

Long-term effects of forest fire on habitat use by siamangs in Southern Sumatra

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Keywords

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Abstract

Forest fires can cause direct mortality to wildlife, and the associated habitat damage can reduce carrying capacity and population densities. However, little is known about long-term responses of animals to fire in the wet tropics. From 2000–2015, we examined siamang ranging patterns in habitat damaged by fire to assess the effects on these arboreal frugivores. We mapped home ranges (HR) of seven siamang groups inhabiting contiguous HR 3–5, 10–12, and 17–18 years post-fire. We predicted that if habitat connectivity or quality improved over time in burned areas, HR should become larger and centroid locations should shift toward recovering areas. Since territoriality constrains siamang ranging, we examined effects of social and habitat factors on ranging. By 18 years post-fire, tree density in the burned area had returned to the 1997 baseline, but composite LandSat images indicated that tree species composition differed in burned and unburned forest. Our data and the associated models indicated that HR sizes in burned forest increased over time whereas those in unburned forest did not. Centroid locations moved little ($15.5 \pm 6.9 \text{ m y}^{-1}$) and their movement appeared to be predominantly influenced by social factors, although HR centroids in burned habitat shifted further into the burned area while those in adjacent unburned forest did not. In a large burned area unused by siamangs before 2012, two new groups were observed 15–17 years post-fire, although one subsequently disappeared. This is the first study of the long-term effects of fire on small ape habitat use. By 18 years post-fire, siamangs had incorporated some burned areas into their HR, but did not use heavily damaged areas. Reduced frugivore densities in burned areas may inhibit forest regeneration by disrupting seed dispersal.

Introduction

Forest fires are occurring at increasing frequencies on Sumatra and Borneo due to anthropogenic climate change, changes in human land use patterns, and deliberate setting of fires during agricultural activities (Kinnaird & O'Brien, 1998; Secretariat of the Convention on Biological Diversity, 2001). Ecological consequences of fire can be more severe than those of other disturbances, such as selective logging (Kinnaird & O'Brien, 1998; Chazdon, 2003; van Nieuwstadt & Sheil, 2005). Fire may destroy the seedling and sapling

layer and can increase canopy tree mortality for ≥ 3 years post-fire (Slik & Eichhorn, 2003; van Nieuwstadt & Sheil, 2005). Canopy connectivity may recover within 5–20 years, but the species composition in recovering forests may differ from that in unburned areas for decades (Slik, Verburg & Keßler, 2002; Toma, Ishida & Matius, 2005). Fires may also affect the density, behavior, and demography of surviving animal populations (Anggraini, Kinnaird & O'Brien, 2003; O'Brien *et al.*, 2003; Sözer & Nijman, 2005; Slik & Van Balen, 2006). While seeds in the soil seed bank may survive (Woods, 1989), the presence of important animal seed

dispersers in a damaged habitat may also affect forest recovery (McConkey *et al.*, 2012). Therefore, understanding animal responses during post-fire recovery is important for quantifying the impacts of fire on threatened populations and habitats.

Animals may respond to fire damage by moving toward or away from damaged habitat, shifting their diets, or changing the size of their foraging area (Russon, Kuncoro & Fersa, 2015). Habitat loss may also force surviving populations into smaller spaces (Sözer & Nijman, 2005). After disturbance, the inability of animals in territorial species to shift their home ranges (HR) due to aggression from neighbors may reduce the local density below carrying capacity (Van Horne, 1983; Nasi *et al.*, 2002), and may reduce the survivorship or reproduction of surviving groups (O'Brien *et al.*, 2003). However, little is known about long-term effects of fire on territorial animals in the tropics. Here, we examine the ranging behavior of a territorial arboreal frugivore, the siamang (*Symphalangus syndactylus*), in and adjacent to habitat damaged by fire in 1997 from 3 to 18 years post-fire. Our goal was to assess the long-term effects of fire on siamang ranging and habitat occupancy, and to evaluate the relative importance of social and ecological constraints on siamang ranging behavior in post-fire landscapes.

Siamangs are endemic to Sumatra and peninsular Malaysia and are Endangered due to habitat loss and degradation (Nijman & Geissmann, 2008). Like most other gibbons (Hylobatidae), siamang groups defend small (5 to > 40 ha) HR as territories (Bartlett, 2011). Gibbon HR sizes and locations tend to be stable over time (Chivers & Raemaekers, 1980; Bartlett, Light & Brockelman, 2016; Cheyne *et al.*, 2019), but few studies span more than a few years, and the long-term effects of fire on gibbon ranging have not been previously evaluated. As siamangs and other gibbons are important, sometimes irreplaceable, seed dispersers for canopy trees (McConkey & Brockelman, 2011; McConkey, 2018), their responses to habitat disturbance may impact the structure, species composition, and functioning of Southeast Asian forests (McConkey *et al.*, 2012).

We used ranging data from seven habituated siamang groups in Way Canguk Research Area (WCRA) collected over 15 years and annual census data from 6–22 other groups, making this by far the longest and largest study of wild siamangs to date. Baseline information about siamang ranging before the 1997 fires is unavailable, as the fires ignited only a few months after WCRA was established. However, observers on site noted a dramatic change in occupancy immediately after the fire. During initial surveys, researchers detected siamang groups throughout WCRA, but following the fires, there were no siamangs in the most severely burned section of southern WCRA (Kinnaird & O'Brien, 1998). Habitat loss or degradation may leave survivors with smaller HR, lower-quality HR, or both. In the only other study of gibbons in fire-affected habitat, HR locations for three neighboring groups of Bornean southern gibbons (*H. albibarbis*) remained stable before and three years after a fire, although habitat within one HR was damaged and was no longer used (Cheyne *et al.*, 2019). Similarly,

from 2000–2002 (3–5 years post-fire), siamangs in WCRA living immediately adjacent to large areas of fire-damaged habitat (*burn groups*) had smaller HR than those in unburned forest (*normal groups*) and their HR contained 48% fewer reproductive figs (O'Brien *et al.*, 2003). Infant and juvenile mortality were higher in burn groups than in normal groups, making the fire-damaged area a demographic sink (O'Brien *et al.*, 2003). Therefore, all available evidence suggests that in the immediate post-fire period, siamang groups in burned areas of WCRA were under considerable stress, whereas their neighbors in unburned habitat were not.

The response of siamangs to post-fire habitat changes may depend on both habitat recovery and the territorial behavior of their neighbors. If vegetation changes in the 18 years post-fire resulted in high habitat quality in the burned areas or improved connectivity between high-quality patches, then we predicted that mean HR size in the fire-affected neighborhood should increase from 2000 to 2015, and that siamang HR centroids should shift toward the burned areas. These changes may affect all groups in the area if ecological factors are the primary constraint on siamang ranging, or may only affect burn groups if the territorial behavior of neighboring groups in unburned habitat prevented compression of their HR after the fire. Alternatively, if post-fire recovery did not restore habitat quality or connectivity by 2015, then we predicted that HR centroids should remain stationary or shift away from the fire-damaged areas. Finally, we examined relationships between time elapsed since the fire, changes in group composition, and movements of HR centroids. If territoriality poses a major constraint on siamang ranging behavior, we predicted that HR locations should shift more when group compositions change due to death, immigration, or emigration/expulsion of an adult than during periods of stable composition.

Materials and methods

Study area

WCRA is in Bukit Barisan Selatan National Park (BBSNP) in southern Sumatra, Indonesia (5° 39' 32" S, 104° 24' 21" E), and includes 900 ha of lowland primary forest (ca. 50 m a s l) interspersed with elephant clearings and areas damaged by flooding, wind, or fire. Wildlife Conservation Society—Indonesia Program and BBSNP established WCRA in 1997 and at this time grids of research trails at 200m intervals were built. In 1997, during a severe drought associated with an El Niño–Southern Oscillation (ENSO) event, anthropogenic fire damaged a 165-ha section of WCRA in the southern WCRA trail grid (Kinnaird & O'Brien, 1998).

Effects of 1997 fire on habitat quality in WCRA

Fire damage was patchy in affected parts of the WCRA, with damage to the leaf litter and light damage to the seedling layer in some areas and damage to all layers of the

forest, including the crown layer, in others (O'Brien *et al.*, 2003). Before the fires, Wildlife Conservation Society—Indonesia Program established 100 vegetation plots (10*50 m) and tagged 2106 trees with dbh > 10 cm (O'Brien *et al.*, 2003). The fires damaged forest in 20 of these plots (O'Brien *et al.*, 2003). Tree mortality was high in the year following the ENSO drought, but mortality was substantially higher in burned plots (25%) than in unburned plots (11%) the first year post-fire and remained higher in burned plots for several years afterward (O'Brien *et al.*, 2003). Trees of many fruiting species died, including siamang food trees (O'Brien *et al.*, 2003). Seedling and sapling mortality were also substantially higher in burned areas, with 100% mortality in the worst-affected areas (Kinnaird & O'Brien, 1998). Changes in forest structure and composition following the fires affected the densities of several bird (Kinnaird & O'Brien, 1998; Anggraini *et al.*, 2003; Adenay *et al.*, 2006) and mammal taxa (Kinnaird & O'Brien, 1998).

Tree mortality from the 1997 drought reduced the basal stem area and standing carbon stock across WCRA (Kinnaird & O'Brien, 1998). By 2004, vegetation in unburned areas had returned to the 1997 baseline, suggesting recovery from the drought (O'Brien, 2015; S3). In burned plots, the basal stem area did not return to baseline until 2012, with the standing carbon stock predicted to reach baseline levels by 2019 (O'Brien, 2015; S3). The reduced standing carbon stock in burned plots indicates a shift in tree species distribution to more early pioneer species (O'Brien, 2015). It is unclear how this shift affected habitat quality from the perspective of canopy-dependent frugivores such as siamangs.

Assessment of forest recovery using Landsat imagery

Boundaries of the burned area (including lightly and heavily damaged forest) were mapped after the 1997 fire (Kinnaird & O'Brien, 1998). We compared burned and unburned sections in WCRA in a circa-2016 Landsat cloud-free image composite (Hansen *et al.*, 2013; Hansen/UMD/Google/USGS/NASA, 2016). First, we projected the 30 m x 30 m-resolution multispectral composite Landsat image in ArcGIS 10.3.1 (ESRI, Redlands, CA, USA 2015) and flattened it to a single-band grayscale image. Because Landsat image pixels are likely to be spatially autocorrelated, we selected a sample of 100 points within southern WCRA using the “spatially balanced points” tool in ArcGIS, which is designed to maximize spatial independence between sampling points. We then determined reflectance values in the pixels corresponding with these points and compared the distributions of values in burned and unburned area of southern WCRA using a Mann-Whitney U test with $\alpha = 0.05$.

Collection of ranging data from focal groups 2000-2015

We collected ranging and group composition data from seven habituated groups during other research activities in

2000-2002, 2007-2009, and 2014, and for this project in 2014-2015 (Table 1). We estimated group locations using a compass and laser rangefinder to the nearest meter along each axis within a local system of x,y coordinates corresponding to the trail system.

From January 2000-December 2001, AN and TO recorded locations of all individuals in groups B, C, F, G, S, and U at 30-minute intervals five days/month. From January-August 2002, SL recorded locations of a focal adult in groups B, C, F, G, and S at 15-minute intervals 4-6 days/month. From 2007-2009, LM recorded locations at 10-minute intervals from focal adults in groups B, C, F, G, L, S, and U 3-4 days/month. In February-March 2014, MS recorded locations of groups B, F, and G at 5-minute intervals four days/month. Finally, from July 2014- June 2015, SL recorded locations from all adults in groups B, C, F, G, L, S, and U at 15-minute intervals three days/month (Table 1). When the locations of multiple group members were recorded, only data from adult females were used to avoid pseudoreplication, as members of social groups are spatially cohesive.

Table 1 Sampling periods and sample years designated for each study group. All data from 2014-2015 were included in the sample year 2014. Authors SL, LM, AN, TO, and MS collected data

Group	Sampling periods for location data (researchers)	Sample year (months included)
B	Feb-Apr 2000 (AN, TO), Jan-Aug 2002 (SL), Sept 2007-Mar 2009 (LM), Feb-Mar 2014 (MS), Jul 2014-Jun 2015 (SL)	2000 (all), 2002 (all), 2007 (Sept 2007 to April 2008), 2008 (May 2008-Mar 2009), 2014 (Feb 2014-Jun 2015)
C	May 2000-Aug 2002 (SL, AN, TO); Sept 2007-Apr 2009 (LM), Jul 2014-May 2015 (SL)	2000 (all), 2001 (all), 2007 (Sept 2007-April 2008), 2008 (May 2008-Apr 2009), 2014 (Aug 2014-May 2015)
F	Apr 2000-Jan 2001 (AN, TO), Jan-Aug 2002 (SL, AN, TO), Oct 2007-Apr 2009 (LM), Mar-Apr 2014 (MS), Sept 2014-Jun 2015 (SL)	2000 (all), 2002 (all), 2007 (Oct 2007-Apr 2008), 2008 (May 2008-Apr 2009), 2014 (Mar 2014-Jun 2015)
G	Feb 2000-Jan 2001 (AN, TO), Jan-Aug 2002 (SL, AN, TO), Feb 2008-Apr 2009 (LM), Mar-Apr 2014 (MS), Oct 2014-Jul 2015 (SL)	2000 (all), 2002 (all), 2007 (Nov 2007-Jul 2008), 2008 (Aug 2008-April 2009), 2014 (Mar 2014-Jul 2015)
L	Jan-Dec 2008 (LM), Sept 2014-Jun 2015 (SL)	2008 (all), 2014 (Sept 2014-Jun 2015)
S	May 2001-Aug 2002 (SL, AN, TO); Jan-Dec 2008 (LM), Aug 2014-Jul 2015 (SL)	2002 (May 2001-Aug 2002), 2008 (all), 2014 (Aug 2014-Jul 2015)
U	Jan-Mar 2002 (AN, TO); Jan-Dec 2008 (LM), Oct 2014-Jul 2015 (SL)	2002 (all), 2008 (all), 2014 (Oct 2014-Jul 2015)

Estimation of HR size and location

We calculated annual HR for each group*year from which at least 12 complete daily follows had been conducted. Where data were collected for a sampling period exceeding 18 months, we divided the period into two “sample years”, with approximately equal sample sizes for each of the two years (Table 1). In the resulting dataset, samples of ≥ 15 days were available for 24 group*years and samples of 12–14 days were available for four group*years. Most (25 of 28) samples were collected across a period of ≥ 8 months, one (group F in 2007) was collected across a period of 7 months, and two (group B in 2000 and group U in 2002) were collected in a 3-month period (Table 1).

We calculated HR size in R (v 3.4.1; R Core Team, 2017) using the *adehabitat* HR package (Calenge, 2006). Sample sizes were much larger for some sample years than others due to differences in sampling between projects and time intervals, with the largest samples from 2000–2008 ($X \pm SD = 27 \pm 10$ days/group*year), and the smallest sample ($X \pm SD = 17 \pm 4$ days/group*year) in 2014–2015. Since HR size estimates may change with sample size, and 15 or more days of data were available from the vast majority of group-years, we estimated the reliability of size estimates produced using 15-day samples by generating 500 randomly selected subsamples of 15 complete days of data from the larger dataset for each group-year from which > 17 days of data were available. We used these values to calculate the mean and associated confidence intervals and used the mean values in our analysis of HR size. For groups from which between 13 and 17 days of data were available, and therefore fewer than 500 combinations of 15 days were possible, we first generated 500 randomly selected subsamples of 10 days for each group*year and used these values to calculate the mean and associated confidence intervals. The confidence intervals for 15-day and 10-day samples were narrow, suggesting that even for samples of 10–15 days, random samples of data produce fairly consistent results. Hence, for samples that included ≤ 15 days of data, we used all of the data (range = 12 to 15 days) to generate a single estimate of 95% kernel density HR size which we used in our analysis of HR size over time. For the two samples that included 17 days of data, we randomly selected 15 days of data and used this sample to generate a single estimate of 95% kernel density HR size which we used in our analysis of changes in HR size over time.

To visualize HR we mapped 95% kernel density HR from 15 randomly selected days from all group*years from which > 15 days were available and from all days for group*years from which ≤ 15 days were available. For this analysis, we modeled 95% kernel density HR in Geospatial Modelling Environment© (v. 0.7.4.0; Beyer, 2015) with R (v 3.4.1; R Core Team, 2017) using Gaussian kernels with smoothed cross-validation and a cell size of 25 and projected them and calculated their centroid locations in ArcGIS 10.3.1© (ESRI Inc. 2015).

To analyze changes in HR size over time, we first built LMMs with estimated HR size (ha) as the outcome variable and different sets of candidate predictors. We used habitat recovery (measured in years, with the value for 2000 set as 0 to avoid placing the zero outside of the range of sampled values) and habitat type (a binary variable distinguishing “burn groups”—groups with HR including and immediately adjacent to large areas of fire-damaged habitat, from “normal” groups—groups living in unburned habitat) singly and in combination as candidate predictors. For the model including both predictors, we also included an interaction term. We included random intercepts for group identity, as each group was sampled repeatedly. VIF for the test predictors in a regression model without the random effects was 1.03, indicating that collinearity was not a problem. We visually inspected QQ plots and the residuals plotted against fitted values to check the assumptions of normally distributed and homogeneous residuals. We selected the model(s) with the best fit with the fewest parameters using AICc and associated AICc weights. Since group C was identified in an earlier study (O’Brien *et al.*, 2003) as an outlier for HR size, we ran this analysis including and excluding group C.

To analyze changes in HR location, we measured the movement of the group centroid between subsequent sampling periods. We divided these distances by years between samples to estimate annual rates of movement (m/y) for each group during each interval. To test the prediction that centroids would move toward the burned area as the habitat recovered we first calculated the mean position of the centroids of the study groups in the first year for which data from each group were available (2000 for groups B, C, F, and G, 2002 for groups S and U, and 2008 for group L) to estimate the geographic center of the HR of the study population. We used the geographic center for the study population, rather than individual HR centroid locations, to develop predictions about movement direction for two reasons. First, our goal was to examine patterns of movement across the neighborhood, so a common standard needed to be selected for the sake of consistency. Second, the centroids of some group HR in some years were located slightly within the boundary of the burned habitat, making defining movement toward the burned area difficult if only individual HR are considered. We then estimated the predicted range of directions of HR movement for the population by measuring the angles from this population center to the two most extreme points on the boundaries of the burned area (i.e., the points that formed the widest angles from the mean centroid; Fig. 1.). These angles represented the boundaries for the predictions for mean direction of movement for the HR centroids for the study population. To estimate the actual trajectory of HR movements across the study population, we calculated the mean direction of centroid movement for the study groups for each interval (e.g., 2000–2002, 2008–2014) in ArcGIS 10.3.1© (ESRI Inc. 2015). We then examined these values to determine whether they fell within the range of predicted values for movement toward the recovering habitat.

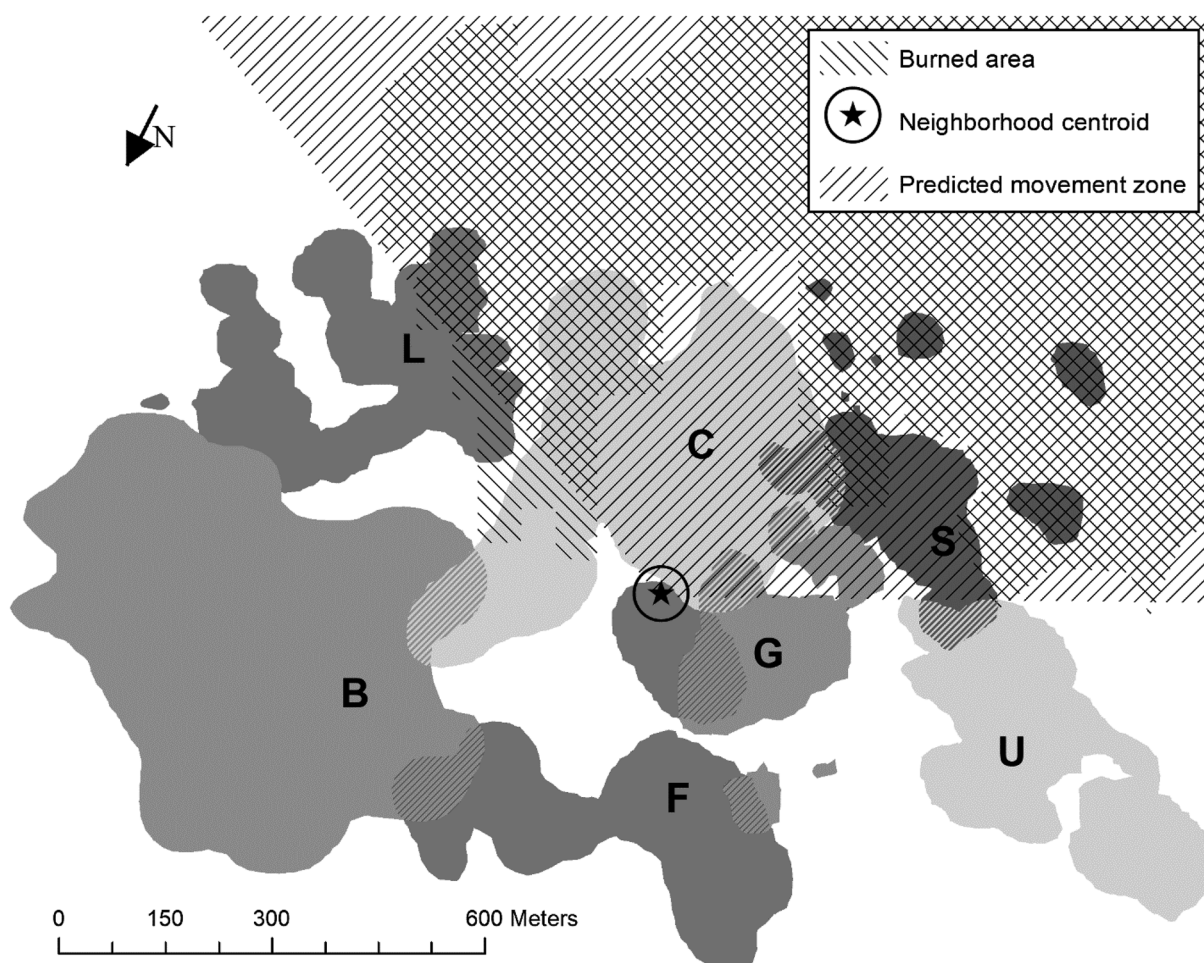


Figure 1 Map showing the location of the burned area relative to the home ranges of the seven focal siamang groups. Home range locations are shown in the first year from which ranging data were available (2000 for groups B, C, F, and G, 2002 for groups S and U, and 2008 for group L). The “neighborhood centroid” was estimated as the geographic center of the centroid locations for all home ranges in the first year from which ranging data were available. The “predicted movement zone” is the area that encompasses the range of angles between rays originating at the neighborhood centroid and intersecting the outer boundaries of the main burned area (excluding a projection of burned forest into the space between and including parts of the home ranges of groups C and L, and a small isolated patch of burned forest in the interior of the group B home range). Note that the map is oriented relative to the Way Canguk Research Area trail grid and coordinate system, rather than the cardinal directions. The burned area is to the south of the neighborhood centroid

Visualization of 2002 and 2012–2017 siamang census data

We mapped the locations of unhabituated siamang groups and individuals to determine whether ranging behavior of habituated groups was constrained by other groups and whether unhabituated groups colonized the burned area. To estimate the locations of the HR of unhabituated groups in the southern WCRA not included in our ranging study, we used locations recorded by Wildlife Conservation Society—Indonesia Program during an annual siamang census in WCRA. During the census, observers searched systematically for siamangs and attempted to follow each group or individual that they located for several hours, mapping their locations as they moved. As

most groups were unhabituated, and fled upon detecting the human observers, observation periods were often short. When groups could not be followed for several consecutive hours to obtain a reliable group composition, the observers attempted to contact the group again to confirm their identity and group composition. However, sample sizes for each group were small in each year. To visualize siamang occupancy of WCRA post-fire, we mapped each location point recorded during the annual census in 2002 (excluding the habituated focal groups) in ArcGIS 10.3.1 (ESRI Inc. 2015). Sample sizes were smaller in later years, so we grouped the data from 2012–2017 to determine whether new groups ranging in the burned areas posed a potential constraint on the ranging of our focal groups in 2014–2015.

Assessment of social and ecological correlates of HR movement

To determine whether changes in HR locations within the neighborhood were primarily associated with social changes (changes in the adult composition of a group or its neighbors), ecological changes associated with habitat recovery in the same interval, or both, we first created a set of candidate LMMs. The response variable was estimated annual change in HR centroid location (m/y) between subsequent sampling periods, $\ln(x + 1)$ transformed. In these initial analyses, group identity was included with a random intercept. However, no variance was explained by group identity. Therefore, we subsequently excluded the random factor and created a set of LMs with the same response variable. Variables included in the candidate models were: a) “habitat recovery”, measured in years since 2000 (the first year from which HR location data were available), b) “social change”, a binary variable measuring changes in the focal group (0 = adult composition remained the same between adjacent time samples, 1 = adult composition changed), and c) “neighbor change” (proportion of neighboring groups that changed in adult composition between adjacent samples, arcsine-square-root transformed). We generated models for all possible combinations of ecological and social variables. For models including both social change and neighbor change, these variables were modeled in interaction, as we assumed that the response to a change in the composition of a neighboring group may depend on the composition of the index group, so these variables may not have independent effects. Finally, we used AICc and associated AICc weights of the LM to select the model(s) that has the best fit with the fewest parameters.

For groups B, C, L, and U, the composition of one neighboring unhabituated group was unknown for some intervals.

In these cases, we assumed that group compositions did not change. When a group composition changed during a sampling year, we scored both affected intervals as having experienced a social change (e.g., if a male was replaced in February 2008, the group was scored as experiencing social changes in the 2007 to 2008 and the 2008 to 2014 intervals). Statistical analyses were conducted in IBM SPSS Statistics v. 24 except where specified.

Ethical note

All research followed the laws of the Republic of Indonesia and was approved by Bukit Barisan Selatan National Park (all years), Wildlife Conservation Society—Indonesia Program (2000–2002), and the Institutional Animal Care and Use Committees of New York University (2000–2002), Rutgers University (2007–2009), Universitas Indonesia (2014) and Appalachian State University (2014–2015). Location data from this endangered species will be provided by the corresponding author upon reasonable request.

Results

Assessment of forest recovery using Landsat imagery

By 2016, the area damaged by fire in 1997 had complete or near-complete forest cover, but the range of reflectance values for the sample of image cells inside the burned area remained different from that of cells in unburned forest ($U = 1459$, $N_1 = 30$, $N_2 = 70$, $p < 0.001$; Fig. 2), which suggests that floristic characteristics of forest in the burned area remained different from those in the unburned area in 2016, 19 years post-fire.

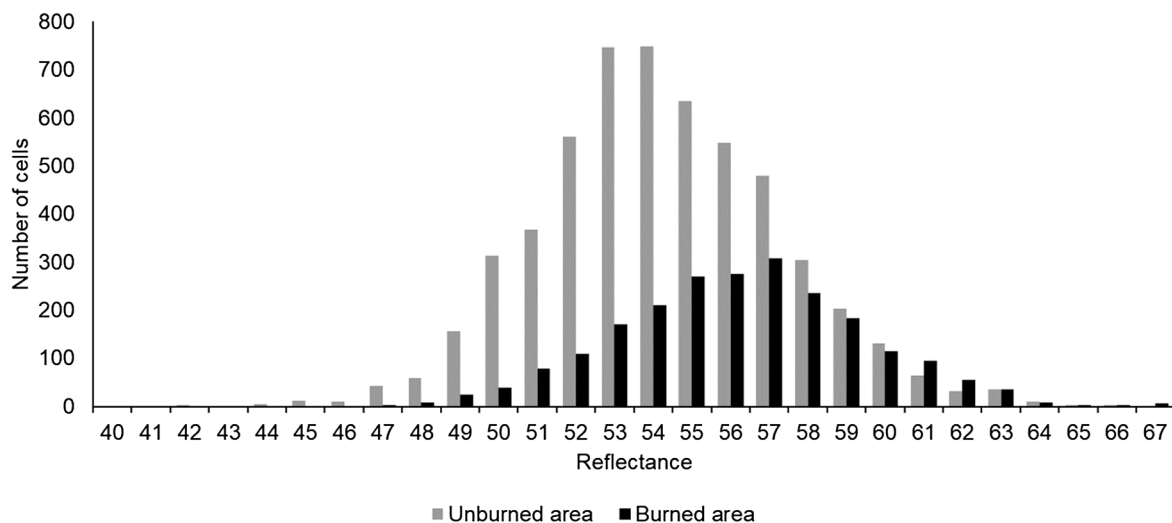


Figure 2 Comparison of flattened reflectance values in the area of the Way Canguk Research Area (WCRA) damaged by fire in 1997 (“Burned area”) and adjacent undamaged areas (“Unburned area”) in the southern WCRA trail system. Reflectance values were derived from a flattened circa-year 2016 Landsat cloud-free composite image at 30 x 30 m resolution (Hansen *et al.*, 2013; https://earthenginepartners.appspot.com/science-2013-global-forest/download_v1.4.html)

HR sizes 2000-2015

The mean 95% kernel density HR size for all groups in our sample was $20.4 \pm \text{SD } 7.8$ ha (mean of group mean annual sizes from 2000-2015). HR sizes of most groups were stable over time (Fig. 3). However, the HR of group S, a burn group, doubled in size between 2002 and 2014 (Fig. 3), and the HR of group G, which ranged in unburned habitat, also expanded. The HR of group U, which likewise ranged in unburned habitat, declined dramatically, such that the HR in 2014 was only 57% of its 2002 size. The model selection procedure favored one model including habitat type (burn versus normal) an interaction between habitat type and forest recovery, and habitat recovery (Table 2). The result was the same if group C, an outlier for HR size among burn groups, was excluded (Table 2). The coefficients suggest that HR size increased over time for burn groups but not normal groups (Fig. 4). In all other models, the confidence intervals around all predictor variables were wide, and spanned zero, indicating that these predictors were not reliable.

HR centroid movement 2000-2015

HR centroids showed little movement over time (mean \pm SD annual rate of movement 15.5 ± 6.9 m/y, $N = 7$ groups; Fig. 5). Annual rates of movement were < 15 m/y in every interval for the subsample including only burn groups and for the whole sample in every year except 2007-2008, when the mean centroid movement distance was 34.4 m (Table 3).

From the mean centroid location in 2008, the burned area spanned an area from 321° clockwise to 92° from the y axis

of the WCRA trail grid (Fig. 1), while the mean direction of movement of the group centroids ranged from 166° to 310° (Table 3; Fig. 5). For the analysis with only burn groups, centroid movement was in the predicted direction in 2008-2014, indicating home range movement into the burned area (Table 3; Fig. 5). However, this pattern did not appear in the larger sample including burn and adjacent normal groups. For this sample, most values are clustered around 300° within the trail grid coordinate system (Table 3), which roughly corresponds to eastward movement (Fig. 1).

Ranging of unhabituated neighbors

In 2002, the siamang census did not detect siamangs in most of the burned area (S1). Several groups had HR around the periphery of the burned area that included small areas of fire-damaged habitat, including three of the habituated groups, but no groups were found on the interior of fire-damaged habitat (S1). By 2012-2017, two new siamang groups had been observed ranging in the interior of the burned area (S1), although only one of these groups was contacted again in subsequent years, and at least two other groups with HR adjacent to the burned area had expanded their ranges into the burned area (S1). On several occasions, solitary individuals were also observed in the interior of the burned area (S1), but the number of individuals involved could not be determined. No siamangs were recorded ranging in the part of the burned area immediately south of the area occupied by groups S and C, however (S1). The unoccupied areas correspond to the areas showing the lowest percentage forest cover in 2000 Land-Sat images (S1).

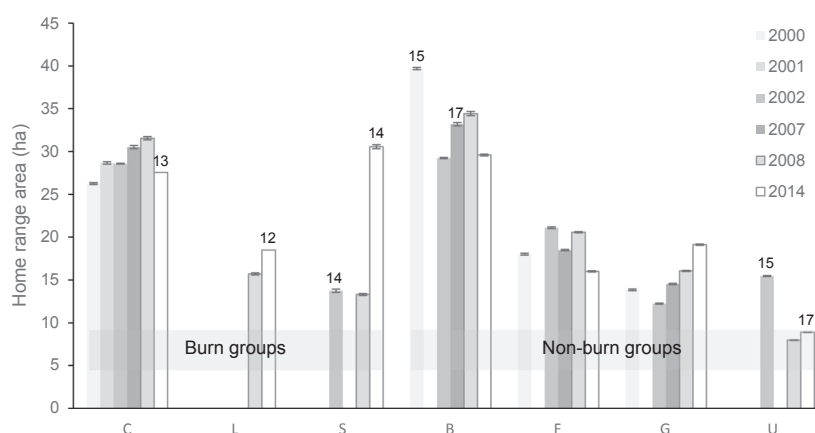


Figure 3 Home range sizes (95% kernel density) for each study group in each year from which data are available. Groups C, L, and S ("burn groups") had home ranges that included or were immediately adjacent to large areas of fire-damaged habitat. Groups B, F, G, and U ("non-burn groups") were in neighboring home ranges that did not include fire-damaged habitat (except an isolated patch in the interior of the group B home range). For group-years for which ≥ 18 days of ranging data were available, and therefore > 500 combinations of days of data are possible, values shown are means of 500 random samples of 15 days of data with 95% CI. For samples for which 14-17 days of ranging data are available, values shown are means of 500 random samples of 10 days of data with 95% CI. For samples for which 12-13 days of ranging data are available, the value, shown without CI, is the 95% kernel density home range calculated using all available days of data. Numbers above the bars are sample sizes for group*years for which < 18 days of data were available

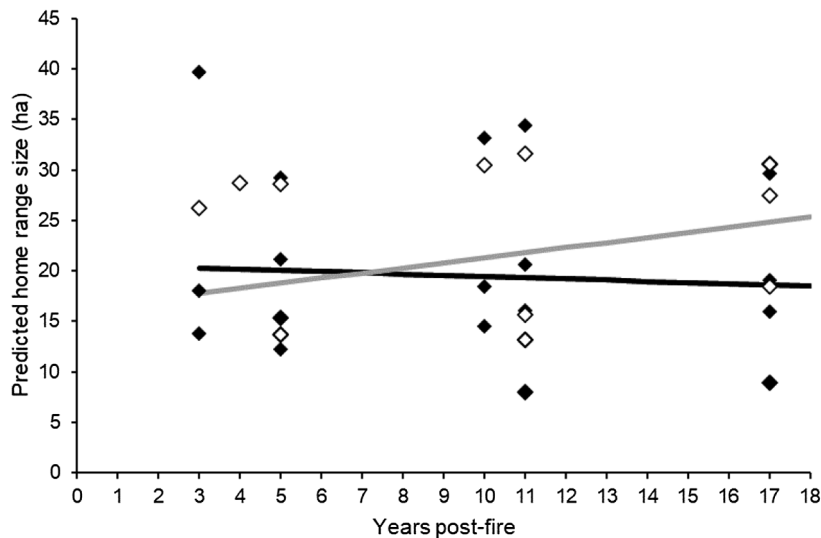


Figure 4 Actual home range sizes (symbols) and modeled values for the best LMM for home range size for siamang groups in the Way Canguk Research Area (lines). The best LMM included group status ("burn" or "non-burn"), forest recovery (measured in years post-fire), and their interaction and random intercepts for group identity. "Burn groups" are groups living in and immediately adjacent to habitat damaged in the 1997 fires, and "non-burn groups" are neighboring groups ranging in habitat not damaged by the 1997 fires. Filled shapes are home range sizes for non-burn groups. Hollow shapes are home range sizes for burn groups. The gray line indicates the slope for burn groups, and the black line indicates the slope for non-burn groups

Social and ecological correlates of HR movement

The composition of the dominant pairs in groups B, C, G, and U changed between 2000 and 2015 as males died, emigrated, and immigrated. No changes in the female composition of the groups were detected. The model selection procedure for centroid movement showed the strongest support for the model including social variables (social change, neighbor change, and their interaction) but not forest recovery (Table 4). The parameter estimates indicated that HR centroids showed greater movement when there was a change in the composition of a focal group or a greater change in the composition of neighboring groups, but that this effect was not additive. In other words, when the composition of the focal group changed, there was no effect of the composition of neighboring groups, but when the composition of the focal group remained stable, centroids moved more when there was more change in neighboring group composition.

Discussion

Almost two decades after the 1997 drought and fire, vegetation in the burned area of WCRA has shown substantial recovery. Canopy connectivity has been restored, and the tree basal stem area in the burned habitat returned to 1997 baseline in 2012 (O'Brien, 2015; S3). Nonetheless, LandSat images from 2016 and vegetation data (O'Brien, 2015; S3) confirm that vegetation in the burned area differed from that

in unburned sections of the WCRA 19 years post-fire, indicating a shift in tree species distribution. It is unclear how this shift affected the quality of this habitat for siamangs relative to unburned forest. These results are consistent with previous studies showing recovery of forest structure and diversity, but not species composition, 15 years post-fire (Slik *et al.*, 2002; Slik & Eichhorn, 2003; Slik *et al.*, 2006).

Some animals, including at least one gibbon population (Lee *et al.*, 2015), thrive in disturbed forests. One of the few studies of primates in fire-damaged habitat showed that Bornean orangutans (*Pongo pygmaeus*) had largely recovered their pre-fire feeding ecology, diets, and ranging behavior 12–15 years post-fire (Russon *et al.*, 2015). Our results show that between 3 and 11 years post-fire, siamangs with HR including fire-damaged habitat had not substantially expanded their ranges into the recovering area, but by 18 years post-fire, two of three burn groups had incorporated substantial areas of burned habitat into their HR. This change was not associated with a general increase in the size of siamang HR in the neighborhood, which indicates that siamang responses to ecological change are very localized.

In the absence of habitat disturbance, gibbon HR appear to remain stationary over long periods of time, but few researchers have closely monitored gibbon ranging over periods exceeding a few years. The HR of a group of white-handed gibbons (*Hylobates lar*) in Mo Singto, Thailand remained stable in location and changed in size by < 10% between 1994 and 2014, despite changes in group membership (Bartlett *et al.*, 2016). Similarly, an agile gibbon (*H. agilis*) HR boundary did not shift detectably following a

Table 2 Results of model selection using AICc with LMM of home range size for seven groups of siamangs in fire-affected habitat at Way Cangkuk Research Area from 2000 to 2015

Analysis	Predictor	β	95% CI	AICc	Δ AICc	$w_i(\text{AIC})$
Excluding group C	Group status[b]	-2.5	-19.8 to 14.9	173.5	0	0.62
	Group status[b] x Forest recovery	0.5	0 to 1			
	Group status[n] x Forest recovery	-0.1	-0.5 to 0.3			
	Forest recovery	-	-			
	Group status[b]	2.4	-14.2 to 19.0	175.4	1.9	0.24
	Group status[b]	2.3	-14.6 to 19.1	176.9	3.4	0.11
	Forest recovery	0.1	-0.2 to 0.4			
	Forest recovery	0.09	-0.2 to 0.4	182.6	9.1	0.01
	Group status[b]	-13.4	-33.6 to 6.7	134.5	0	0.95
	Group status[b] x Forest recovery	1.2	0.4 to 2			
	Group status[n] x Forest recovery	-0.1	-0.5 to 0.2			
	Forest recovery	-	-			
	Group status	-1.3	-21.3 to 18.7	141.6	7.1	0.03
	Group status[b]	-1.6	-21.7 to 18.6	142.8	8.3	0.02
	Forest recovery	0.1	-0.3 to 0.5			
	Forest recovery	0.1	-0.3 to 0.5	148.6	14.1	0.00

Predictors were group status (burn versus non-burn, with non-burn as reference category), forest recovery, and an interaction between group status and forest recovery. We included random intercepts for group identity. A null model with the same structure but with the predictors excluded had AICc = 181.0, Δ AICc = 7.5, $w_i(\text{AIC})=0.01$. A null model with the same structure but with the predictors excluded and group C excluded had AICc = 147.4, Δ AICc = 12.9, and $w_i(\text{AIC})=0.00$.

male replacement (Koda *et al.*, 2012), and the HR locations of three Bornean southern gibbon groups were stable over a three to nine year period during which a fire damaged the HR of one of the groups (Cheyne *et al.*, 2019). Our results show the same pattern in a larger sample of siamang groups over a 15-year period, confirming that stability of HR sizes and locations is common for gibbons, and showing that this pattern persists even in areas experiencing ecological changes. Unburned areas in southern WCRA were saturated with siamang territories throughout the study period. Given the poor quality of siamang habitats adjacent to fire-damaged areas in 2002, siamang groups living in these areas should have shifted or expanded their HR to include larger areas of healthy forest if possible. The fact that they had not done so by 2008, 11 years post-fire (Fig. 3), suggests that territorial behavior can act powerfully to prevent gibbons from adjusting their boundaries with neighboring groups in response to changes in habitat quality, leaving the most severely affected groups few behavioral options for mitigating the costs of habitat loss and degradation. Gibbons may also benefit from detailed ecological knowledge about the distribution of resources and risks within relatively small HR, which may favor long-term fidelity to a specific site (Brockelman *et al.*, 2005, Brockelman *et al.* 2014). Our results, therefore, are consistent with our knowledge of the behavioral biology of territorial gibbons specifically and animals in general. However, few long-term studies of territorial species have been conducted in tropical landscapes recovering from fire damage.

Only very small movements in centroid location were observed between 2000 and 2015, and the tendency across the neighborhood was for centroids to shift slightly east,

perpendicular to the direction predicted if movement was toward or away from the area recovering from fire damage. This does not fit the pattern expected if the primary driver of changes in HR location in the entire neighborhood was improved habitat quality in the burned areas. Instead, the eastward shift may have resulted from changes in group compositions. The model selection procedure indicated that changes in the adult composition of social groups were predictors of larger shifts in HR locations for the affected groups and their immediate neighbors during the same time period. Specifically, HR locations for the study population showed greater annual movement from 2007 to 2008 than in any other time period. In 2007 and 2008, the composition of groups B, C, G, and U changed due to emigration (groups B and C), takeovers (groups B and G), and the probable death of an adult male (group U). If territoriality maintains stable HR, changes in group composition may create rare opportunities to renegotiate boundaries with neighbors.

In 2002, no siamang groups were observed in the burned area interior (S1), but between 2012 and 2017, two groups and ≥ 2 solitary individuals were observed ranging there (S1). The HR of groups C and S also shifted between 2000 and 2015 to include more fire-damaged habitat, but this did not lead to a neighborhood-wide shift toward the recovering area. These results align with our other results in suggesting that the effects of habitat recovery on siamang ranging were highly localized. The fact that group L did not expand its HR into the burned area may reflect local differences in the pattern of habitat recovery. Even 18 years post-fire, the most heavily affected areas (which appear to be concentrated in areas that had been damaged in an earlier fire the same year [S1]) remained unoccupied. Similar long-term avoidance of

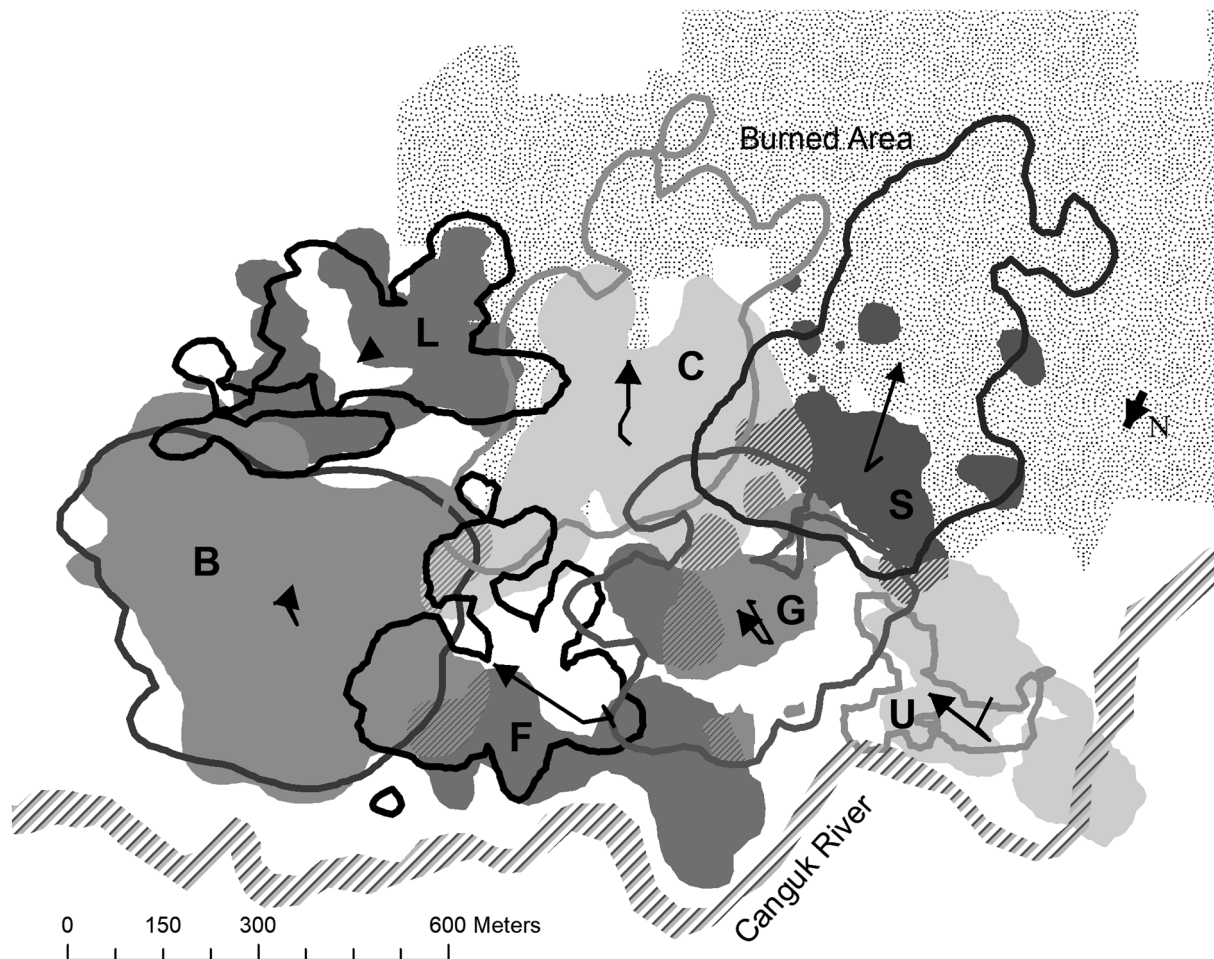


Figure 5 95% kernel density home ranges of groups B, C, F, G, L, S, and U from 2000 to 2015. Shaded areas represent home ranges in the first year that they were mapped (2000 for groups B, C, F, and G, 2002 for S and U, 2008 for group L), and dashed outlines represent 2014-2015 home ranges. Arrows indicate the movement of the group centroids. The stippled area indicates forest that was damaged by fire in 1997

an isolated area of fire damage on the interior of a HR can be seen in the ranging behavior of group B (S2).

Understanding the behavioral biology of a species is critical to predicting their responses to habitat loss and degradation. While siamangs have a strong dietary preference for ripe fruits and figs, they may respond to abrupt changes in habitat quality by adjusting their diets, rather than their ranging behavior. Indeed, the ability of siamang groups to persist on the edges of the burned areas from 1998 to 2008, despite the small size and low quality of their HR (O'Brien *et al.*, 2003), indicates ecological flexibility. Given that siamang reproductive lifespans may reach two or more decades, this flexibility may prevent or delay extirpation in severely disturbed habitats, especially habitats contiguous with large areas of undisturbed forest. However, since gibbon reproductive success is lower in poor-quality habitat (O'Brien *et al.*, 2003; Marshall, 2009), gibbons may be vulnerable to

extirpation in fire-damaged and fragmented landscapes, when large areas are burned, or when fires affect the same landscape repeatedly. Management authorities should closely monitor fire-damaged habitat and intervene as necessary to prevent further damage and support the recovery of resident gibbon populations. Loss of fauna can disrupt plant-animal relationships, resulting in plant reproductive failure and changes in plant species composition of forests (Harrison, 2001; Brodie & Aslan, 2012; Harrison *et al.*, 2013). Gibbons are important, and in some cases irreplaceable, seed dispersers for canopy trees, including species with fruits that are consumed in large numbers, but are not efficiently dispersed, by other tropical frugivores (Brockelman, Nathalang & McConkey, 2005; Hai *et al.*, 2018; McConkey, 2018). Therefore, the inability of gibbons to rapidly recolonize fire-damaged habitats could inhibit post-fire habitat recovery in Asian forests, with implications for entire ecosystems.

Table 3 Mean direction and distance of movement for the centroids of siamang home ranges in Way Cangkuk Research Area in southern Sumatra between 2000 and 2002, 2002 and 2007, 2007 and 2008, and 2008 to 2014

Interval	Direction of movement	Distance moved (m)	Annual movement (m)
2000 to 2002	295°	25.1	12.6
2002 to 2007	166°	32.9	7.8
2007 to 2008	305°	34.4	34.4
2008 to 2014	310°	87.0	14.4
2002 to 2008 (burn only)	311°	46.0	7.7
2008 to 2014 (burn only)	340°	78.9	13.2

The predicted range of movement directions if movement was driven by vegetation changes in the burned area was from 321° clockwise to 92° (corresponding to values of $\geq 321^\circ$ and values $\leq 92^\circ$). Intervals in which movement was in the predicted direction are shaded. Directions of movement are calculated relative to the trail system rather than the cardinal directions, with movement in the positive direction along the y axis of the trail system corresponding to 0° and movement in the positive direction along the x axis corresponding to 90°. Mean annual movement was calculated as the total distance moved during an interval divided by the number of years in that interval. "Burn only" indicates samples including only groups C, L, and S, which have home ranges including and adjacent to large areas damaged by the 1997 fires.

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Table 4 Results of model selection procedure for centroid movement between sampling periods (2000-2001 or 2000-2002, 2002-2007 or 2002-2008, 2007-2008, and 2008-2014) for neighboring siamang groups A, B, C, F, G, L, S, and U at Way Cangkuk Research Area

Variables	β	95% CI	AICc	Δ AICc	$w_i(\text{AICc})$
Social change	1.03	−0.14 to 2.21	52.1	0	0.76
Neighbor change	0.44	−1.11 to 1.98			
Social change x Neighbor change	−0.72	−2.54 to 1.11			
Forest recovery	−0.05	−0.13 to 0.03	55.2	3.1	0.16
Social change	1.13	−0.04 to 2.30			
Neighbor change	0.54	−0.99 to 2.07			
Social change x Neighbor change	−0.74	−2.54 to 1.06			
Neighbor change	0.76	−0.09 to 1.60	57.8	5.7	0.04
Social change	0.47	−0.26 to 1.20	59.7	7.6	0.02
Forest recovery	−0.03	−0.11 to 0.05	61.8	9.7	0.01
Neighbor change	0.82	−0.05 to 1.69			
Forest recovery	−0.02	−0.11 to 0.06	63.9	11.8	0.003
Social change	0.50	−0.26 to 1.26			
Forest recovery	−0.02	−0.10 to 0.07	65.6	13.5	0.001

Measurements of centroid movement were $\log(x + 1)$ transformed. "Forest recovery" is the number of years elapsed since the 1997 fire and the end of the sampling period, "Social change" is a binary variable indicating that the adult composition of the group did (1) or did not (0) change during the interval, with 0 as the reference category, "Neighbor change" indicates the proportion of neighboring groups that experienced a change in their adult composition during the sampling interval (arcsine-square-root transformed). When both "social change" and "neighbor change" were included in the model, an interaction term was included. Coefficients for social change are values for groups with a social change, and coefficients for social change x neighbor change indicate values for social change[1]x neighbor change. AICc for a null model was 61.2, Δ AICc = 9.1, $w_i(\text{AICc})=0.01$

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Supporting information

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

Figure S1. Map illustrating the absence of siamangs in most of the burned area in 2002, and the colonization or attempted colonization of some, but not all, of the burned area by 2012–2017

Figure S2. Figure showing avoidance of a burned area on the interior of the group B home range. Each symbol represents a location point collected during behavioral observations of group B in 2000, 2002, 2007, 2008, or 2014–2015

Figure S3. Temporal changes in A) aboveground biomass; and B) above ground carbon in burned (“Damaged forest”) and unburned (“Intact forest”) habitat in Way Canguk Research Area, Lampung, Indonesia (from O’Brien 2015)