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・Title

Rushing for “burned” food: Why and how does a group of patas monkeys (*Erythrocebus patas*) reach freshly burned areas?

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Abstract

Recently, considerable attention has been paid to animal adaptations to anthropogenic environments, such as foraging in burned areas where plants are promoted to regenerate by anthropogenic burning. However, among primates, reports on the utilization of resources that are available immediately after burning have been limited to a few primate species. In this study, we investigated and compared the activity budgets and food categories of a group of patas monkeys (*Erythrocebus patas*) in freshly burned areas by comparing them with those in previously burned areas and unburned areas. We also assessed the proportion of time spent in the freshly burned area before and after the fire: GPS collars were fitted to five of the six adults in the group, and their patterns when they traveled toward freshly burned and unburned feeding areas were compared. Patas monkeys spent more time in freshly burned areas after the fire, and they visited such areas mostly for feeding, particularly on roasted seeds of *Cissus populnea*. Furthermore, patas monkeys traveled faster and in a more synchronized way toward freshly burned areas. This “apparent goal-directed” travel began at least 1 hr before arriving. Results indicate that the group recognized freshly burned areas as valuable, and the monkeys were able to travel in a goal-directed manner to them despite their variable locations. We suggest that smoke from freshly burned areas provides a visual cue with which to orient to the burned areas. Our results also support the notion that some primates are flexible enough to adapt to and benefit from anthropogenic environmental changes.

Keywords: Anthropogenic environments, Goal-directed behavior, Temporal synchrony, Travel direction, Collective movement, Group living

Introduction

At present, given the increasing human population and continuous development worldwide, almost all living organisms live in human-induced environments (Lee 2010; Sih et al. 2011; Treves 2009). In primatology, the process by which primates change their behaviors in anthropogenic habitats has received increasing interest (Hockings et al. 2012; Humle and Hill 2016; Strier 2017). Behavioral adaptations include changes in activity budgets, ranging behavior, social organization, and most commonly, diet (McLennan et al. 2017). In anthropogenic habitats, primates have been widely fed on agricultural crops, garbage, and provisioned items (McLennan et al. 2017). One anthropogenic habitat change that may cause behavioral adaptations is burning, such as slash-and-burn agriculture, which is a traditional practice (Eriksen 2007). Controlled burning is a method used in parts of Africa to manage savannah-type national parks as part of habitat management. Once a fire is set, grasses burn vigorously, temporarily reducing their biomass (Sinclair 1977). Consequently, animals such as grazers (those that rely on grasses) must adapt to such instantaneous changes in their habitat (Vieira and Marinho-Filho 1998). Most animals can flee when fires approach, whereas some animals suffer from smoke asphyxia (Barlow et al. 2002; Peres 1999). Animals that survive the fire and smoke may suffer in other ways, for example, starvation, if they cannot find a new place to settle (Cochrane 2002).

Although burning may have several negative effects on animals, post-burning environments can be beneficial. Burns facilitate the regeneration of grasses over time (Everson and Everson 1987), and regenerated grasses often have high nutritional values and bulk density (van de Vijver et al. 1999). Immediately after the fires, invertebrates and plant seeds may become accessible. For example, green monkeys (*Chlorocebus sabaeus*) utilize burned invertebrates (Harrison 1983); vervet monkeys (*C. pygerythrus*) easily prey on ants that appear on the surface when they are escaping from fire and smoke (Jaffe and Isbell 2009), and chimpanzees (*Pan troglodytes*) forage on roasted seeds (Brewer 1978). Compared with grasses, these foods do not continue to regenerate, and thus such foods have limited availability. The limited accessibility and abundance of such resources can result in the home-range expansion into burned areas as animals take advantage of the foods in them (Herzog et al. 2014; Rasmussen 1983). However, few systemic studies have focused on the utilization of burned areas by primates (but see Herzog et al. 2014, 2020; Jafe and Isbell 2009).If burned areas are attractive feeding sites for primates, then how do they find and access the places? The general foraging theory of primates may be applied to answer this question: In general, a primate group tends to travel fast and linearly toward feeding sites that they visited before when the resource is of high quality, in quantity, or both (Janmaat et al. 2006; Noser and Byrne 2007; Pochron 2001; Salmi et al. 2020). Such fast and linear travel patterns indicate that the monkeys are using their spatial memory to navigate to a specific feeding site (Bell 1991; Noser and Byrne 2007; Salmi et al. 2020). For example, yellow baboons (*Papio cynocephalus*) accelerated and directed travel an hour before arriving at valuable feeding sites despite their inability to see or smell the food (Pochron 2001). Notably, studies consider the feeding site as rare, isolated, or highly clumped, such as a specific fruit tree. However, high-quality feeding sites can be widely distributed. Patas monkeys (*Erythrocebus patas*) are terrestrial primates living in savannahs. Although they form one-male multi-female groups, multimale situations occur because of male influx in a distinct mating season (Chism and Rogers 1997; Chism and Rowell 1986; Ohsawa et al. 1993). They rely on particular types of food, namely insects and gums (Isbell 1998; Nakagawa 2000), and selectively feed on a small number of high-quality foods (Nakagawa 2003). Given the relatively heavy body mass of patas monkeys among primates whose diet is gummivorous and insectivorous, they have a unique diet (Isbell 1998) in accordance with the principle of physiological ecology (Jarman 1974; Bell 1971). Studying whether the general foraging theory can be applied to patas monkeys is interesting, but previous studies on the theory have paid little attention to such species.

When foods such as insects and gums become available in burned areas, patas monkeys might employ goal-directed travel to those areas. However, the locations of naturally burned areas are unpredictable, and even in the case of controlled burning by authorized agencies, the location of fires may change annually. Compared with primates that rely on spatial memory to guide their goal-directed travel, patas monkeys would need to use a different cue to travel to the burned area.

Individuals within a group must also coordinate their travel, especially during goal-directed traveling. Either they must reach a consensus on where to go or manipulate other members' travel (Boinski 2000) because individual choices lead to the final decision of a group movement (King and Cowlishaw 2009; King and Sueur 2011; Pillot and Deneubourg 2010). In general, collective movements result from the low variance of travel velocity (e.g., the coefficient of variation [CV]) and the synchronized direction among individuals (i.e., travel direction). Therefore, these parameters are important for understanding how animals in groups achieve a coordinated movement (Herbert-Read 2016; Strandburg-Peshkin et al. 2017). However, in primates, previous studies have focused more on identifying goal-directed travel than on the travel variability of velocity and synchrony of travel direction among individuals when traveling toward feeding sites. In addition, they substituted data from the observer's location for the group's location (e.g., Noser and Byrne 2007) or used data from the location of particular individuals in the group (e.g., Normand and Boesch 2009). Moreover, these studies did not collect data on the positions and movements of each individual in groups.

Previous studies on group decision-making in savannah-dwelling primates are limited to baboons (*Papio spp.*) (Altmann 1979; King and Cowlishaw 2009; Rhine

1975; Stueckle and Zinner 2008). Baboons are considered as suitable subjects for this field of research because they often spread out when traveling (often up to 320 m wide; Harel et al. 2021), and their travel coordination is assumed to be more challenging when groups spread. Patas monkeys are also known to spread out during traveling (up to 300 or 500 m wide; Chism and Rowell 1988). Moreover, they tend to move laterally or at angles across the group's center of mass rather than along with others (Isbell et al. 1999). Such conditions make patas monkeys interesting subjects for studying the process of traveling toward feeding sites and their collective movements.

In this paper, we aimed to investigate the adaptability of patas monkeys to anthropogenic burning and examine the difference in the proportion of time spent in the freshly burned area before and after the fire and their activity budget and diet in the area. We also aimed to explore the process by which patas monkeys find and access freshly burned areas and compare their travel patterns toward freshly burned areas with those toward unburned feeding areas.

Methods

Study site and subjects

We conducted our study from December 2022 to March 2023 in the Mole National Park, Ghana (09°12′–10°06′ N, 01°25′–02°17′ W, and 150 m above sea level), which is located in the Guinea savannah zone, and the open savannah woodland with a layer of grass is the dominant vegetation (Lawson et al. 1968). The average annual rainfall is approximately 1100 mm, and the average temperature is approximately 28 °C. The dry season lasts from November to March, and the rainy season lasts from April to October (Schmitt and Adu-Nsiah 1993). Controlled burning is carried out by the park staff every year from December to early February during the dry season to promote the growth of new herbaceous plants in the park. The location and timing of burning vary annually, with some areas left unburned to protect animals with cover from predators and poachers.In this study, we investigated a group (named Motel group) of patas monkeys consisting of 17 individuals, including one adult male, five adult females, and 11 juveniles and infants. The home range of the group is in the southeastern part of the national park, which includes the headquarters.

Spatial data collection

We fitted GPS collars (GLT-02, Circuit Design, Inc.) to the sole adult male (MC) and four of the five adult females (Sa, Sk, Kr, and Sh) of the group. Veterinarians (YM or RS) immobilized the animals with zoletil (5 mg/kg) and medetomidine (0.1 mg/kg) with a blowpipe and later reversed the drugs with atipamezole (0.5 mg/kg). The GPS collar (less than 250 g) was less than 5% of the body mass (6.2–10.8 kg ($N = 5$); YM, unpublished data) as suggested by the American Society of Mammalogists (1998). See Supplementary Information for the details on the process. The GPS collars recorded data on the location (latitude, longitude), time, and positional dilution of precision (PDOP, an index of position accuracy) every 10 min from 7 a.m. to 5 p.m. between December 12, 2022, and March 1, 2023. After data collection, we successfully removed the collars from all the monkeys by remote electronic drop-off systems. We calculated the three-dimensional positioning success rate (the number of successful positioning attempts divided by the total number of positioning attempts) to remove large position errors. Results showed that all data had the three-dimensional positioning success rate of 100%, and only the data with PDOP of six or less were used (D’Eon and Delparte

2005). Consequently, we collected 28,849 pt of GPS fixes (Table S1).

Ethical note

The procedures carried out in this study were approved by the Animal Experimentation Committee of Kyoto University in Japan (# 202021) and by the Wildlife Division of the Forestry Commission of Ghana (WD/A.185/VOL. 13/69).

Behavioral data collection

We also observed the group from 7 a.m. to 5 p.m. by following one of the GPS-collared individuals for an hour at a time from a distance of 3 to 5 m. We selected the next focal animal as the one which we have not observed on the day to record all the individuals evenly each day. If we lost the focal individual but found it within 20 min, then recording was resumed until the total following time reached 1 h. Consequently, we observed the individuals for 708 h in total (Table S1). During the focal follow, we recorded the individual’s activities, (i.e., foraging, feeding, traveling, resting, and others) of the individuals every 10 min instantaneously corresponding to the timing of the GPS fixes. Foraging was defined as searching for food such as moving rocks, digging up the ground, or looking at the ground and surrounding trees while moving forward or not; feeding was defined as having food in the mouth or manipulating food with the hands; traveling was defined as continuing to move without looking at the ground or surrounding trees. Food items (the species and the part eaten) were recorded whenever possible. However, in this paper, we primarily used the following food categories for analyses: animal matter (e.g., insects, lizards, birds, and bird eggs), flowers and buds, fruits, gums, seeds, leaves, and garbage (e.g., human food waste). We also recorded the following location types where the focal individual was observed every 10 min: “freshly burned area” (where observers had detected fire or smoke at the time), “previously burned area” (with ash but no fire or smoke), and “unburned area” (with no evidence of burning during the research period).

Statistical analyses

Changes in the time proportion of land use by burning

First, we plotted all GPS fixes in freshly burned areas onto a map in Quantum GIS (QGIS; 3.30.1). Next, we created areas within the radius of 100 m around the GPS fixes because the observer could see whether the land 100 m from the focal animal was burned or not, and 95% of all the distances between the focal animal and other individuals were within 100 m. If the time interval between the data point at the freshly burned area was longer than 1 h, then the visited areas were considered different, although such areas were in close proximity to one another. If the time interval was less than 1 h, then the overlapping areas were merged and considered as one data point. Consequently, we identified 14 discrete “estimated freshly burned areas” (Figure S1, Table S2). However, these estimated areas do not represent all freshly burned areas in the study site. Thus, this study aimed to compare the percentage of time spent before and after the fire in the freshly burned areas visited by the group.

We compared the proportion of GPS fixes with the total number of GPS fixes by using a generalized linear mixed model (GLMM) with a binomial distribution and a logit link function (Model 1) to examine the difference in time spent by individuals in estimated freshly areas before and after the fire. Each period included all days before and after the fire. Predictor variables included the period (before or after the fire) and ID of all individuals to avoid pseudoreplication. We did not add ID as a random effect because it is generally suggested to only fit a random effect if it has six levels or more in the mixed model (Bolker et al. 2009; Harrison et al. 2018). We also added an observation-level random effect (ORLE; assign an independent ID to each data point) to account for overdispersion (Harrison 2015). We also incorporated the number of days of observation elapsed from the beginning of the research as a random intercept and the period within the observation elapsed days as a random slope into the model to consider the differences based on the length of the observation elapsed days.

Dietary benefits of burned areas for patas monkeys

In examining whether or not patas monkeys use burned areas for feeding, we calculated and compared the percentage of each activity (see the Behavioral data collection section) in freshly burned areas, previously burned areas, and unburned areas by combining the behavioral data of five focal individuals. Then, we examined the percentage of feeding-related behavior (consisting of foraging and feeding activities) based on areas by running the following GLMMs with binomial distribution and logit link function. We included behavior (feeding-related behavior/not) as the response variable as well as the areas (freshly burned area/previously burned area/unburned area) and focal ID as predictor variables. We incorporated the observation date as a random intercept.

Moreover, we calculated the percentage of each food category eaten by five focal individuals in freshly burned areas, previously burned areas, and unburned feeding areas. As for unburned feeding areas, we used the feeding data points included in a session defined in the following paragraphs. Then, we examined whether the food category, which was most eaten in freshly burned areas (i.e., *Cissus populnea* seeds), was eaten significantly more than in other areas. We also included whether *C. populnea* seeds were eaten or not (yes/no) as response variables as well as the areas (freshly burned area/previously burned area/unburned area) and focal ID as predictor variables. We added the observation date as a random intercept.

Group travel to freshly burned areas versus unburned feeding areas

In this analysis, we only handled data from GPS collars at freshly burned areas and unburned areas. The data at previously burned areas were excluded because the group sometimes just passed by the area without feeding, which was considered a questionable destination for a feeding site. We defined a session as the time when the group is in either area using the data of focal individuals to examine the differences between the group's travel before arriving at freshly burned areas and their travel before arriving at unburned feeding areas. Considering that the distance between focal individuals and other members when starting each session was almost within 100 m (Figure S2), we assume that all individuals were in the same area when starting sessions.

First, we defined a session in freshly burned areas as when the focal individual was in the fresh burned area for more than 30 consecutive minutes, and this session was considered independent if the next data point at freshly burned areas was more than an hour away from the last data point. Second, we defined a session in unburned feeding areas as when a focal individual was in the unburned area for more than 30 consecutive minutes, and non-feeding-related behaviors (i.e., traveling and resting) of the individuals were not observed for more than 10 consecutive minutes. We only used sessions in unburned feeding areas when the individuals included more than 80% of feeding-related behavior to clarity whether it is the uniqueness of freshly burned areas or the certain characteristics of the feeding area that determine the travel patterns. In addition, the travel distance of individuals from a place 1 h before starting session was between 300 and 900 m. We also included the food category that was observed in freshly burned areas and whose characteristics were the same as those of the freshly burned area. We could not completely control the diet because the monkeys had usually eaten multiple food categories in the unburned feeding areas. Third, we further selected the sessions that included more than two feeding data points (to exclude foraging-only sessions) and that had complete data of all focal individuals from 1 h before the sessions (to analyze group movements before the sessions). Consequently, we extracted nine sessions in freshly burned areas and eight sessions in unburned feeding areas. Regarding the former sessions, every session had a diferent date, which indicates the absence of the travel among freshly burned areas.

In examining temporal changes in travel before arriving at freshly burned areas or unburned feeding areas (e.g., whether they went fast from the beginning or not), we further divided pre-arrival data (i.e., from 1 h before each session) into three segments (50–60 min, 30–40 min, and 10–20 min) and compared the trends in group travel at each segment.

Then, we examined the travel of all individuals before arriving in each destination (freshly burned area/unburned feeding area) by running the following GLMMs. Travel distances and angles of all individuals were calculated using the adehabitatLT package in R statistical analysis (Calenge 2006). For all models, the session ID was included as a random intercept to cope with the non-independence of the data.

First, we investigated whether travel velocity difered depending on the destination by using a model with a t-distribution and identity link function (Model 2a). The degree of freedom of the t-distribution was 1.531. We calculated the individuals' velocity (m/min) for each sampling point from the travel distance to the point 10 min immediately afterward. Then, we included the log-transformed values as the response variables. In this model, we included the destination, pre-arrival time (three segments: 50–60 min, 30–40 min, and 10–20 min), their interaction, and focal ID as predictor variables. We added the interaction because the travel at certain pre-arrival times may change with destination.

Second, we examined whether travel linearity difered depending on the destination. Travel linearity was calculated as the direct distance from where the individual was positioned 1 h before each session divided by the travel distance through the travel route (Normand and Boesch 2009). Both distances have 1 cm as a significant digit. Travel linearity indicates that if travel was maximally direct, then the value approaches 1. We used the degree of linearity as a response variable using a beta distribution and a logit link function (Jang et al. 2019; Model 2b). In this model, the destination, focal ID, interaction between them, and ORLE were included as predictor variables. The interaction was also added because the potential individual variation in linearity has been confirmed by destination.

Third, we investigated whether the variation in the individual's velocity difered depending on the destination using a model with a gamma distribution and a log link function (Model 2c). We calculated the CV as the standard deviation of the velocity of all individuals every 10 min divided by the mean of the velocity of the corresponding periods. CV was used as a response variable, and the destination, prearrival time, and their interaction were included as predictor variables.

Finally, we investigated the differences in the synchrony of the travel direction among group members depending on the destination using a model with a binomial distribution and a logit link function (Model 2d). We represented the travel of each individual in 10-min increment to estimate the synchrony of the travel direction among individuals. The angle between consecutive vectors (θ) ranged from 0° to 180°. Then, we regarded the travel direction by two individuals as synchronous when θ was less than 45° (otherwise asynchronous) in accordance with previous studies (Jacobs et al. 2011; Nishikawa et al. 2021; Sueur and Petit 2008). In this model, we included the proportion of the number of synchronized pairs as a response variable. We included the destination, pre-arrival time, their interaction, and focal ID as predictor variables, as well as ORLE.

Model implementation

All analyses were conducted using R (version 4.2.1, R Core Team 2022). GLMMs were fitted with the "glmmTMB" package (Brooks et al. 2023). No problems with the GLMMs were detected when checking the model assumptions, including under/overdispersion and zero-inflation, using the "simulateResiduals" function in the DHARMa package (Hartig and Lohse 2022). Variance inflation factors (VIFs) were revealed for all test predictors using the "check_collinearity" function in the performance package (Lüdecke et al. 2021), indicating low collinearity (VIF < 10; Roberts and Roberts 2015). If models included interaction terms, then we performed post hoc pairwise comparisons to compare the estimated marginal means among destinations within each pre-arrival time for Models 2a, 2c, and 2d and within each individual for Model 2b. We used the "estimate_contrasts" function in the model-based package (Makowski et al. 2020) to conduct this analysis, and p values were adjusted using the Holm's method. The alpha level was set at 0.05.

RESULTS

Do patas monkeys use freshly burned areas?

In Model 1, the proportion of GPS fixes at the estimated freshly burned areas to the total number of GPS fixes after the fire was higher than that before the fire ($\beta = 2.283$, SE = 0.469, 95% CI = [1.363, 3.203], $z = 4.863$, $p < 0.001$, Table S3; Figure S3). However, three areas were identified (area ID: 10, 11, and 12) showed relatively higher usage proportions before the fire (mean prop, ID: 10 = 0.00142, ID: 11 = 0.000645, ID: 12 = 0.000728) than after the fire (mean prop, ID: 10 = 0.00112, ID: 11 = 0.000347, ID: 12 = 0.000686). Two of the areas (ID: 10 and 11) included places where the group regularly visited to drink water, and the remaining one area (ID: 12) largely overlapped with another area (ID: 3) that had been burned 29 days earlier.

What did patas monkeys do in freshly burned areas?

Patas monkeys spent most of their time feeding and foraging in freshly burned areas (84.1%) and more so than in previously burned (51.3%; $\beta = 1.793$, SE = 0.351, 95% CI=[0.953, 2.634], z =5.109, $p < 0.001$; Figure S4) and unburned areas (39.6%; β = 2.457, SE=0.695, 95% CI = [0.793, 4.120], $z = 3.535$, $p < 0.01$). No significant differences in the percentage of feeding-related behavior were found between previously burned areas and unburned areas ($\beta = 0.663$, SE = 0.624, 95% CI = [− 0.830, 2.156], z = 1.064, $p = 0.287$). In freshly burned areas, the monkeys primarily ate *Cissus populnea* seeds (77.8% of scan samples), followed by animal matter (13.9%; Fig. 1). Compared with freshly burned areas, in previously burned areas, the monkeys focused less on *Cissus* seeds (34.3%), and they ate animal matter (20.7%) and gums (16.0%) more often. The percentage of samples involving *Cissus* seed eating was signifcantly in previously burned areas than freshly burned areas ($\beta = -1.793$, SE = 0.351, 95% CI = [− 2.634,− 0.953], $z = -5.109$, $p < 0.001$). Similarly, the monkeys spent less time feeding on *Cissus* seeds in unburned feeding areas (7.1%) than in freshly burned areas ($\beta = -2.457$, SE = 0.695, 95% CI = [− 4.120, − 0.793], $z = -3.535$, $p < 0.01$) and spent more time feeding on fruits (35.7%) and gums (28.6%). No signifcant diference in the percentage of *Cissus* seed eating was found between previously burned and unburned feeding areas ($\beta = 0.663$, SE=0.624, 95% CI = [− 0.830, 2.156], $z = 1.064$, $p = 0.288$). When foraging on *Cissus* seeds, individuals searched for a small clump of seeds sometimes buried in the ground with ash, dug them out to feed, and then continued searching for another clump.

Differences in travel patterns to freshly burned areas and unburned feeding areas

The details of each model are shown in Table S4 and Table 1. The differences in travel velocity in Model 2a indicate that individuals traveled significantly faster during the first 20 min of the hour before arriving at freshly burned areas compared with unburned feeding areas (mean velocity 50–60 min; freshly burned area, 8.34 m/min; unburned feeding area, 5.96 m/min; Fig. 2; Model 2a, Table 1). By contrast, no significant differences in other pre-arrival times were observed (mean velocity 30–40 min; freshly burned area, 8.55 m/min; unburned feeding area, 8.75 m/min; 10–20 min; freshly burned area, 8.50 m/min; unburned feeding area, 10.9 m/min).

In Model 2b, no significant differences by destination in the travel linearity of individuals were found (mean linearity to freshly burned area, MC = 0.784, Sa = 0.808, Sk = 0.809, Kr = 0.787, Sh = 0.792; unburned feeding area, MC = 0.876, Sa = 0.903, Sk = 0.893, Kr = 0.873, Sh = 0.942; Fig. 2; Model 2b, Table 1). The linearity before arriving at freshly burned areas showed higher variation in the all individuals than that before arriving at unburned feeding areas (freshly burned area, 0.239–0.985; unburned feeding area, 0.672–0.986). Adult male MC had greater variation in linearity before arriving at freshly burned areas than adult females after excluding outliers (MC = 0.285–0.978, Sa = 0.586–0.981, Sk = 0.494–0.985, Kr = 0.703–0.952, Sh = 0.787–0.977). The mean travel distance of individuals to freshly burned and unburned feeding area was 507 m (283–930 m) and 511 m (303–938 m), respectively.

In Model 2c, the CV of velocity was significantly lower 50–60 min before arriving at freshly burned areas than that before arriving at unburned feeding areas (mean CV of velocity 50–60 min, freshly burned area = 0.332, unburned feeding area = 0.570; Fig. 2; Model 2c, Table 1). By contrast, no significant differences by destination in the other prearrival times were found (mean CV of velocity 30–40 min, freshly burned area = 0.413, unburned feeding area = 0.483; 10–20 min, freshly burned area=0.453, unburned feeding area=0.427).

In Model 2d, the proportion of pairs with a synchronized travel direction was significantly higher 50–60 min before arriving at freshly burned areas than that before arriving at unburned feeding areas (mean prop 50–60 min, freshly burned area = 0.867, unburned feeding area=0.644; Fig. 2; Model 2d, Table 1). However, no significant differences by destination in the other pre-arrival times were observed (mean prop 30–40 min, freshly burned area = 0.811, unburned feeding area=0.781; 10–20 min, freshly burned area=0.739, unburned feeding area=0.794).

DISCUSSION

Collective movements toward freshly burned areas as feeding sites

We showed that the proportion of GPS fixes in estimated freshly burned areas was generally higher after the fire. This result indicates that patas monkeys spent less time in estimated freshly burned areas before the fire. We also found that the percentage of feeding-related behavior was higher in freshly burned areas than in previously burned areas and in unburned areas, which suggested that patas monkeys visited freshly burned areas for foods. In addition, freshly burned areas are not suitable for resting because of smoke or heat, and feeding-related activity may have increased. More than 70% of the feeding records of the focal animal in freshly burned areas were seeds of *Cissus populnea*, which belongs to the Vitaceae family and common and scattered in tropical western African savannahs. This perennial liana species with branched tendrils often covering trees and fruits ripens during the rainy season (Arbonnier 2004).

Regarding travel movements toward feeding sites of the group, the monkeys traveled at high velocity with less variation among individuals when they were farthest away (50–60 min) an hour before arriving at freshly burned areas compared with unburned feeding areas. These results indicate that the group may have detected the location of freshly burned areas at least an hour before arriving and purposefully traveled toward the location. Several studies demonstrated that when primates headed to a particular feeding site, they often used landmarks along familiar routes (Di Fiore and Suarez 2007; Garber and Brown 2006; Milton 2000), which is known as a topological or network map (Byrne 2000). However, it is not possible to know where the burning has “occurred” from only previous memories about the geographical information of the geography. Nevertheless, the group has traveled at high velocity with less variation among individuals in the first 20 min of the hour before arriving at freshly burned areas. Therefore, this goal-directedness may be facilitated by the presence of smoke. The large amount of smoke may effectively indicate the location of the currently burned area and could facilitate a shared perception of the direction by all group members. Moreover, the smoke was visible to human observers from a distance of 0.5–1 km away. This range in visibility to humans is similar to the distances the group traveled to freshly burned areas in the hour before arriving at such locations. On the contrary, in the time frames 30–40 min and 10–20 min before arriving, no significant differences in velocity were found between freshly burned and unburned feeding areas: This is probably because they start to travel in a goal-directed manner based on spatial memory to guide unburned feeding areas. When heading to freshly burned areas, the monkeys travel long distances (up to 930 m) at a stably high velocity. This high ability of locomotion could be related to their unique morphological adaptation in savannah. They have longer legs, hind foot digitigrady, and longer tarsal bones (Isbell 1998; Isbell et al. 1998), which reduce the cost of traveling over long distances and result in flexible movements for foods.

Although the linearity of travel did not significantly differ among destinations, some of the linearity measures were considerably low when heading to freshly burned areas, causing a large variation compared with the case of unburned areas. Predicting when and where the burning occurs may be difficult because it happens suddenly, and the location and timing may change annually. Thus, the group will need to instantly reroute and change their destination even if they were on their way to another destination. The group may have had to take large detours of obstacles (e.g., large trees or dense grasses) depending on where they decided to change their destination, which may have resulted in high variation in linearity. By contrast, when they travel toward the unburned feeding area, they may follow linear paths with advance planning on how to approach resources despite being out of sight, similar to other primates (Noser and Byrne 2007).

Less variation in velocity was observed in velocity among individuals, and more synchrony in travel direction was found among pairs in the first 20 min of the hour before the group arrived at freshly burned areas. In general, when the benefit at a destination for each individual is greater, individual decision-making becomes more consistent; consequently, individuals travel more synchronized (Boinski 2000). The *Cissus* seeds observed in freshly burned areas were dispersed in small clumps. Considering that the distance between clumps was close, low-ranking individuals may find an alternative clump with relatively low search costs, although they are supplanted from clumps by high-ranking individuals. In Japanese macaque (*Macaca fuscata*), no difference in feeding time was observed in relation to rank when the distance between patches was close, which indicates a decrease in within-group feeding contest competition (Saito 1996). However, this study did not quantify the distribution of seed clumps in freshly burned areas, the search costs of each individual, or antagonistic interaction over seeds. Thus, further research is necessary.

Behavioral adaptability to burned habitats

We revealed that patas monkeys also showed a high degree of behavioral plasticity in response to anthropogenic burning, which creates unpredictable and temporary environments. This flexibility is tuned in accordance with the unique diet and the socioecological and morphological characteristics of the patas monkeys adapted to the savannah environment. In other savannah-dwelling primates, it has been reported that predator-related behaviors are less likely to occur in burned areas because visibility is improved, which helps them to find terrestrial stealth predators easily (Herzog et al. 2020; Jaffe and Isbell 2009). Although this study focused on the utilization of burned areas as a feeding site, future studies considering multiple benefits of using of anthropogenic environments will be helpful in providing a comprehensive understanding of the value of adaptation in primates.

This empirical study is the first to establish that patas monkeys, who have rarely been examined for group movements, travel at high velocity and with high synchrony with other members when heading to freshly burned areas. The “goal-directed” travel mode was observed when they were heading to a place where their spatial memory could not be used (because the location of the fire changes annually). This finding is quite different from heading to a fruiting tree (for which they can easily use spatial memory). Therefore, we hypothesize that primates might be able to locate a sudden appearance of a feeding site even by detecting dynamic visual information that appears temporarily and unexpectedly, such as smoke. This study sheds new light on the ability to recognize the location of feeding sites in primates.

Author contributions

Conceptualization: [Maho Hanzawa (lead)]; Formal analysis: [Maho Hanzawa (lead)]; Funding acquisition: [Maho Hanzawa (equal)], [Yoshiki Morimitsu (equal)], [Naofumi Nakagawa (equal)]; Investigation: [Maho Hanzawa (lead)], [Yoshiki Morimitsu (equal)], [Richard D Suu-Ire (equal)], [Naofumi Nakagawa (equal)], [Erasmus H Owusu (supporting)]; Methodology: [Maho Hanzawa (lead)], [Yoshiki Morimitsu (supporting)]; Visualization: [Maho Hanzawa (lead)]; Writing – original draft: [Maho Hanzawa (lead)]; Writing – review and editing: [Maho Hanzawa (lead)], [Naofumi Nakagawa (equal)]; Project administration: [Erasmus H Owusu (lead)], [Richard D Suu-Ire (lead)], [Naofumi Nakagawa (equal)], Supervision: [Naofumi Nakagawa (lead)].

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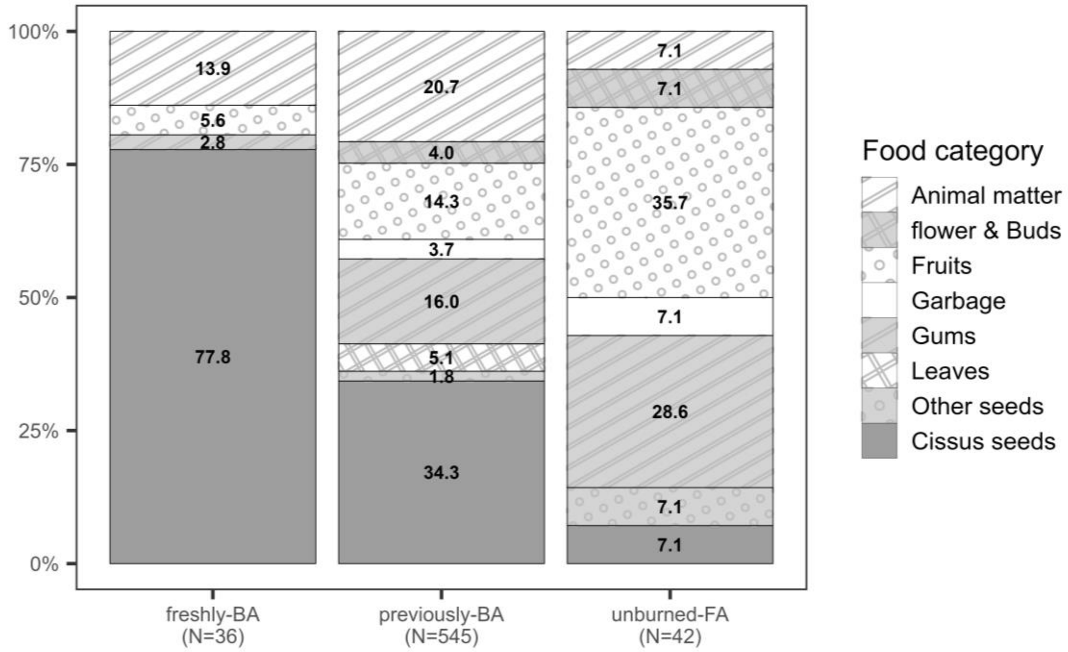
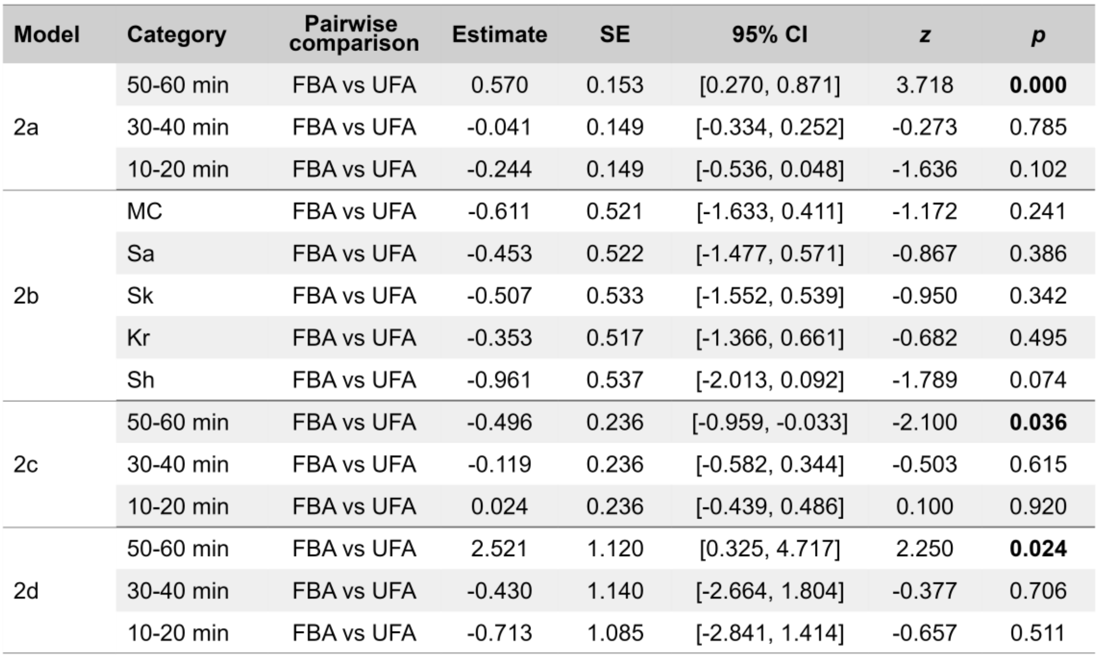


Fig. 1 Numbers in bars show the percentage of each food category of individuals in each area (freshly-BA, freshly burned area; previously-BA, previously burned area; unburned-FA, unburned feeding area). We calculated the percentage of "*Cissus* seeds" with "Other seeds" since we focused on the *Cissus*, which was obviously most eaten by monkeys in freshly burned areas.



Model	Category	Pairwise comparison	Estimate	SE	95% CI	*z*	*p*
2a	50-60 min	FBA vs UFA	0.570	0.153	[0.270, 0.871]	3.718	**0.000**
	30-40 min	FBA vs UFA	-0.041	0.149	[-0.334, 0.252]	-0.273	0.785
	10-20 min	FBA vs UFA	-0.244	0.149	[-0.536, 0.048]	-1.636	0.102
2b	MC	FBA vs UFA	-0.611	0.521	[-1.633, 0.411]	-1.172	0.241
	Sa	FBA vs UFA	-0.453	0.522	[-1.477, 0.571]	-0.867	0.386
	Sk	FBA vs UFA	-0.507	0.533	[-1.552, 0.539]	-0.950	0.342
	Kr	FBA vs UFA	-0.353	0.517	[-1.366, 0.661]	-0.682	0.495
	Sh	FBA vs UFA	-0.961	0.537	[-2.013, 0.092]	-1.789	0.074
2c	50-60 min	FBA vs UFA	-0.496	0.236	[-0.959, -0.033]	-2.100	**0.036**
	30-40 min	FBA vs UFA	-0.119	0.236	[-0.582, 0.344]	-0.503	0.615
	10-20 min	FBA vs UFA	0.024	0.236	[-0.439, 0.486]	0.100	0.920
2d	50-60 min	FBA vs UFA	2.521	1.120	[0.325, 4.717]	2.250	**0.024**
	30-40 min	FBA vs UFA	-0.430	1.140	[-2.664, 1.804]	-0.377	0.706
	10-20 min	FBA vs UFA	-0.713	1.085	[-2.841, 1.414]	-0.657	0.511

Table 1 Pairwise comparison of destination (FBA, freshly burned area; UFA, unburned feeding area) for pre-arrival time or ID in Model 2a, 2b, 2c, and 2d. Response variables; the velocity of individuals (Model 2a), linearity for each session (Model 2b), CV of velocity (Model 2c), the proportion of pairs with synchronized travel direction (Model 2d). Bold values indicate $p < 0.05$. SE, standard error; 95% CI, 95% confidence intervals; *z*, z value; *p*, p value.

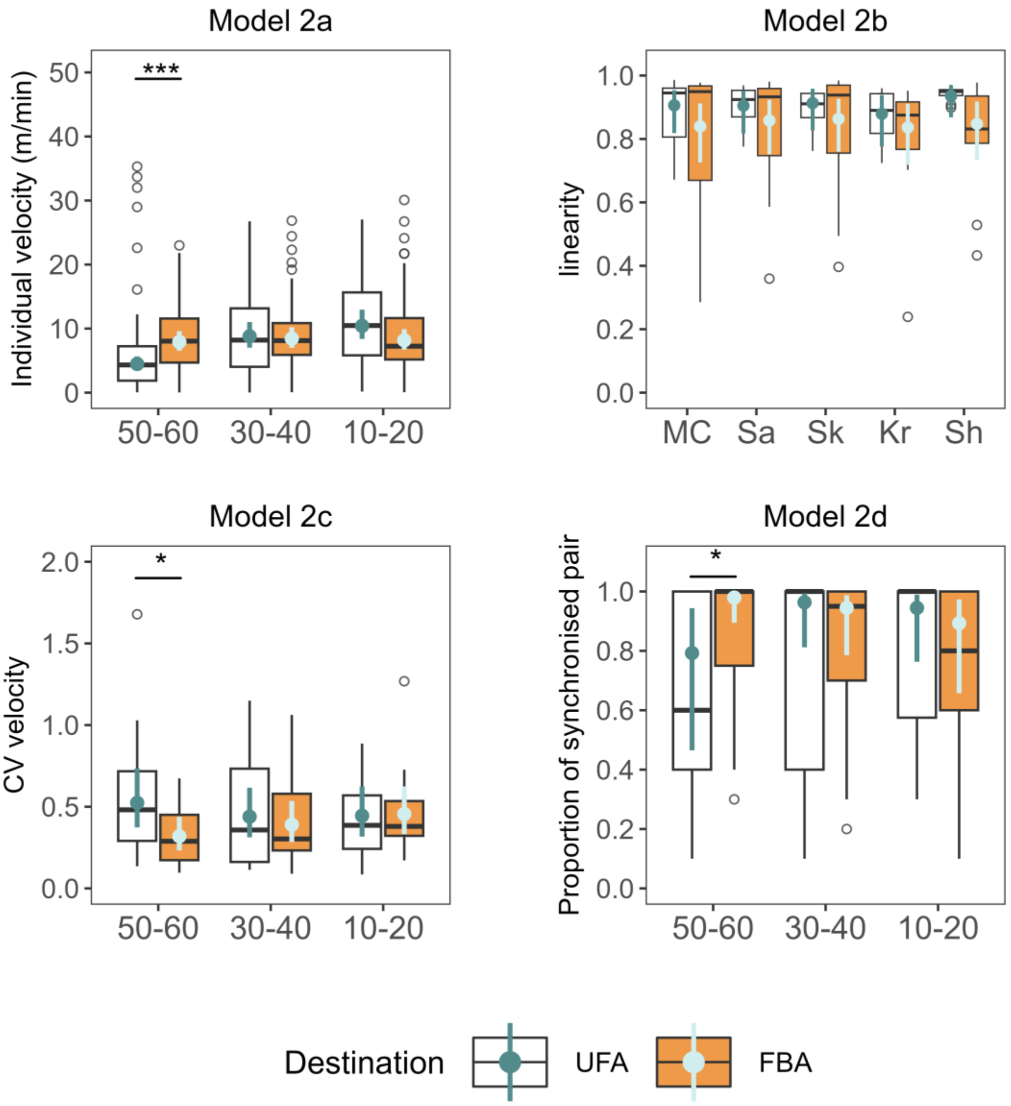
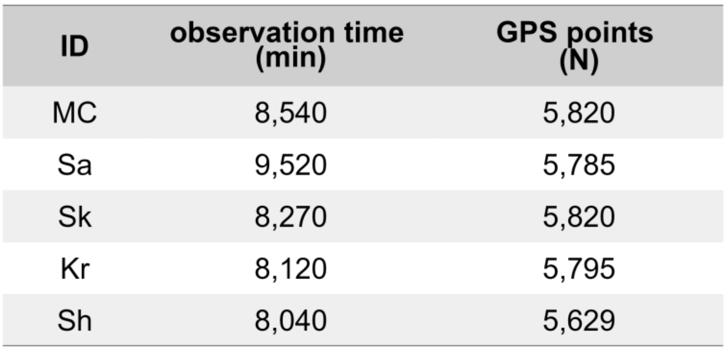


Fig. 2 Differences in individual velocity (Model 2a), linearity (Model 2b), CV velocity (Model 2c), the proportion of pairs with a synchronized travel direction (Model 2d) by destination (UFA unburned feeding area; FBA freshly burned area) with GLMM. The horizontal axis indicates pre-arrival times, colored circles represent the marginal mean of the response variable value, and colored vertical lines show its 95% confidence interval fitted estimated by each model. *, $p < 0.05$; ***, $p < 0.001$.

Supplementary Information

Capturing patas monkeys

Let us describe additional details on the process of capturing patas monkeys. We fitted GPS collars to five adults (sole adult male and four adult females) of the group. We did not fit the device to one of the adult females because she was not fully habituated to observers. We (veterinarians YM or RS) immobilized individuals with a combination of zoletil (5 mg/kg) and medetomidine (0.1 mg/kg) from a distance of 3-5 m using a blowpipe. After injecting the target, two researchers followed the other members of the group. Once the target was immobilized and the group was out of sight, we fitted the individual with a GPS collar and collected morphometric and other biological data in the shade. In a few cases, subcutaneous fluids were administered to assist with rehydration. We completed all processes within an hour, and veterinarians reversed the medetomidine with atipamezole (0.5 mg/kg). After a full recovery of the individual, we returned it to the group and monitored until it was ambulatory. After data collection, we dropped the collar with a remote control while observing the individual. Then, we continued to observe them for a few days to ensure no problems with their bodies or their behavior.



ID	observation time (min)	GPS points (N)
MC	8,540	5,820
Sa	9,520	5,785
Sk	8,270	5,820
Kr	8,120	5,795
Sh	8,040	5,629

Table S1: The observation time (min) and the number of recorded GPS fixes (collected by GPS device and collars) used in the analysis for each individual.

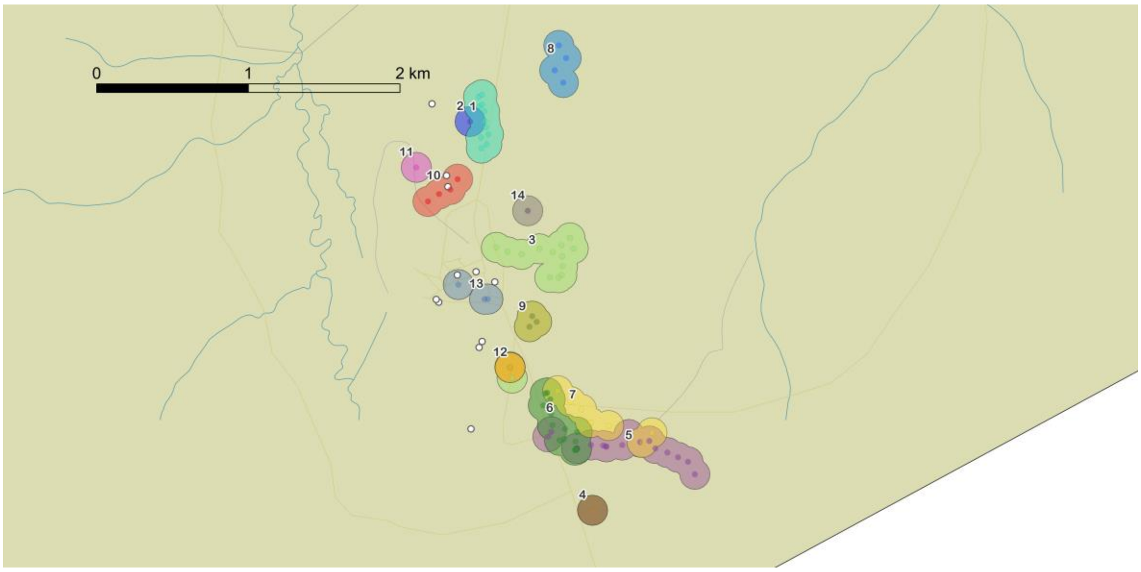


Figure S1: The colored dots represent GPS fixes of the focal individual in freshly burned area and the areas around them indicate "estimated freshly burned areas" (N=14). White circles show the location of water place used by the group during the study period.

area_ID	burned_date
1	2022-12-14
2	2022-12-15
3	2022-12-20
4	2022-12-21
5	2022-12-22
6	2022-12-23
7	2022-12-24
8	2022-12-30
9	2023-01-09
10	2023-01-10
11	2023-01-11
12	2023-01-18
13	2023-01-23
14	2023-02-01

Table S2: Date of each "estimated freshly burned area" burned.

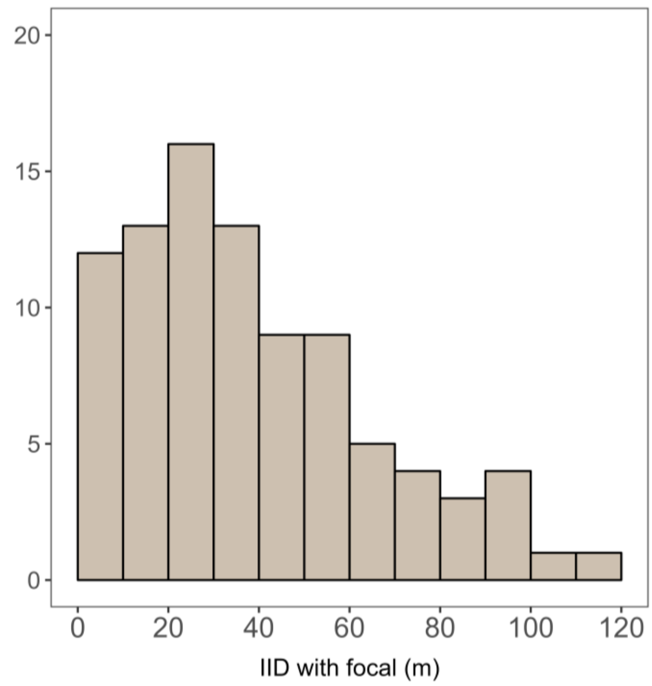
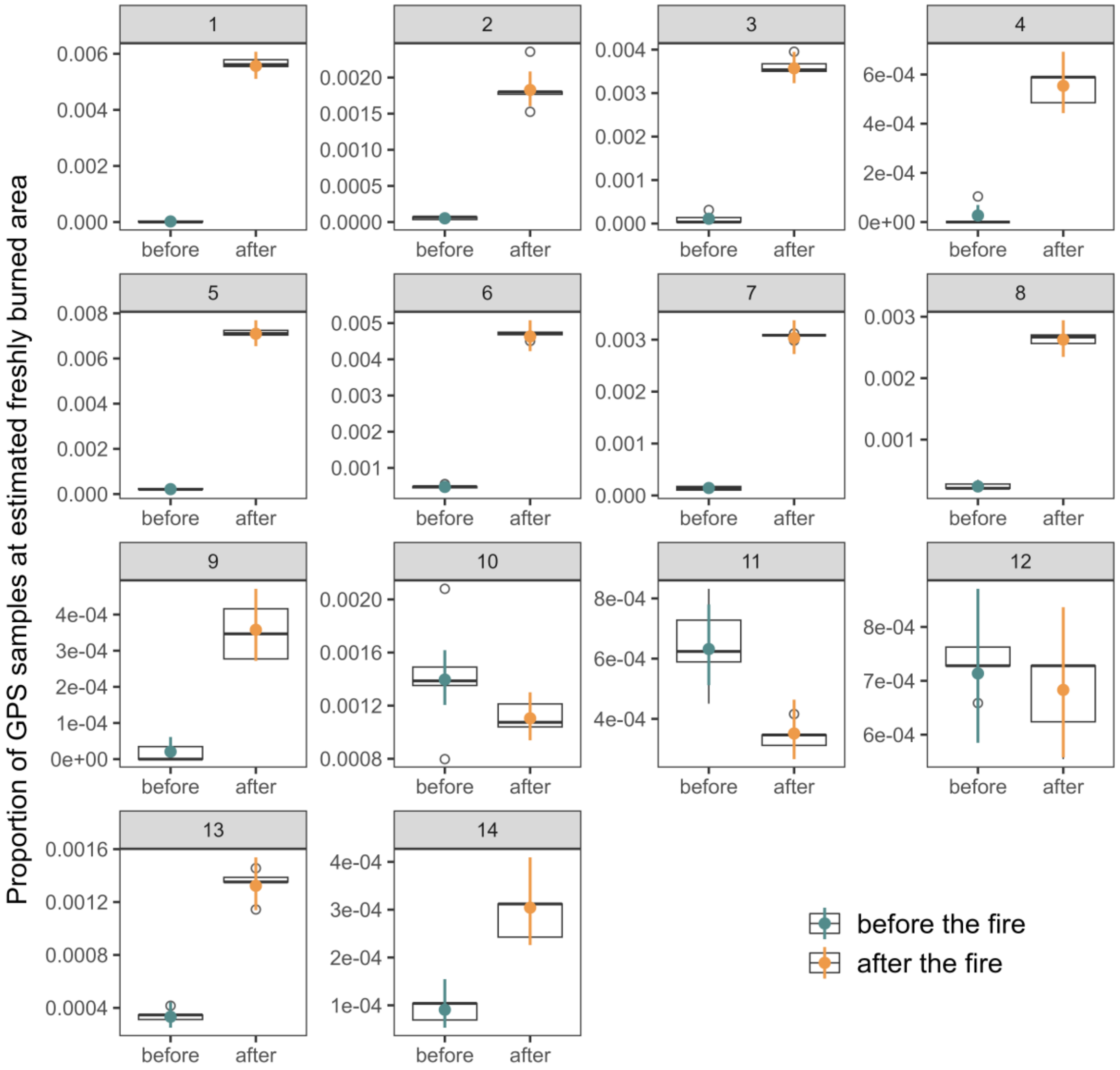


Figure S2: Amount of data of distance between the focal animal and other collared individuals when starting each session. The horizontal axis indicates the inter-individual distance (IID) with the focal animal (m).

Predictor variables		Estimate	SE	95% CI	z	p
Intercept		-8.813	0.380	[-9.559, -8.067]	-23.168	**< 0.001**
Period	after vs before	2.283	0.469	[1.363, 3.203]	4.863	**< 0.001**
ID	Sa vs MC	0.017	0.043	[-0.067, 0.102]	0.407	0.684
	Sk vs MC	-0.005	0.043	[-0.089, 0.080]	-0.108	0.914
	Kr vs MC	0.039	0.043	[-0.044, 0.123]	0.917	0.359
	Sh vs MC	0.006	0.043	[-0.078, 0.091]	0.151	0.880

Table S3: Differences of the proportion of GPS fixes at estimated freshly burned areas before or after the fire (GLMM). Response variables; the proportion of GPS fixes at estimated freshly burned areas in the total number of GPS fixes. Predictor variables; the period (before or after the fire) and ID of all individuals.
Bold values indicate $p < 0.05$. GLMM, generalized linear mixed model; SE, standard error; 95% CI, 95% confidence intervals; z, z value; p, p value.



FigureS3: The proportion of GPS fixes each estimated freshly burned areas before or after the fire (N = 14) in Model1 (GLMM). The number above each graph indicates the number of days of observation elapsed from the beginning study. Colored circles represent the marginal mean of response variable value, and colored vertical lines show its 95% confidence interval fitted estimated by each Model.

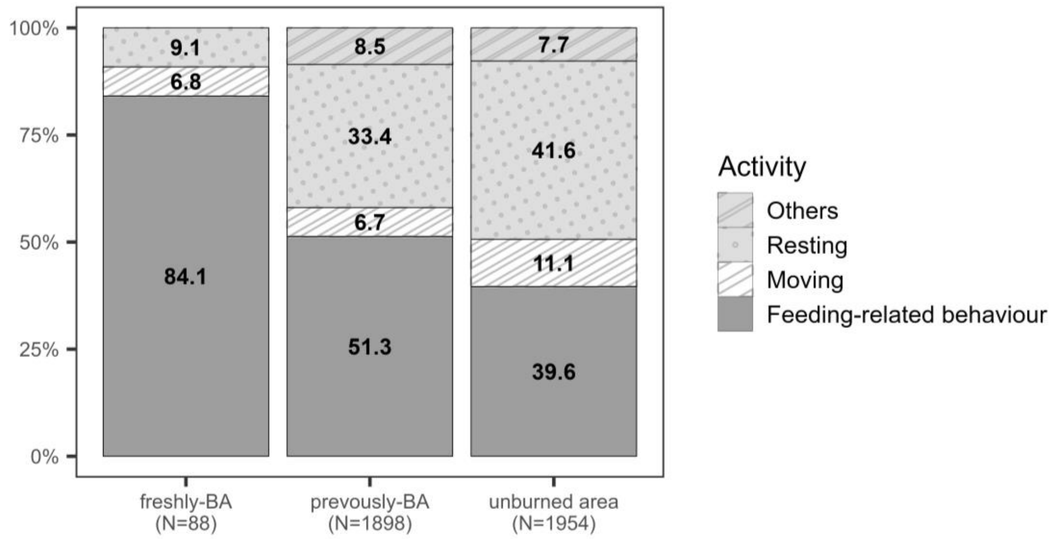


Figure S4: Numbers in bars show the percentage of activity of individuals at each area (freshly-BA, freshly burned area; previously-BA, previously burned area).

Model	Predictor variables		Estimate	SE	95% CI	*z*	*p*
2a	Intercept		1.504	0.134	[1.241, 1.767]	11.206	**< 0.001**
	Destination	FBA vs UFA	0.570	0.153	[0.270, 0.871]	3.718	**< 0.001**
	Pre-arrival time	30-40 vs 50-60	0.675	0.118	[0.443, 0.906]	5.713	**< 0.001**
		10-20 vs 50-60	0.844	0.114	[0.620, 1.068]	7.378	**< 0.001**
	ID	Sa vs MC	-0.027	0.087	[-0.197, 0.143]	-0.316	0.752
		Sk vs MC	0.023	0.089	[-0.152, 0.198]	0.258	0.797
		Kr vs MC	-0.013	0.092	[-0.193, 0.167]	-0.140	0.889
		Sh vs MC	-0.005	0.088	[-0.178, 0.168]	-0.056	0.955
	Destination (FBA) × Pre-arrival time (30-40)		-0.611	0.144	[-0.894, -0.328]	-4.233	**< 0.001**
	Destination (FBA) × Pre-arrival time (10-20)		-0.814	0.143	[-1.094, -0.533]	-5.681	**< 0.001**
2b	Intercept		2.267	0.389	[1.505, 3.029]	5.832	**< 0.001**
	Destination	FBA vs UFA	-0.611	0.521	[-1.633, 0.411]	-1.172	0.241
	ID	Sa vs MC	-0.014	0.292	[-0.586, 0.558]	-0.047	0.962
		Sk vs MC	0.084	0.317	[-0.537, 0.705]	0.264	0.792
		Kr vs MC	-0.283	0.282	[-0.836, 0.270]	-1.003	0.316
		Sh vs MC	0.409	0.309	[-0.197, 1.015]	1.323	0.186
	Destination (FBA) × ID(Sa)		0.158	0.369	[-0.566, 0.882]	0.428	0.669
	Destination (FBA) × ID(Sk)		0.104	0.389	[-0.657, 0.866]	0.268	0.788
	Destination (FBA) × ID(Kr)		0.258	0.362	[-0.450, 0.967]	0.714	0.475
	Destination (FBA) × ID(Sh)		-0.350	0.386	[-1.105, 0.406]	-0.907	0.364
2c	Intercept		-0.646	0.173	[-0.984, -0.308]	-3.742	**< 0.001**
	Destination	FBA vs UFA	-0.496	0.236	[-0.959, -0.033]	-2.100	**0.036**
	Pre-arrival time	30-40 vs 50-60	-0.177	0.195	[-0.559, 0.206]	-0.906	0.365
		10-20 vs 50-60	-0.164	0.204	[-0.563, 0.236]	-0.802	0.423
	Destination (FBA) × Pre-arrival time (30-40)		0.377	0.270	[-0.152, 0.906]	1.397	0.162
	Destination (FBA) × Pre-arrival time (10-20)		0.519	0.275	[-0.020, 1.059]	1.887	0.059
2d	Intercept		1.340	0.755	[-0.140, 2.820]	1.775	0.076
	Destination	FBA vs UFA	2.521	1.120	[0.325, 4.717]	2.250	**0.024**
	Pre-arrival time	30-40 vs 50-60	1.933	1.095	[-0.213, 4.078]	1.765	0.077
		10-20 vs 50-60	1.497	1.050	[-0.560, 3.554]	1.426	0.154
	Destination (FBA) × Pre-arrival time (30-40)		-2.951	1.538	[-5.965, 0.064]	-1.919	0.055
	Destination (FBA) × Pre-arrival time (10-20)		-3.234	1.494	[-6.162, -0.307]	-2.165	**0.030**

Table S4: Differences in movement of the group before arriving at each destination (FBA, freshly burned areas; UFA, unburned feeding areas) in Model2 (GLMM). Response variables; the velocity of individuals (Model 2a), linearity for each session (Model 2b), CV of velocity (Model 2c), the proportion of pairs with synchronized travel direction (Model 2d). Bold values indicate $p < 0.05$. GLMM, generalized linear mixed model; SE, standard error; 95% CI, 95% confidence intervals; *z*, z value; *p*, p value.