

Fire, demography and the persistence of siamang (*Symphalangus syndactylus*: Hylobatidae) in a Sumatran rainforest

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Abstract

We show a direct impact of El Niño/Southern Oscillation (ENSO) related fires on the demography and persistence of the siamang (*Symphalangus syndactylus*), a frugivorous, Southeast Asian rainforest primate. Siamang groups affected by ENSO-related wildfires in a Sumatran rainforest were significantly smaller and experienced significantly lower infant and juvenile survival. Likelihood of infants surviving to subadults was higher by a factor of 2.8 for groups in undisturbed habitat. Burn groups had access to 48% fewer reproductive-size strangling fig trees in their territories, compared to non-burn groups. Dietary and foraging behaviour changes associated with habitat disturbance may result in lower productivity and higher mortality of young animals. Reproductive potential of burn groups is insufficient to offset low survival and groups are unlikely to persist for more than two generations. Increasing frequency of ENSO events increases the likelihood that siamang and other long-lived species that rely on fruiting trees will experience multiple fires within one generation; the resulting reduction in seed dispersal services will slow recovery of burned forest.

INTRODUCTION

Fires associated with El Niño/Southern Oscillation (ENSO) are recurring events in Southeast Asia, and within the past two decades major fires have occurred during five ENSO events (Meijaard & Dennis, 1997; Barber & Schweithelm, 2000). In Indonesia, the scale of ENSO-related fires ranges dramatically, from 160,000 ha of forest burned in 1994 to more than 3.6 million ha of forest and scrub burned in 1982–83. During 1997–98, fires in the Indonesian province of East Kalimantan on Borneo damaged 2.9 million ha of concession and conservation forests (Siegert *et al.*, 2001). Wildfires often invade forest reserves and national parks; in 1997 wildfire damaged at least 17 parks and protected areas in Indonesia (Kinnaird & O'Brien, 1998; Siegert *et al.*, 2001). Consequences of fires in protected areas include loss of primary forest, large-scale habitat change and loss of the biodiversity that parks are meant to protect (Singer *et al.*, 1989; Kinnaird & O'Brien, 1998; Barber & Schweithelm, 2000). Specific changes to wildlife communities resulting from fires, however, are poorly understood (Whelan, 1995; Kinnaird & O'Brien, 1998; Barlow, Haugassen & Peres, 2002).

Intensity of disturbance and species-specific characteristics such as abundance, demography, body size, dietary flexibility and social system all interact to define

a wildlife community's response to forest disturbance (Terbourgh & Winter, 1980; Karr, 1982; Johns & Skorupa, 1987; Lambert, 1990; Kinnaird & O'Brien, 1998). Several researchers have argued that longitudinal studies within sites are imperative to explore the long-term consequences of severe habitat disturbance on wildlife populations (Johns, 1992; Plumptre, 1996; Chapman & Lambert, 2000), but unfortunately few such studies have been published.

Another major limitation of most studies concerning impact of fires and other forms of forest disturbance on wildlife is the sole reliance on density estimation as a measure of impact. Although density estimation yields clues to the gross effects of disturbance on population abundance, the underlying mechanisms of these effects remain elusive, especially for large mammals.

We report the effects of ENSO-related wildfires on the demography and persistence of the siamang (*Symphalangus syndactylus*). Siamang are frugivorous apes of the gibbon family, Hylobatidae. They form an important component of the large-mammal community of Southeast Asian forests and, as seed dispersers, are considered important for forest dynamics. Gibbons are the most widespread apes, and among the best-studied primates in Asia. However, with the exception of *Hylobates agilis* (Mitani, 1990), we know very little about the demography of gibbons and most information comes from studies of only a few groups (Chivers, 1974; Tenaza, 1975; Palombit, 1992). Our data are derived from

a longitudinal study, including intensive monitoring of eight siamang groups and 4 years of censuses, and are the most complete data set available for siamang in the wild.

METHODS

Study area

Bukit Barisan Selatan National Park (BBSNP) is the third-largest protected area (3568 km²) on the Indonesian island of Sumatra (Fig. 1). Located in the extreme southwest of the island (4° 31' to 5° 57' S and 103° 34' to 104° 43' E), the park spans the provinces of Lampung (82% of the park) and Bengkulu for more than 150 km along the Barisan Mountain Range. BBSNP contains some of the largest tracts of lowland rainforest remaining on Sumatra and is the major watershed for southwest Sumatra. The park is bordered by villages, agriculture and plantation forestry. The park's thin elongate shape results in more than 700 km of borders, and encroachment for logging and agriculture are major problems (O'Brien & Kinnaird, 1996; Kinnaird *et al.*, 2003). Two roads bisect the park in the north and the south. Rainfall is weakly seasonal and ranges from 3000 mm to more than 4000 mm, except during ENSO events when severe droughts may occur. Temperatures fluctuate from 22 to 35° C.

The Way Canguk Research Station is located in the southern part of BBSNP (5° 39' 32" S, 104° 24' 21" E; Fig. 1) at 50 m elevation, in a mosaic of primary forest, and forest damaged by drought, wind throws, earthquakes and fire. The study area encompasses 900 ha of forest, is split by the Canguk River and is crossed by trails at 200 m intervals. The area is contiguous to large tracts of undisturbed lowland forest as well as areas disturbed by illegal logging and agricultural activity.

At the height of the 1997 ENSO event, fires broke out in many locations in southern BBSNP damaging approximately 100 km² of forest, including 165 ha of forest within the southeast portion of the Way Canguk Research area. Further damage to the study area was limited by efforts of park rangers and Way Canguk staff, who worked for 3 weeks to control the spread of the fire. Damage was patchy in the affected area. In 27% of the forest that was burned, fire destroyed leaf litter and lightly damaged the sapling layer. In 38% of burned forest, the sapling layer was damaged up to 5 m but the canopy suffered little damage. In the remaining 35% of burned forest, fire destroyed the sapling layer, severely damaged the mid-canopy layer and damaged the crown layer (Kinnaird & O'Brien, 1998; O'Brien *et al.*, 1998; Sunarto, 2000).

Prior to the fire, we established 100 vegetation plots (10 × 50 m) and tagged and measured 2106 trees with diameter at breast height (DBH) ≥ 10 cm (M. F. Kinnaird,

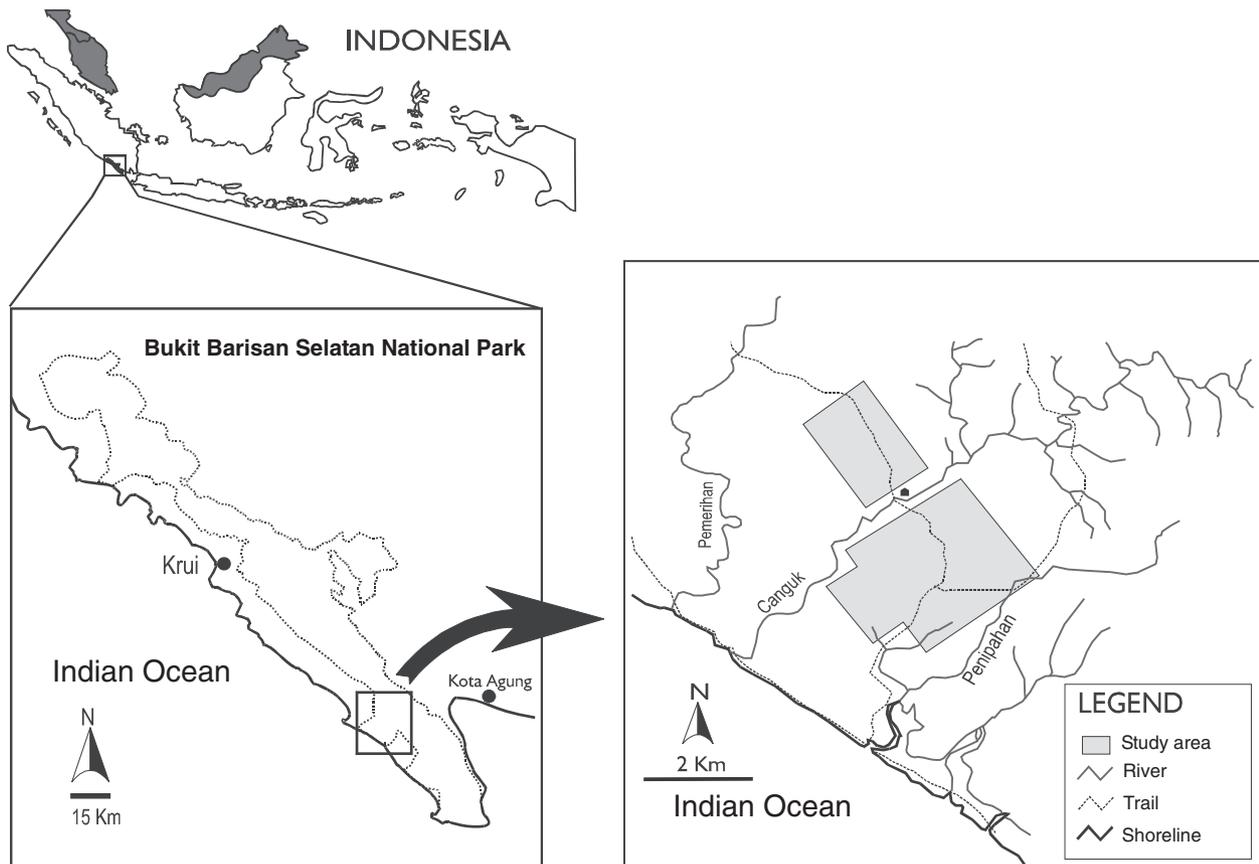


Fig. 1. Location of Bukit Barisan Selatan National Park and the Way Canguk research area. Shaded areas indicate the limits of the study area on the northwest and southeast sides of the Canguk River.

unpubl. data). The 1997 fire burned 20 of these plots, allowing us to estimate fire damage to forest structure. Prior to the fire, the vegetation plots in the eventual burn area possessed significantly fewer trees/plot ($\bar{X}_{\text{burn}} = 18.2 \pm 6.90$ trees, $\bar{X}_{\text{unburned}} = 21.8 \pm 5.16$ trees; 2-sample $T = 2.17$, d.f. = 24.6, $P = 0.04$), but average DBH size was not significantly different ($\bar{X}_{\text{burn}} = 22.9 \pm 6.22$ cm, $\bar{X}_{\text{unburned}} = 23.4 \pm 5.04$ cm; 2-sample $T = 0.37$, d.f. = 25.6, $P = 0.72$) and the distribution of DBH size classes was similar (Kruskal–Wallis $Z = 0.80$, $P = 0.54$) between unburned and burned plots.

Post-fire tree mortality was high and prolonged in the burn area (M. F. Kinnaird, unpubl. data). In the first year, tree mortality was 25.5% in the burn plots compared to 11.0% in the unburned plots. The abnormally high mortality in the unburned plots reflects the effects of the ENSO drought prior to the fires. Annual mortality in the unburned plots in subsequent years dropped to between 1.2 and 1.8% whereas annual mortality in the burn plots ranged from 3.6 to 6.7% through 2001. Seedling and sapling mortality was also much greater in the burn plots (Kinnaird & O'Brien, 1998; Sunarto, 2000). Although the fire destroyed most trees before identification was possible, 50 trees that were identified to species died more than 1 year post-fire; of these, 23 were known to be siamang food trees.

Census

In 1998 we initiated a systematic annual survey of siamang groups within the research area at Way Canguk. Siamang are the largest (≥ 10 kg at adulthood) member of the family Hylobatidae and inhabit the forests of peninsular Malaysia, Myanmar, Thailand and Sumatra. They are strictly arboreal, highly territorial and primarily monogamous. Infants are produced singly after a gestation period of 8.5 months (Leighton, 1987) and the interbirth interval is 3.0–3.5 years (Leighton, 1987; Palombit, 1992). Although primarily folivorous in mainland Asia (Chivers, 1974; Raemaekers, 1984), the species is primarily frugivorous on Sumatra (Palombit, 1992; Nurcahyo, 1999), with 25% of feeding records on fruiting figs (*Ficus* spp., family Moraceae) and an additional 38% of feeding records on other fruits.

Eight groups of siamang were followed for 5 days monthly between 1998 and 2002 during periods ranging from 6 months to 2 years as part of a siamang behaviour study (Nurcahyo, 1999; N. Nurcahyo, unpubl. data). An additional four groups were followed for 10–15 consecutive days in order to map home ranges and fruit resources. We know approximate ranges for the remaining groups in the study area based on contacts during monthly line transect censuses for ungulates and hornbills. Each year during October and November, we conducted searches to locate all groups in the research area. Once located, we classified all siamang group members to age and sex class (see Palombit (1992) for age classifications), although we are often not able to classify first year infants by sex. Counts were conducted by two groups of two to three people. Siamang groups were

followed between 6 and 20 hours to be sure that a complete count was obtained for each group. Siamang groups are easily counted because they tend to move less than 1 km during the course of the day, they spend more than 80% of their days at distances greater than 200 m from neighbouring groups, they have little overlap in territories, and groups rarely subdivide (approximately 15% of records during monthly behavioural observations). When subdivision does occur, subunits are usually within 100 m of one another and normally rejoin within 3 hours. By using multiple observers and teams, we were able unambiguously to census neighbouring groups. Data on births were collected opportunistically throughout the study.

Because we did not measure ranging patterns of groups prior to the fire, we were unable to determine the degree to which individual home ranges were directly affected by fire and we could not measure subsequent changes in the size or configuration of home ranges. Therefore, a group was classified as 'burn group' if the territory included forest that was damaged by the fire or if the territory was directly adjacent to areas burned in 1997. Otherwise, the group was considered a 'normal' group.

We calculated annual survival rates for infants and juveniles based on the presence or absence of individuals in successive censuses over a 4-year period, 1998–2001. Thus, an infant's fate through the first year of life was calculated for all infants that were observed as born in year i (scored as a 1) and either alive (score 1) or dead (score 0) in year $i + 1$. Survival was calculated by $\sum(\text{alive year } i + 1) / \sum(\text{alive year } i)$. Survival for other age classes was calculated in a similar fashion. This method may under-sample infants since an unknown proportion of infants dies within the first few days of life (Geissmann, 1991), but any bias should be random with respect to infants born to burn groups and normal groups. If bias does exist and more infants die undetected in the burn groups, we would expect longer observed interbirth intervals among burn groups.

Figs are among the top five diet items in every month and *Dracontomelum dao* (family Anacardiaceae) is the top diet item whenever it bears ripe fruit (5–6 months/year: Nurcahyo, 1999; WCS-IP, unpubl. data). The number of important fruit resources in a home range has important implications for siamang foraging success and home-range quality. We therefore conducted inventories of siamang home ranges to determine the number of reproductive-sized strangling figs (family Moraceae) among the 23 species present in the study area and the number of reproductive-sized *D. dao*.

RESULTS

We censused members of 24 to 37 groups/year in the Way Canguk study area; 11 groups were categorized as burn groups and 26 groups as normal groups (Table 1). Each group was censused for an average of 3.4 years (range 1–4 years; 130 group-years). In 1998 (1 year after the fire), group size of burn and normal groups were similar ($N_{\text{normal}} = 3.7$, $N_{\text{burn}} = 3.8$; 2-sample $T = 0.445$,

Table 1. Details of siamang census in Way Canguk research area. Differences between numbers of groups censused/year reflect establishment of new groups during the study period, and inclusion of groups with partial ranges in the study area.

Year	1998	1999	2000	2001
Dates of census	Nov–Dec	Nov–Dec	Oct–Nov	Oct–Nov
No. of census groups	24	32	37	37
Group size range burn	3–5	3–5	3–6	2–5
Group size range normal	2–5	2–6	2–6	2–6

d.f. = 10.31, $P = 0.665$) but by 2001 the size of burn groups had declined significantly ($N_{normal} = 4.0$, $N_{burn} = 3.2$; 2-sample $T = 2.187$, d.f. = 22.32, $P = 0.039$). Differences in the size distribution of burn groups in 2001 include a large proportion of groups composed of pairs and a lack of groups in the five to six size range (Fig. 2). Population structure in 2001 also varied significantly between the burn and the normal groups ($\chi^2 = 83.9$, d.f. = 4, $P < 0.001$). The burn population was composed of 74.3% adults and subadults whereas the normal population was 62.6% adult and subadult. Burn groups had 30% fewer infants, 24% fewer small juveniles and 39% fewer large juveniles compared to normal groups.

Much of the difference in group and population structure between the burn and normal groups is attributed to differences in survival of infants and juveniles. Infant survival rates in the first and second years are 1.3 and 1.4 times greater, respectively, for infants in the normal groups (Table 2). Combined juvenile survival over 4 years is 1.5 times greater in normal groups compared to burn groups. These consistent survival differences imply that an infant born into a normal group is almost twice as likely to survive to the juvenile age class and three times more likely to survive to the subadult age class compared to an infant born into a burn group.

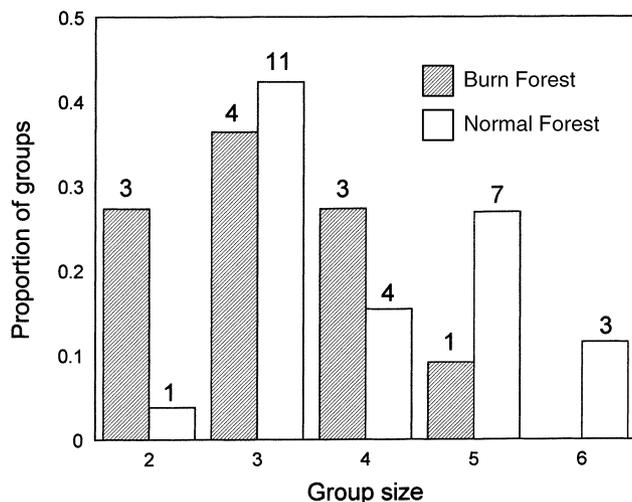


Fig. 2. Distribution of siamang group sizes for burn and normal forest. The number of groups is indicated above bars.

Table 2. Age-specific survival rates for siamang infants and juveniles born in normal and burn groups. P indicates significance level for binomial test.

Age class	Normal	Burn	P
Infant year 1	0.848	0.667	0.017
Infant year 2	0.867	0.600	0.027
Juvenile (combined)	0.839	0.556	0.003
Infant to subadult	0.617	0.220	

We counted reproductive-size strangling figs and *D. dao* trees in the home ranges of seven burn groups and five normal groups (Fig. 3). Home ranges in normal forest were larger on average (19.5 ± 8.0 ha) compared to burn forest (15.1 ± 7.5 ha) but differences were not significant (Mann–Whitney $U = 13$, $P = 0.53$; Fig. 4). Neither frequency ($N_{normal} = 32.4 \pm 18.2$, $N_{burn} = 22.7 + 14.1$) nor density ($D_{normal} = 1.40$, $D_{burn} = 1.38$) of *D. dao* trees was significantly different in the normal and burn group ranges (Mann–Whitney $U = 13$, $P = 0.53$, for both frequency and density). Frequency of reproductive-sized strangling figs was significantly higher for normal groups than for burn groups ($N_{normal} = 28.6 \pm 4.4$ figs, $N_{burn} = 15.1 + 9.6$ figs; Mann–Whitney $U = 4.5$, $P = 0.03$; Fig. 4). Density of large strangling figs was also higher for normal groups ($D_{normal} = 1.68$, $D_{burn} = 1.06$; Mann–Whitney $U = 8.0$, $P = 0.15$), but this difference was not significant. The second-largest home range belonged to the largest burn group (group B-4; Figs 3 and 4) containing five members from 1998 to 2001. The home range was 28 ha and retained high densities of figs (Fig. 4) and *D. dao*. Elimination of this apparent outlier, however, does not change any of the results. The difference in abundance of reproductive-sized strangling figs is consistent with the expectation that burn forest is poorer-quality habitat for siamang.

DISCUSSION

Monogamy and strict territoriality may limit the range of possible responses to fire (and other severe disturbances) by siamang. Whereas many colobine and cercopithecine primates may shift ranges in response to habitat disturbance (Berenstain, 1986; Johns & Skorupa, 1987) siamang habitat tends to be saturated (Leighton, 1987), limiting opportunity for territory shifts or expansions, and limiting opportunity for new territory formation or dispersal. In our study population, some groups exhibit home-range overlap (Fig. 3) and most groups have very small vacancies between home ranges, except around the burn area. In such a situation, groups that occupy territories affected by fire have little chance to expand into adjacent areas to accommodate degradation and loss of habitat. Thus, even though groups may have survived the fire, the consequences may persist in the form of smaller ranges and reduced habitat quality.

Territories of siamang in normal forest averaged 29 reproductive strangling figs versus 15 figs in burned forest. Because figs are highly preferred by siamang and contribute to 25% of all feeding records, these data suggest an important difference in habitat quality, as

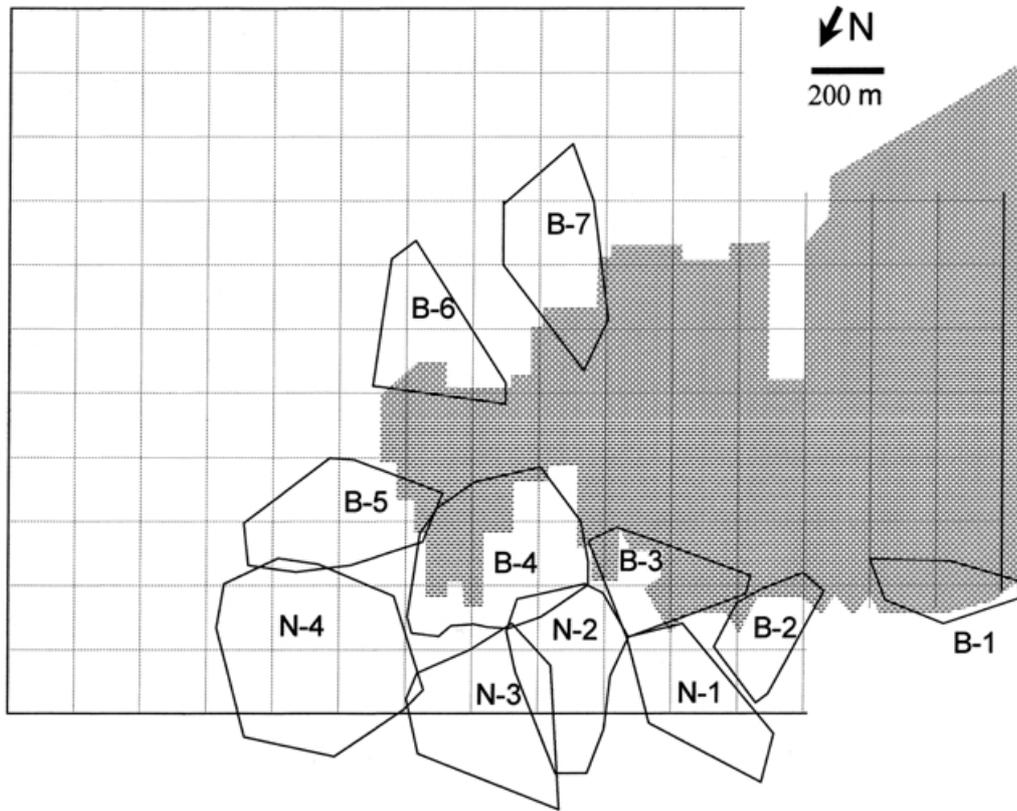


Fig. 3. Extent of the 1997 fire (shaded) in the southeast Way Cangkuk research area and positions of measured home ranges relative to the fire. ‘B’ indicates a burn group and ‘N’ indicates a normal group. One normal group range in the northwest study area is not shown.

measured by the availability of our study groups’ primary fruit resource. Figs fruit asynchronously throughout the year, and a lower number of fruiting fig species and individuals in a territory reduces the probability that these

preferred fruits are available during any given month. Groups in normal forest may have access to abundant fruit resources year-round, while groups in burned habitat are likely to suffer periods of fruit shortage. During these periods, siamang will have to forage and move more often, or switch their diet to leaves.

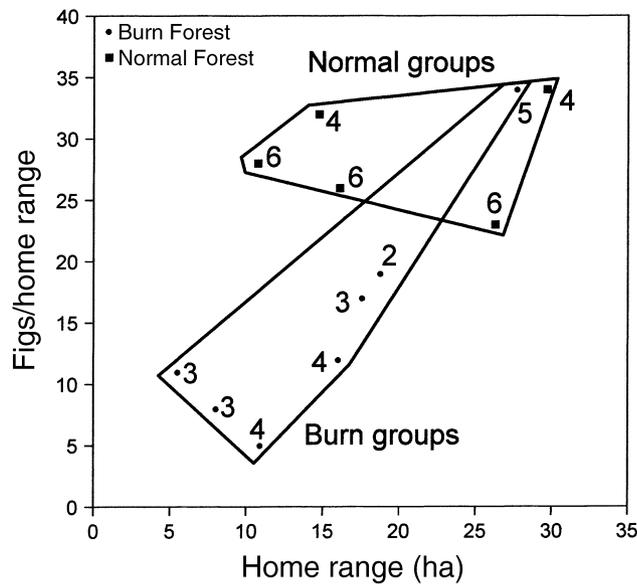


Fig. 4. Number of reproductive size strangling figs (*Ficus* spp.) in home ranges and home-range sizes for burn and normal forest groups. Numbers indicate the group size associated with each home range.

Only one group in the burn forest had five members, compared with the average size of 2.8 members for the remaining groups (B-4 in Fig. 3). The large burn group also possessed the second-largest home range, containing many strangling figs, and managed to maintain its group size as the average size of burn groups declined. This group’s similarity to normal groups in resource availability and maintenance of group size suggests that inadequate fruit resources typical of the burn group home ranges do have significant effects on the structure and demography of siamang groups.

Johns & Skorupa (1987) found that, among primate species, large body size and degree of frugivory shows a significant negative correlation with the ability to persist in recently logged forests, as expressed by comparative population densities in unlogged and adjacent logged forests. Dietary diversity, on the other hand, did not appear to affect vulnerability because typical logging operations changed abundance but not diversity of potential food types. The most important factor affecting a species’ persistence was the ability to change the relative proportions of different food types in the diet, specifically

to exploit available new leaves in the absence of fruit. Highly specialized frugivores are less able to do this and the most successful species are those which can survive on a largely folivorous diet, despite being primarily frugivorous (Johns, 1997).

By these criteria siamang should be highly vulnerable to fire-related habitat disturbance. Siamang are large bodied, have a relatively diverse diet (> 160 species, T. O'Brien, unpubl. data) and appear to prefer fruits to leaves. Although siamang usually are described as folivorous (Chivers, 1974; Raemaekers, 1984), our study population more closely resembles other gibbons in that the diet is composed primarily of fruit (> 60%; Nurcahyo, 1999; N. Nurcahyo, unpubl. data), especially fig fruits (*Ficus* spp.) and fruits of *D. dao*. Palombit (1992) argues that siamang are flexible foragers, preferring fruit when available but able to switch to leaves when necessary. Such flexibility may help reduce siamang vulnerability to habitat disturbance but it is not without costs.

Johns (1986) reported behavioural changes in gibbon groups after habitat disturbance due to logging. He cited a loss of 51% of trees in all size classes (Johns, 1988) and a dramatic reduction in fruit availability associated with an increase in folivory and time spent resting, and a decrease in time spent feeding and travelling. Altmann (1980) showed that female baboons (*Papio cynocephalus*) with infants are believed to be under nutritional stress, and decreases in food quality and feeding time presumably reduce nutritional intake, increasing risk to mother and infant. In such circumstances, infant mortality often increases (Altmann, 1980; Jolly, 1985). Decreases in feeding time are also detrimental to juvenile primates. Janson & van Schaik (1993) argue that, because juveniles are growing rapidly but are inefficient foragers (Altmann, 1980), they must spend more time foraging than adults. Juvenile primates also may have more problems digesting leaves than adults (Janson & van Schaik, 1993), making them more at risk as fruit resources decline. Thus juvenile siamang may face a higher risk of mortality through starvation. In situations where adult group members in disturbed forest rest more and forage less, juveniles are constrained to follow the adults' lead or forage solitarily. Following the adults may result in a low-quality diet (more leaves) and less time spent feeding whereas foraging alone increases the juvenile's risk of predation. Either option increases the likelihood of juvenile mortality among siamang groups in fire-disturbed forests.

What is the long-term future for siamang groups occupying burned habitat? Palombit (1992) calculated the reproductive potential of an average siamang female based on a 3-year interbirth interval as approximately five offspring/female/lifetime. Our data also suggest that five to six offspring is an appropriate value for reproductive potential based on a 2.6-year interbirth interval for normal groups and 2.8 years for burned-forest groups. Given the low survival rates for infant and juvenile siamang in burn groups, the estimated reproductive potential is insufficient to allow replacement of the population in burned habitat. Burn groups may be expected, on average, to produce 1.1 to 1.3 infants that survive to the subadult class compared

to 3.1 to 3.7 infants in normal groups. Without rapid improvement in habitat quality, reproductive effort will be insufficient to sustain groups in burned habitat and they will go extinct within one to two generations after a fire. Unfortunately, the periodicity of ENSO-cycles is 3.5 to 5.6 years (Curran *et al.*, 1999), increasing the likelihood that siamang living in fire-damaged forests will be subjected to multiple fires within one generation. Loss of seed dispersal services by siamangs will further slow the recovery of burned forest. Our results highlight the fact that simple comparisons of wildlife densities between control and disturbed areas do not tell the entire story, and longitudinal studies are critical for understanding species' abilities to persist in the increasingly disturbed habitats of the tropics.

Acknowledgements

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