandom and selects for substantial clearings through the forest, such as logging roads, rather than small animal trails and dense primary forest.

The experimentally relocated latrines indicated that dung removal and/or decomposition rates were much higher in the forest than on the road, as uncaged latrines in the forest lost significantly more mass (by an order of magnitude) than those on the road (Figure 2f). The mesh diameter of 0.22 mm excluded dung (scarab) beetles, which we observed removing dung from the uncaged treatment but were rarely from latrines on the road. These high rates of dung decay in the forest are in accordance with similar studies, for instance, van Vliet, Nasi, and Lumaret (2008) found that in the forests of north-east Gabon (Ipessa Reserve), decay of duiker dung is mainly because of an intense dung beetle activity that can effectively “hide” duikers’ presence. Alternatively, the scarabs avoid foraging in vegetation clearings due to the lack of cover, because the cost of predation is much higher than the foraging gains. Avoiding clearings despite food availability is well known for a wide range of small animals (Lima & Dill, 1990). This behavior might be particularly accentuated for forest species, as has been shown for some birds and small mammals, which do not, or rarely, cross even small clearings such as roads (Develey & Stouffer, 2001; Goosem, 2001; S. G. W. Laurance, Stouffer, & Laurance, 2004).

More specifically, coprophagous scarabs residing in a woodland-savannah mosaic habitat have been found to not forage on dung more than 1–2 m from protective woodland cover, while dung within the woodland patches was regularly consumed (Mann and Marais unpubl.). If so, duikers appear to be selecting for drier, more exposed latrine sites to avoid removal by dung beetles, while simultaneously enhancing detectability by conspecifics.

We could not discern whether the defecation sites were indeed latrines (individuals) or middens (groups of individuals) but we conservatively refer to each as a latrine. Our failure to locate latrines in the forest could partly be due to faster removal by coprophagous beetles than on the road, but this does not fully explain the complete absence of latrines. Even uncaged latrines moved into the forest took several days to deteriorate, whereas latrines on the road were refreshed on a nightly basis. It thus appears that duikers position their latrines on roads to maximize their detection, probability of encounter, and longevity, thus maximizing the efficiency of their chemical signaling.

Chemical signaling forms a crucial part of an organism’s extended phenotype and has several advantages over more
FIGURE 2  Observational findings of latrines positioned along the logging road. Over a 10-day period, 90 latrines were recorded and assessed for: (a) latrine frequency per nearest neighbor distance; (b) latrine frequency by distance to the nearest intersection; (c) latrine frequency by standard distance from the road Center; (d) percentage canopy cover per site, road, and forest; (e) percentage ground cover per site, road, and forest; and (f) mean daily dry mass loss per location (forest and road) by treatment (caged and uncaged). ***indicates $p < .001$
direct (e.g., visual, behavioral) forms of signaling such as safety from competitors or predators (K. F. Haynes & Yeargan, 1999; Schaedelin & Taborsky, 2009). Chemical signals such as latrines simultaneously transmit multiple channels of information about the signaller including sex and breeding status (Jordan, 2007), dominance (Binz, Foitizka, Staab, & Menzel, 2014), frequency of visitation (Eltz, 2006), individual identity (Burgener, Dehnhard, Hofer, & East, 2009), and even health status (Zala, Potts, & Penn, 2004) without the need for direct contact. In terrestrial mammals, chemical signaling is particularly adaptive in species that are solitary, wide-ranging, occur at low densities, or occupy closed habitats in which direct conspecific interactions are rare (Heinsohn & Packer, 1995). We, therefore, argue that, with the removal of clearings the chemical signals of Weyns’s Duiker will be much less effective due to lower detectability by conspecifics and much higher removal/decomposition rates, and that this is likely to negatively impact their social ecology (Blake & Inkamba-Nkulu, 2004).

In undisturbed African forests, elephants (Loxodonta cyclotis) serve as ecosystem engineers, creating and maintaining substantial, permanent trails similar to forest roads (Vanleeuwe & Gautier-Hion, 1998). These trails are used by numerous other forest species, such as duikers, for various functions including territorial marking, and their social biology has coevolved with the effects of elephants (Blake & Inkamba-Nkulu, 2004). Currently, forest elephant populations are in steep decline and suffer very slow recovery rates, even where effectively protected (Blake, 2002; Breuer et al., 2016; Poulsen et al., 2017; Turkalo, Wrege, & Wittemyer, 2018). This compromises their role as ecosystem engineers, reducing elephant trails in forests, with probable cascading effects on other dependent species. Counterintuitively, we argue that anthropogenic clearings, such as logging roads, can substitute for this functional role of elephants, as evident through our study by the provision of open, dry microhabitats suitable for latrine placement. In challenging terrain, logging company engineers deliberately build roads on existing elephant trails. Elephants choose to travel along ridgelines and flat riversides, creating economical contour paths. They suffer the same drawbacks as heavy logging trucks finding it hard to climb steep slopes. Thus, logging roads in hilly country already replace the location of elephant trails and their usefulness to duikers. In mountainous areas of western Cameroon, where elephants are locally extinct, local people said their own paths followed the old elephant trails (Maisels, Keming, Kemei, & Toh, 2001). Unfortunately, the reality is that this adaptive response to elephant declines and newfound dependence on anthropogenic roads increases the likelihood of exposure to poachers, bushmeat traders, and other edge effects of commercial forestry (Johns, 1988). Thus, the disappearance of elephants may indirectly accelerate the loss of trail-dependent species that are forced to frequent risky roads. Nevertheless, where human traffic on roads can be controlled, conservation practitioners should consider the merits of maintaining forest roads where they occur in areas receiving attention for biodiversity protection and restoration. In addition to serving as surrogates for elephant trails, roads can be patrolled to monitor dung middens as an index of duiker abundance. Also, the risk of roads being used by poachers can be turned into an opportunity for detecting them using cryptic, remote camera sensors that can be efficiently deployed along roads. A caveat is that roads are often cut through the forest in straight lines and anthropogenic linear features are known to upset predator–prey interactions (DeMars & Boutin, 2018). Nevertheless, using creativity and judicious selection of which intersecting road segments to conserve and which to remediate, a substitute may emerge for elephant trails through African forests. That is until such time as local elephant populations are allowed to recover.

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CONFLICT OF INTEREST

The authors declare no potential conflict of interest.

AUTHOR CONTRIBUTIONS

V.N., W.V., and J.M conceived the study and designed the experimental protocols with input from J.T.d.T. Data were collected by V.N., W.V., and J.M. Analyses were conducted by V.N. and F.B. All authors discussed and interpreted the data. V.N. and F.B. wrote the manuscript with invaluable guidance from J.T.d.T.

DATA ACCESSIBILITY

Data are available in the supplementary materials section (Table S1) or upon request from the corresponding author.

ETHICS STATEMENT

As all sampling was noninvasive and collected materials were processed with the Kibale Forest National Park, no
ethics approval was required to conduct this research. All research conducted within the park was overseen by researchers from the Makerere University Biological Field Station and park officials.

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**SUPPORTING INFORMATION**

Additional supporting information may be found online in the Supporting Information section at the end of this article.