



## Non-territorial Macaques Can Range Like Territorial Gibbons When Partially Provisioned With Food

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### ABSTRACT

Human food supplementation can affect components of animal socioecology by altering the abundance and distribution of available food. We studied the effect of food supplementation by comparing the ranging patterns and intergroup interactions of two groups of northern pigtailed macaques (*Macaca leonina*), a non-territorial primate species. One group was partially reliant on food provisioning, whereas the other group foraged wild food. We also compared the macaques' movement with that of a group of white-handed gibbons (*Hylobates lar*), a territorial species inhabiting the same site. Home range, core area, and daily path lengths were significantly smaller for the semi-provisioned group than for the wild-feeding group. In contrast to wild-feeding macaques, supplemented macaques showed higher fidelity to home range, core area, and particularly to the region where human food was most accessible and abundant. The relationship of daily path length and home range indicated a low defendability index for wild-feeding macaques; the higher index for the semi-provisioned group was consistent with the territorial pattern found in gibbons. Semi-provisioned macaques showed further traits of territoriality with aggression during intergroup encounters. These findings indicate that human modification of food availability can significantly affect movement patterns and intergroup competition in macaques. The observed ranging dynamics related to food provisioning may decrease the efficiency of macaques as seed dispersers and increase predation on their home range, and thus have important consequences for plant regeneration and animal diversity.

Abstract in Thai is available with online material.

*Key words:* core area; home range; Khao Yai National Park; *Macaca leonina*; northern pigtailed macaque; site fidelity; socioecological models; white-handed gibbons.

SOUTHEAST ASIA HAS BEEN ONE OF THE MAJOR ZONES OF SYMPATRY BETWEEN HUMAN AND NONHUMAN PRIMATES for at least the last 10,000 yr (Fuentes 2006), and this long interaction has created a form of co-ecology where both taxa affect one another significantly (Fuentes 2006, Riley *et al.* 2011). The particularly strong anthropogenic disturbance and consequent fragmentation of tropical landscapes during recent decades have generated many new areas where animals and humans are compelled to interact (Biquand *et al.* 1994, Woodroffe 2000, Hill *et al.* 2002, Lee & Priston 2005, Corlett & Primack 2011, Laurance *et al.* 2011). With this proximity, animals may lose their fear of humans while discovering the ease of feeding from garbage, leftovers, or crops (Sprague 2002, Lee & Priston 2005, Albert *et al.* 2011, 2013a,b).

This is aggravated by deliberate feeding of animals by people in lodges, temples (Brennan *et al.* 1985, Else 1991, Fa & Lind 1996, Richter *et al.* 2009, Knapp *et al.* 2013), and even protected areas (Orams 2002, Sangjun *et al.* 2006, Albert *et al.* 2011, 2013a,b).

This human–animal coexistence provides an opportunity to explore animal socioecology models that link resource defensibility and predation pressures with social systems and intra- and intergroup interactions (Crook & Gartlan 1966, Wrangham 1980, Janson & van Schaik 1988, van Schaik 1989, Sterck *et al.* 1997). Living in groups has benefits, such as enhancing the likelihood of avoiding predators, but also increases the level of resource competition (van Schaik 1989, Janson & Goldsmith 1995, Chapman & Chapman 2000). Two basic competition regimes, contest and scramble, can be described based on the distribution of resources. Contest competition emerges when a resource can be economically defended, and thus, hierarchical relations and aggression are expected; scramble completion emerges when a resource is not

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economically defendable or is equally accessible among contestants, and thus, individuals are expected to show weak or non-existent hierarchies and low levels of aggression. The competitive regime affects the spatial organization of groups. For example, defense of a territory indicates between-group contest competition, whereas the spatial patterns of scramble competition are thought to be related to population density (van Schaik 1989, Sterck *et al.* 1997). Scramble competitors would increase travel distances under high population densities or dispersed and scarce resources to satisfy their energetic requirements (Wrangham *et al.* 1993, Chapman *et al.* 1995, Janson & Goldsmith 1995). Anthropogenic effects can influence key factors, for example, the abundance and spatial distribution of food resources, thereby providing scenarios that allow us to test socioecological models.

Food enhancement can affect animal socioecology (Kanurai 2004, Sapolsky & Share 2004, Silva & Talamoni 2004, Fuentes 2006, Riley *et al.* 2011). Food provisioning may alter movement ecology (*sensu* Nathan 2008) and consequently the spatial and social decisions of animals (Southwick *et al.* 1965, Kawanaka 1973, Lindburg 1977). Movement alterations may be observed as changes of ranging patterns such as the home range, for example, the area used over a given period of time excluding occasional ‘sallies’ (Burt 1943, Jewell 1966); the core area, that is, the most used regions inside home ranges (Kaufmann 1962, Asensio *et al.* 2012a); or the daily path length (Carbone *et al.* 2005). When animals rely on human food, a concentrated hyper-caloric source of energy, they do not travel in search of wild food as much as non-provisioned animals do (Fa 1986). In general, both home range and daily path length greatly decrease when animals are food-provisioned (Altmann & Muruthi 1988, Boutin 1990, Monadjem & Perrin 1998, Kreiter & Wise 2001, Silva & Talamoni 2004). Because the supplied food is usually concentrated in specific spots, greater levels of contest competition may arise given the forced proximity between individuals and the economical defendability of the resource (Brennan *et al.* 1985). Food provisioning may affect another key aspect of movement ecology, the recurrent visit and use of particular regions of the home range or site fidelity, which generally varies according to the spatial distribution of resources over time (Easley & Kinzey 1986, Switzer 1993, Asensio *et al.* 2012b).

We can expect that food provisioning would also affect movement ecology, as the distribution and availability of resources are major influences on ranging patterns and territoriality. Non-territorial animals shift their ranging areas over time in response to variation in the spatial distribution of food (Burt 1943, Börger *et al.* 2008), while territorial species concentrate in exclusive, non-overlapping regions that have key resources such as mates, nest sites, or food (Wrangham *et al.* 2007, Wartmann *et al.* 2014). Therefore, territories are usually centered within the home range and not at the overlapping zones adjacent to its borders (Mitani & Rodman 1979). Under a regime of food provisioning, we might expect species to shift these patterns in response to a changed distribution of resources. Moreover, the existence of strong site fidelity is thought to reflect predictability of defendable resources as they can be monopolized by displaying

aggression or hierarchy (Mitani & Rodman 1979, Doncaster & MacDonald 1991, Kie *et al.* 2010, Rivrud *et al.* 2010).

Like other cercopithecines, macaques (*Macaca* spp.) show great ecological and socioecological flexibility, adjusting their diet, group size, feeding strategies, and movement patterns to resource availability and habitat structure (Albert *et al.* 2014). Consequently, they are better able to tolerate human environments than many other species (Richard *et al.* 1989, Albert *et al.* 2014). The genus contains several of the last large seed dispersers remaining in the disturbed habitats of South-East Asia (Corlett 1998, Lucas & Corlett 1998, Kitamura *et al.* 2002, Albert *et al.* 2013c). The northern pigtailed macaque (*Macaca leonina*) is a non-territorial and semi-terrestrial primate that lives in multi-male/multi-female groups (Melnick & Pearl 1987, Choudhury 2008, Albert *et al.* 2011). Although the species is omnivorous, fruit often constitutes most of its diet (Choudhury 2008, Feeroz 2012, Albert *et al.* 2013a). The species has home range sizes varying from 83 ha for troops living in well-preserved forests to 347 ha for groups living in degraded forests (Choudhury 2008, Albert *et al.* 2013b).

At Khao Yai National Park (Thailand), some wild northern pigtailed macaques inhabit the park headquarters, the main tourist areas, and areas next to bungalows (Albert *et al.* 2011). Since the early ‘90s, these macaques have frequently fed from garbage bins, sometimes stolen food from careless humans, and occasionally broken into houses in search of food (W.Y. Brockelman pers. comm.). Despite the interdiction of feeding wildlife in the park, some people deliberately provide food to macaques (Albert *et al.* 2011, 2013a,b). Macaques at the site live in sympatry with two species of gibbons (*Hylobates lar* and *H. pileatus*). Gibbons are arboreal ripe-fruit specialists, and although they feed on a broad number of species, 3–7 species usually constitute the base of their monthly diet (Savini *et al.* 2008, McConkey 2009, Asensio *et al.* 2014). They often live in small pair-bonded groups comprising one breeding pair and one to four offspring, within a relatively small and stable home range (*ca* 25–40 ha: Bartlett 2009, Suwanvecho & Brockelman 2012). They are territorial and defend non-overlapping areas of their home range from neighboring groups (Brockelman *et al.* 2014).

We aimed to examine the effect of food provisioning on the movement ecology and intergroup interactions of northern pigtailed macaques by comparing two free-ranging groups in Khao Yai National Park, one large wild-feeding group (WF) and a smaller semi-provisioned group (SP) that forages on human food. We also compared their movement patterns with those of a group of white-handed gibbons living at the same site. We hypothesize that partial food provisioning modifies the movement patterns of macaques, making them range similar to a territorial species (gibbons), and altering the nature of their intergroup interactions. First, we predict that SP will have smaller home ranges and core areas and shorter daily path length than WF. Second, SP and gibbons will have core areas in fixed areas at the center of the home range, the area where supplemented food is found for SP groups and in boundary areas for the gibbon group. However, WF will have a core area frag-

mented in several nucleuses throughout the home range, shifting over time in response to the naturally changing location of food. Third, site fidelity will be greater for SP and gibbons compared to WF. Particularly, SP will have an especially strong fidelity to areas where human food is accessible, where resource defense is theoretically feasible. Fourth, SP and the gibbon group will have a higher defendability index (Lowen & Dunbar 1994) than WF in accordance with the movement of a territorial animal. Fifth, site fidelity to human areas of SP will be more related to the number of visitors to the park (used as a proxy of human food influx) than to the general fruit abundance in the forest. Finally, SP will have more agonistic inter-group encounters than WF.

## METHODS

**STUDY SITE.**—We conducted the study at Khao Yai National Park, Thailand (14°26' N, 101°22' E), which covers 2168 km<sup>2</sup> ~130 km NE of Bangkok. This park is the most visited protected site in Thailand, averaging up to 800,000 visitors per year with the main influx between November and February (DNP 2014). The study area was in the Mo Singto forest area, covering approximately 10 km<sup>2</sup> and including the park headquarters and some tourist zones. The study area consists mainly of seasonally wet evergreen forest between 700 and 890 m asl (Savini *et al.* 2008). It has a monsoonal climate with a wet season (June to October), a cold dry season (November to February), and a hot dry season (March to May). The annual average rainfall is 2504 mm, ranging from 69 mm during the dry season to 353 mm during the wet season; the mean monthly temperature ranges from 19°C in December and January to 24°C in March and April (Albert *et al.* 2011), and mean humidity ranges from 64.6 to 77.1% (Savini *et al.* 2008). Due to the consistent rainfall patterns, Khao Yai has a marked and regular seasonality in food abundance with a high-abundance period from March to September and a low-abundance period from October to February (Savini *et al.* 2008, Bartlett 2009, Albert *et al.* 2013b).

**PRIMATE GROUPS.**—We studied two northern pigtailed macaque groups (WF and SP) and one group of white-handed gibbons habituated to researchers (Savini *et al.* 2009, Albert *et al.* 2011). WF comprised 60–67 individuals: 3–4 males, 19–20 females, and 37–44 immatures (2–3 subadults, 20–29 juveniles, and 7–14 infants); and behavioral data were collected during 12 consecutive months (852 h). The troop mainly ranged at the north and northwest of the park headquarters and the visitor center. They did not search actively for food on the road or forage from garbage bins, and on only three occasions was the dominant male observed receiving food on the road from visitors in cars. SP included 30–39 individuals: 1–3 males, 12–13 females, and 17–26 immatures followed for 12 mo (1029 h) by Albert *et al.* (2013a). SP ranged in the surroundings of the park headquarters and had a diet partly based on food provided by humans food, and the yearly percentage of total feeding time devoted to acquiring provisioned food was 28.1 percent ±23.2 SD

(max = 68.7% in January, min = 1.5% in June,  $N = 12$ ; Albert *et al.* 2013b). Each primate group was followed for a total of 12 mo. The gibbon group consisted of 1 adult male, 1 adult female, and 2 immatures. WF was observed from July 2012 to June 2013; SP from April to July 2009, December 2009 to March 2010, and August to November 2010 (Albert *et al.* 2013a,b,c); and the gibbon group from January to December 2002.

**ANIMAL LOCATIONS, HOME RANGE, CORE AREA, AND DAILY PATH LENGTH.**—We followed all three groups for five to eight full days (sleeping site to sleeping site) a month. We recorded the geographical position of the macaque groups every 30 min using a handheld global positioning system (GPS). We plotted the position of gibbons every 30 min on a detailed map of research trails across their home range. The trails were ground-truthed and imported into ArcGIS 9.3 (Environmental Systems Research Institute, Redlands, CA, USA), which allowed extracting gibbon positions in relatively accurate UTM coordinates. We estimated yearly and monthly home ranges and core areas of macaques and gibbons groups using characteristic hull polygons (CHPs). CHPs are calculated using the Delaunay triangulation in which a triangulated irregular network is built from each point to other points without intersecting lines, so that all resulting triangles do not overlap (Duckham *et al.* 2008, Downs & Horner 2009). The rationale behind the CHPs method is that short-perimeter triangles represent areas of high ranging activity and long-perimeter triangles represent areas of low or null activity. To determine which triangles formed the home range and the core area, we applied a spatial statistical tool, the 'Hot Spot Analysis with Rendering' in ArcGIS 9.3. This tool assesses whether short- or long-perimeter triangles are statistically clustered or dispersed in space. We discarded the longest triangles that were statistically clustered, and the remaining triangles formed the home range. The shortest triangles that were statistically clustered defined the core area. We quantified the percentage of core area within the home range. Daily path length was calculated by summing the distances of consecutive 30-min track points across full days.

**GROUP MASS.**—Following Grant *et al.* (1992), we calculated the group mass (kg) per unit area (ha) for each group. We took into account the known weight averages of adult males and females of both species (macaques: Fooden 1975, Malaivijotnond *et al.* 2012; gibbons: Jungers & Stern 1984). The mass of an immature individual was considered as half the weight of an adult (Clutton-Brock & Harvey 1977), and infants were excluded. For each group, we calculated the yearly mass values for the home range and core area.

**HOME RANGE AND CORE AREA FIDELITY.**—The degree of site fidelity to home ranges and core areas was estimated by quantifying the number of months in which different home range or core area regions overlapped following the method of Ramos-Fernandez *et al.* (2013). This method creates an interception map overlaying all monthly home ranges and core areas and then

generates a figure with a gradient of the use of all overlapping regions. Based on this method, we estimated a monthly fidelity index ( $f$ ) to either a home range or a core area using the formula

$$f = \frac{\sum_i^j p_i o_i}{nA}$$

where  $j$  is the number of overlapping areas in a given month,  $p$  is the number of times that each area overlapped over all months,  $o$  is the overlap area size,  $n$  is the number of study months, and  $A$  is the corresponding monthly home range or core area size. Fidelity index values range from 0 to 1 with values close to 1 indicating high site fidelity.

**DEFENDABILITY INDEX.**—We calculated the defendability index as the fractional monitoring rate ( $M$ ) following Lowen and Dunbar (1994):

$$M = N \left( \frac{sv}{d^2} \right)$$

where  $N$  is the mean number of independently foraging parties,  $s$  is the detection distance (the distance at which intruders can be detected),  $v$  is the mean of daily path length, and  $d$  is the diameter of a hypothetical circle with an area equal to the yearly home range. Territorial animals should have  $M \geq 0.08$ , suggesting that the mobility of the animals allows them to reach home range boundaries at least once daily. By contrast, non-territorial animals usually have  $M < 0.08$ , suggesting reduced mobility in relation to the size of the home range and boundary length, which does not permit the defense of a territory.

**TOURIST EFFECT ON FIDELITY TO HUMAN AREAS.**—We defined the human area by applying a minimum convex polygon to the locations of buildings (houses, cafeteria, visitor center), and we estimated a fidelity index within the human area ( $f'$ ) using the above formula where  $o$  is the overlap area size inside the human area.

**MACAQUE INTRA- AND INTERGROUP INTERACTIONS.**—We recorded *ad libitum* (Altmann 1974) the occurrence of intergroup encounters (encounters/hour) and classified them as agonistic (screams, chases, or attacks between groups) or not agonistic (affiliative or avoidance behavior). Intergroup encounters were defined as occurring when two groups came into visual contact.

**DATA ANALYSIS.**—We compared the ranging patterns between WF and SP using the following monthly variables: home range size, core area size, and daily path length. In addition, we compared fidelity to home range and core area between gibbons and macaque groups. For comparisons with normally distributed data, we applied a Student's  $t$ -test. When data were non-normally distributed, we applied the inverse transformation. If data did not follow a normal distribution even after transformation, we used a Mann–Whitney  $U$ -test.

We ran a generalized linear model (GLM) to test the effect of supplemented food on the SP fidelity to human areas. As dependent variable, we used the home range and core area fidelity to human areas on a monthly basis separately. Explanatory variables of the GLM were the monthly total number of visitors (used as a proxy for the availability of human food) to the park (DNP 2014) and the fruit abundance index (FAI; Albert *et al.* 2013b) during the period when SP was followed. We tested all combinations of explanatory factors and their interactions as possible models. The smallest second-order information criterion (AICc) was used to select the best model in agreement with the small sample size ( $N = 12$ ). The parameters of the GLM tests and their standard errors were estimated with the weighted generalized estimating equations.

## RESULTS

**HOME RANGE, CORE AREA, AND DAILY PATH LENGTH.**—We analyzed 1784 location points for WF (80 d), 2125 for SP (90 d), and 1431 for gibbons (79 d), with a monthly average of  $148.7 \pm 26.1$  (SD),  $177.08 \pm 23.72$  (SD), and  $119.25 \pm 26.38$  (SD) location points per day, respectively. The lower number of locations for gibbons resulted from their shorter daily activity period.

The yearly home range and core area sizes were 306.8 and 115.5 ha, respectively, for WF, 56.3 and 40.1 ha for SP, and 11.6 and 3.5 ha for the gibbon group (Fig. 1, Table 1). The core area of both macaque groups was roughly at the center of their home range. The gibbons' core area was at the north of their home range with an unused region at the center, creating a donut-like home range.

Home ranges and core areas of macaques varied widely in size and shape over the study period (Fig. 2). Monthly home ranges and core areas were significantly larger for WF than for SP ( $t_{12} = 4.543$ ,  $P < 0.001$ ; core area:  $\chi_{12} = -2.243$ ,  $P < 0.05$ ; Table 1). Both macaque groups and the gibbons exhibited core areas formed by several nuclei over 12 mo (Fig. 2). The yearly proportion of core area within the home range was remarkably large for SP (71.3%) compared to WF (37.6%) and the gibbons (30.3%).

We calculated the daily path length using a sample of 69 full days for WF, 86 for SP, and 63 for gibbons (Table 1). Daily path lengths were significantly longer in WF than in SP ( $\chi_{69,86} = 5.492$ ,  $P < 0.001$ ).

**GROUP MASS.**—When considering the yearly home range, the group mass of WF (0.7 kg/ha) was close to four times less than the group mass of SP (2.6 kg/ha), and two times less than the group mass of gibbon group (1.6 kg/ha). When considering the yearly core area, the group mass of WF (1.85 kg/ha) was much smaller than that of SP (3.59 kg/ha) and gibbons (5.28 kg/ha).

**HOME RANGE AND CORE AREA FIDELITY.**—The three study groups showed more fidelity to a home range than to core area (Figs 3 and 4 and Table 1). However, WF had significantly lower site fidelity than SP to both home range ( $t_{12} = -5.972$ ,  $P < 0.001$ )



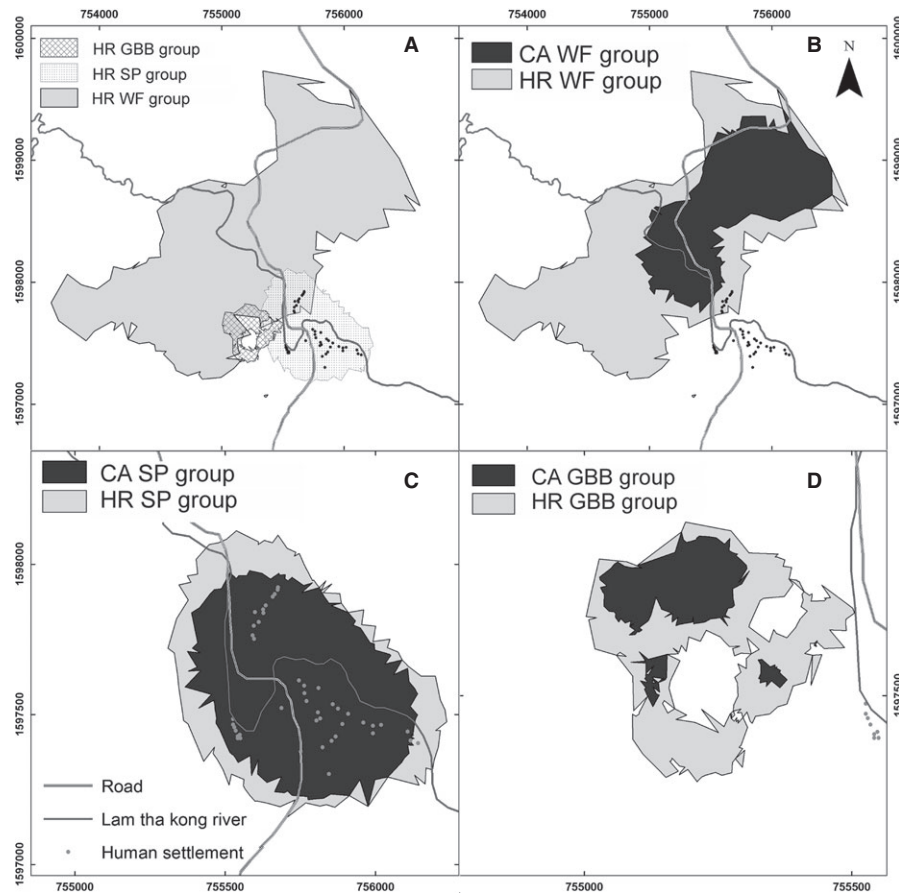


FIGURE 1. Study site and group locations at Mo Singto forest in the Khao Yai National Park (Thailand). (A) Location of the three groups' home ranges and human settlements in the study site; home range and core area size for (B) wild-feeding macaque group (WF), (C) semi-provisioned macaque group (SP), and (D) gibbon group (GBB). Universal Transverse Mercator (UTM) coordinates for latitude and longitude are given in meters in the horizontal and vertical axes of the frame.

and core area ( $t_{12} = -7.723$ ,  $P < 0.001$ ). WF macaques also had smaller fidelity values than gibbons to home range ( $t_{12} = -8.102$ ,  $P < 0.001$ ) and core area ( $t_{12} = -5.63$ ,  $P < 0.001$ ). While SP had greater fidelity to core area than gibbons ( $t_{12} = 3$ ,  $P < 0.01$ ), fidelity to home range did not follow this pattern ( $t_{12} = 0.407$ ,  $P > 0.05$ ).

No part of the WF's home range or core area was used in every month. Therefore, these macaques did not have complete fidelity to any region of their home range or core area (Figs 3 and 4). However, both SP macaques and gibbons had areas used for up to 12 mo and for up to 10 mo in the home range and core area, respectively (Fig. 4). WF home range and core area area-fidelity curves (Figs 3 and 4) decreased steeply in the beginning, indicating that most area was used in a matter of few months. After the steep decrease, the curves became smoother, showing that the maximum site fidelity occurred in a very small region. The home range-fidelity curve of SP also indicated large areas used only during one and two months. However, the curve decreased gently and constantly (as in gibbons' fidelity curve), which reflected high fidelity to home

range. SP and gibbon core area fidelity curves depicted a similar pattern, with greater levels of fidelity than those of WF. Finally, SP macaques displayed more site fidelity to core area than did gibbons because the SP macaques revisited large areas more frequently.

**DEFENDABILITY INDEX.**—The defendability index ( $M$ ) of WF was 0.027, a value corresponding to a non-territorial pattern; SP showed an  $M$  value of 0.111, indicating territoriality; and gibbons presented a defendability index of 0.341, reflecting a highly territorial pattern.

**TOURIST EFFECT ON FIDELITY TO HUMAN AREAS.**—Greater site fidelity to home range and core area for SP was found within the human polygon (Fig. 5). The best GLM model explaining home range fidelity to a human area included only the number of visitors (Table 2), which had a positive significant effect on fidelity to home range ( $F_{1,12} = 14.2$ ,  $P = 0.003$ , Fig. 6). Similarly, only the number of visitors best explained fidelity when considering the core area with significant effect ( $F_{1,12} = 4.6$ ,  $P = 0.003$ ).

TABLE 1. Total and monthly average values of ranging patterns for the three study groups: wild-feeding macaques (WF), semi-provisioned macaques (SP), and gibbons (GBB).

	WF	SP	GBB
Yearly HR (ha)	306.8	56.3	11.6
Yearly CA (ha)	115.5	40.1	3.5
Monthly HR (ha $\pm$ SD)	105.1 $\pm$ 48**	37.8 $\pm$ 17.7**	8.2 $\pm$ 2.9
Monthly CA (ha $\pm$ SD)	13.6 $\pm$ 5.5*	8.9 $\pm$ 4.3*	1.3 $\pm$ 0.4
DPL (m)	2.123 $\pm$ 611**	1.588 $\pm$ 412**	1.088 $\pm$ 348
Yearly CA in HR (%)	37.6	71.3	30.3
Group mass in HR (kg/ha)	0.7	2.6	1.6
Group mass in CA (kg/ha)	1.8	3.6	5.3
Defendability index ( <i>M</i> )	0.027	0.111	0.341
Fidelity index to HR ( $\pm$ SD)	0.32 $\pm$ 0.07	0.61 $\pm$ 0.15	0.63 $\pm$ 0.11
Fidelity index to CA ( $\pm$ SD)	0.11 $\pm$ 0.07	0.42 $\pm$ 0.12	0.29 $\pm$ 0.08

HR, home range; CA, core area; *M*, defendability index; DPL, daily path length.

Significant differences in HR, CA, and DPL between WF and SP: \* $P < 0.05$  and \*\* $P < 0.001$ .

Averages are given as mean ( $\pm$ SD).

MACAQUE INTRA- AND INTERGROUP INTERACTIONS.—SP showed a smaller frequency of intergroup encounters (0.008/h) than WF (0.041/h). However, SP macaques were aggressive in all encounters ( $N = 9$ ), whereas WF macaques were aggressive in only 9 of 35 encounters.

## DISCUSSION

Our findings show that partial food provisioning modifies the socioecology of macaques, altering their movement patterns and competitive regime regarding intergroup interactions. Home range, core area, and daily path length were smaller for macaques living under a human food supplement context. The presence of food in fixed spots meant that food-supplemented macaques did not need to travel in search of wild food. Food provisioning (using the number of park visitors as proxy for the abundance of human food) explained the site fidelity of SP better than did natural fruit abundance (measured using fruit abundance index, or FAI). Predictable supplementation of food in a relatively small area ( $\pm 20$  ha) made the resources economically defensible, increasing macaque density (group mass per ha) and intensifying site fidelity at the same level as gibbons. However, while the highest site fidelity regions for gibbons occurred within the home range boundaries, SP macaques were especially loyal to human areas. Therefore, their site fidelity varied according to the monthly tourist influx to the park. This intense and disproportional use of a great part of the home range by SP macaques created a large core area compared to that of WF.

SP showed a defendability index that corresponds to that of a territorial species, whereas the index of WF corresponds to the pattern expected for the non-territorial macaque. Furthermore, SP macaques had more aggressive encounters toward other conspecific groups than did WF. Both between-group contest and scramble competition depend on the abundance of food resources and the population density (Janson & van Schaik

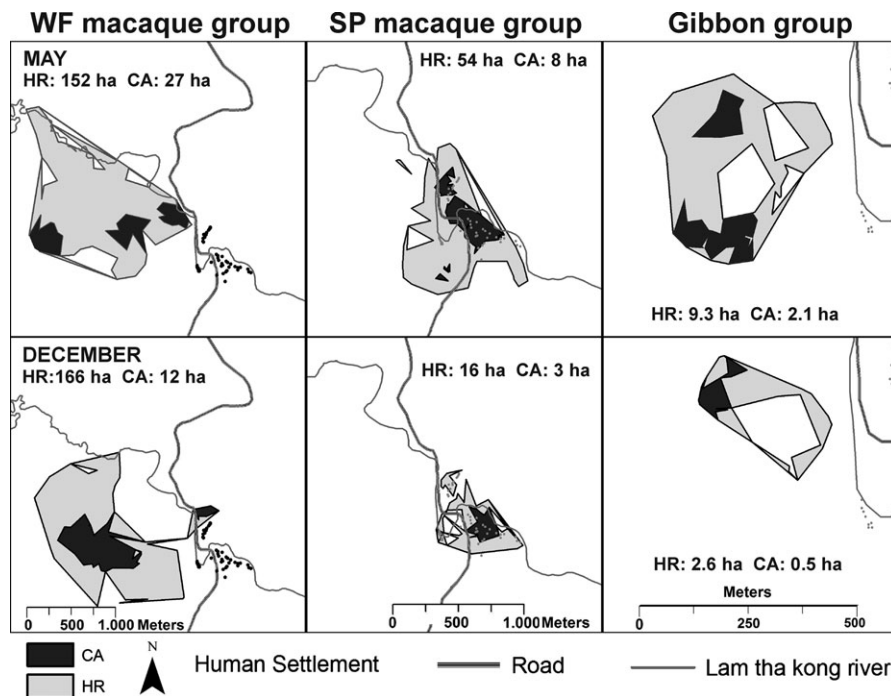


FIGURE 2. Size and locations of monthly home ranges and core areas for the wild-feeding macaque group (WF), semi-provisioned macaque group (SP), and gibbon group.

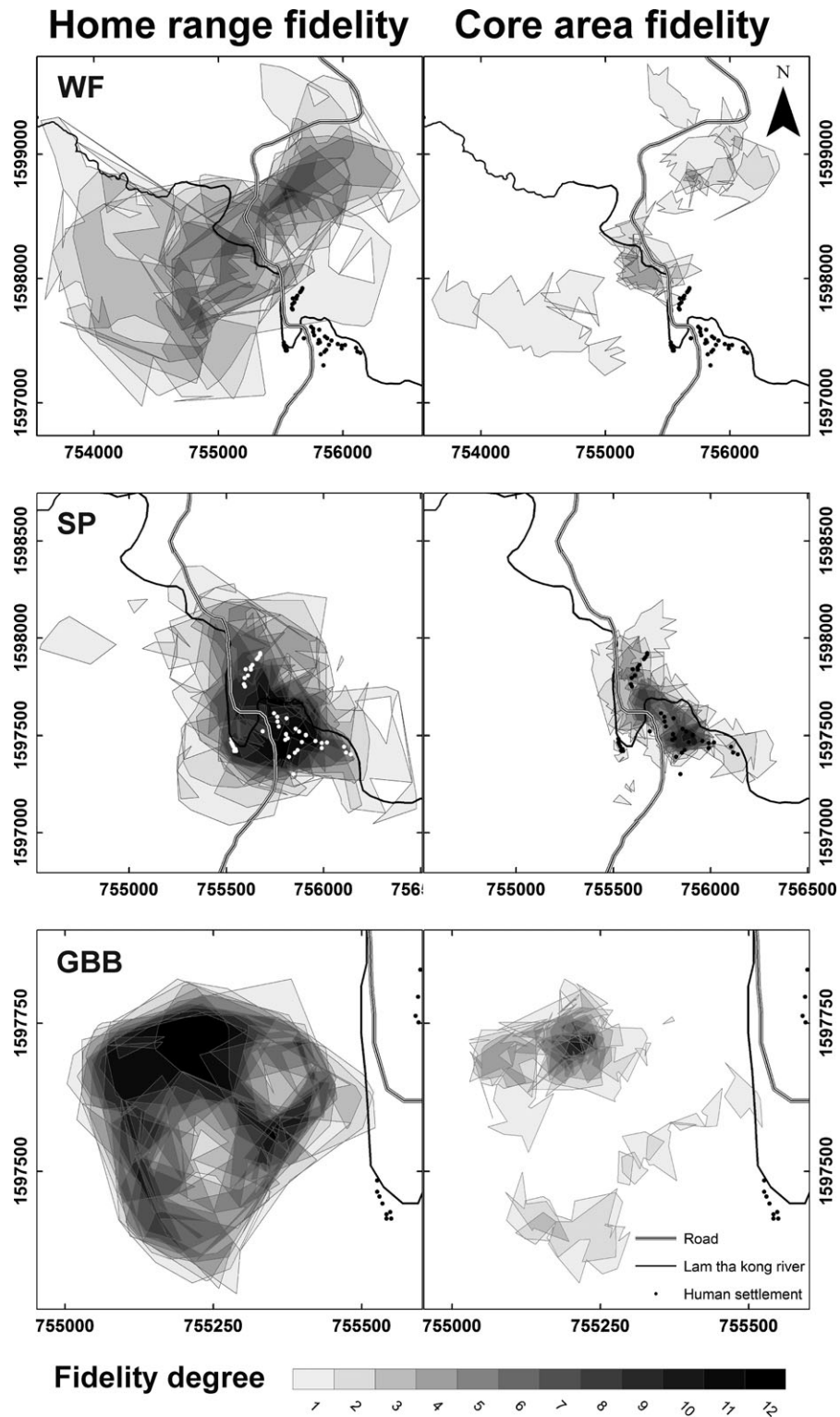


FIGURE 3. Site fidelity to home range and core area by wild-feeding macaque group (WF), semi-provisioned macaque group (SP), and gibbon group (GBB). The fidelity degree (gray gradient) shows the numbers of months an area was used. Universal Transverse Mercator (UTM) coordinates for latitude and longitude are given in meters in the horizontal and vertical axes of the frame.

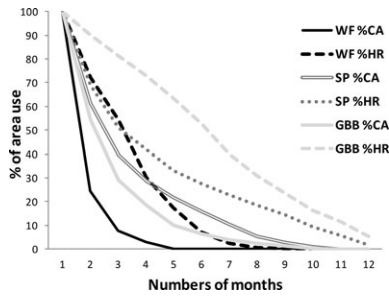


FIGURE 4. Percent of area used over the months (from 1 to 12 mo) by the wild-feeding macaque group (WF), semi-provisioned macaque group (SP), and gibbon (GBB) group. Horizontal axis represents numbers of months that the determinate area was used (fidelity degree), and vertical axis is the total percent of the area used in a determinate number of months. Solid and dotted lines represent home range (HR) and core area (CA), respectively, of the three groups.

1988), but scramble competitors are not expected to fight over resources (van Schaik 1989, Sterck *et al.* 1997). Group encounters of non-territorial animals usually involve passive avoidance and/or tolerance (southern pigtailed macaques: Caldecott 1986; northern pigtailed macaques: Choudhury 2008; mangabey: Waser 1976; red howlers: Sekulic 1982; brown capuchins: Terborgh 1983). Aggressive encounters in non-territorial species can occur due to occasional clumping of key resources (rhesus macaques: Southwick *et al.* 1965 and Lindburg 1977; Japanese macaques: Kawanaka 1973). However, if key food resources occur in an economically defensible pattern over long periods, as is the case for SP macaques, territorial behavior may occur (Oates 1987). Therefore, assuming that territoriality is a form of contest competition transferred to the defense of an area containing the

resources on the condition of resources being stable and located within a defensible range (Brown & Orians 1970), our results indicate that changes in food distribution can substantially alter the naturally non-territorial macaque's patterns, ranging, and even behavior as a territorial species. These patterns also support our understanding of socioecological models as variation of one of its key elements, that is, resource distribution and availability, can cause significant changes in ranging and social behavior.

Some primates, especially cercopithecines, show a high ecological flexibility and tolerance of human disturbance. Because of their behavioral and ecological plasticity (*i.e.*, diet, range, group size), most cercopithecine species (79%) can live in disturbed habitats and use the human food found in anthropogenic areas (Chapman *et al.* 2002, Brotcorne *et al.* 2011, Albert *et al.* 2014). Moreover, a morphological feature, the cheek pouch, lets them store food under stress or competition, providing an additional advantage in a human environment (Lambert & Whitham 2001, Warren 2008, Warren *et al.* 2011). In our study, pigtailed macaques had the flexibility to modify their ranging patterns to better exploit an altered scenario of predictable human food concentrated in particular locations. As opposed to WF relying on wild food, SP restricted their movement to a small home range and a core area centered on regular human food spots as found in other taxa living in human environments (Fa 1986, Altmann & Muruthi 1988, Boutin 1990, Monadjem & Perrin 1998, Kreiter & Wise 2001). However, when human food is dispersed over a greater area, both home range and core area could increase (Sha & Hayna 2013).

CONSERVATION IMPLICATIONS.—The establishment of protected areas and their management creates a matrix of interconnected areas of interaction between humans and wildlife, affecting the elements upon which socioecological models are based (*e.g.*, food abundance and distribution) (Fuentes 2006). The genus *Macaca* is particularly well adapted to human-modified habitats; however,

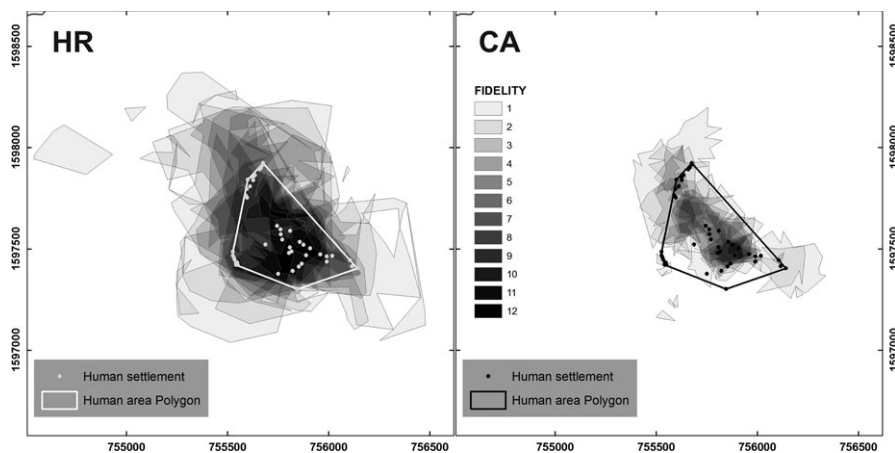


FIGURE 5. Semi-provisioned group (SP) site fidelity to home range (HR) and core area (CA) in relation to the human settlement polygon along the study period. Fidelity degree (gray gradient) shows the numbers of months that an area was used. Universal Transverse Mercator (UTM) coordinates for latitude and longitude are given in meters in the horizontal and vertical axes of the frame.



TABLE 2. GLMs used to explain fidelity to human areas in relation to home range (HR) and core area (CA) with their corresponding AICc and Delta AICc values.

Model HR	AICc	Delta AIC	Model CA	AICc	Delta AIC
#Visitors	-3.9	0	#Visitors	-12.88	0
#Visitors, FAI	-2.17	-1.73	#Visitors*FAI	-8.67	-4.21
FAI	0.61	-4.51	FAI	-5.88	-7
#Visitors*FAI	2.59	-6.49	#Visitors, FAI	-2.4	-10.48

FAI, fruit abundance index.

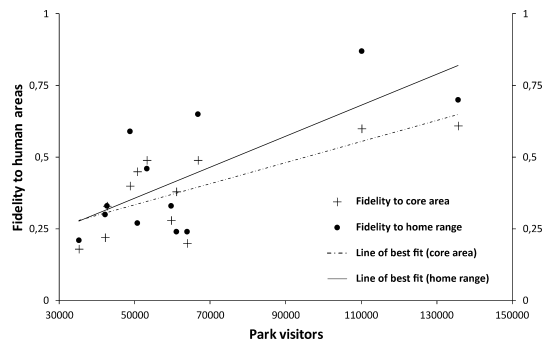


FIGURE 6. Relationship between the number of visitors and the home range (HR) and core area (CA) fidelity to human areas for the semi-provisioned group (SP). Dots and crosses represent the monthly home range and core area fidelity, respectively, related to the monthly number of visitors at the park. The best fitting lines are presented for illustrative purposes.

negative effects on their population and ecosystem may arise. Animals relying on human food, like the SP macaques in this study, come in close contact with humans, which can have demographic consequences for the animals and may affect human well-being. Pathogens can be transmitted bidirectionally between human and nonhuman primates (Engel *et al.* 2002, Wolfe *et al.* 2004, Rouquet *et al.* 2005). For example, Sapolsky and Else (1987) reported high baboon mortality when a bovine tuberculosis outbreak was transmitted to a group that frequently fed on garbage. Additionally, animals are often killed by motor vehicles in places where they spend long periods along the road feeding from human food (Kanurai 2004, Mallapur 2013, Sha & Hayna 2013), as occurs in Khao Yai National Park (J.M. José-Domínguez pers. obs.).

Macaques are one of the last large seed dispersers remaining in the disturbed habitats of South-East Asia (Corlett 1998, Lucas & Corlett 1998, Albert *et al.* 2013c). As fruit is an important part of their diet, groups of northern pigtailed macaques include many individuals that cover large ranges and travel long distances (Choudhury 2008). This pattern results in a great number of seeds being dispersed over large areas. However, with partial food provisioning, macaque home ranges become smaller and daily

path length shorter, decreasing the positive effect of macaques on the forest ecosystem of Khao Yai National Park. A food-provisioned group would disperse few seeds over short distances and some seeds would likely be transported into places where their establishment is not possible (e.g., roads and roofs) or even disperse invasive species present in human areas (e.g., *Syzygium cumini*, *Solanum melongena*) like the SP group does (Albert *et al.* 2013a). Moreover, as macaques are efficient passerine nest predators (Pierce & Pobprasert 2013), a high macaque density within a small area may affect local passerine recruitment. This means that food supplementation has consequences far beyond the common negative effects on animal health such as obesity or poisoning. Food provisioning can ultimately affect the geographical patterning and regeneration of the plant and animal diversity. Managers of protected areas must consider this possibility when implementing policies on garbage management and rules against feeding wildlife.

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