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Social Polyandry Among Siamangs:
The Role Of Habitat Quality

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Abstract

In species where females do not associate spatially with other females, males usually range over an area including the home ranges of multiple females or defend the home range of one female. Nevertheless, social polyandry (multimale–unifemale grouping) occurs in some species. We examine an ecological constraints model relating habitat quality to facultative social polyandry in siamangs, Symphalangus syndactylus, by testing predictions of two hypotheses: (H1) variation in the size and density of important food trees affects the size of siamang home ranges and areas of exclusive use; (H2) socially polyandrous groups benefit from cooperative defence of the home range and area of exclusive use. Crown volume/ha of freestanding or strangler figs (Ficus), the most important siamang food, was negatively related to the size of the home range but not to the size of the area of exclusive use. Density and crown volume/ha of the second-most important plant food, Dracontomelon dao, was not related to the size of the home range or to the size of the area of exclusive use. Multimale groups had larger home ranges and areas of exclusive use than unimale groups, and the home ranges and areas of exclusive use of multimale groups encompassed more freestanding or strangling figs than those of unimale groups. Models of home range size including fig abundance (density or crown volume/ha) and the number of males as predictor variables suggested that multimale groups have larger home ranges than predicted by the relationship between fig abundance and home range size alone. While some other facultatively polyandrous species have larger home ranges in areas of poorer habitat quality, our results suggest a more complex situation for siamangs at our study site. Specifically, the density of large figs may constrain siamang ranging patterns, but multimale groups live in home ranges with more figs than those of unimale groups. Our results suggest that multimale groups may defend higher-quality territories than unimale groups.

Social polyandry among siamangs: the role of habitat quality

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In species where females do not associate spatially with other females, males usually range over an area including the home ranges of multiple females or defend the home range of one female. Nevertheless, social polyandry (multimale—unifemale grouping) occurs in some species. We examine an ecological constraints model relating habitat quality to facultative social polyandry in siamangs, *Symphalangus syndactylus*, by testing predictions of two hypotheses: (H1) variation in the size and density of important food trees affects the size of siamang home ranges and areas of exclusive use; (H2) socially polyandrous groups benefit from cooperative defence of the home range and area of exclusive use. Crown volume/ha of freestanding or strangler figs (*Ficus*), the most important siamang food, was negatively related to the size of the home range but not to the size of the area of exclusive use. Density and crown volume/ha of the second-most important plant food, *Dracontomelon dao*, was not related to the size of the home range or to the size of the area of exclusive use. Multimale groups had larger home ranges and areas of exclusive use than unimale groups, and the home ranges and areas of exclusive use of multimale groups encompassed more freestanding or strangling figs than those of unimale groups. Models of home range size including fig abundance (density or crown volume/ha) and the number of males as predictor variables suggested that multimale groups have larger home ranges than predicted by the relationship between fig abundance and home range size alone. While some other facultatively polyandrous species have larger home ranges in areas of poorer habitat quality, our results suggest a more complex situation for siamangs at our study site. Specifically, the density of large figs may constrain siamang ranging patterns, but multimale groups live in home ranges with more figs than those of unimale groups. Our results suggest that multimale groups may defend higher-quality territories than unimale groups.
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Animal ranging patterns and home range sizes should be affected by resource distribution and abundance. Where resources are economically defensible, groups may defend some or all of the home range as a territory, and territory size should depend on the costs and benefits of defending areas of different sizes (Brown, 1964). The costs of territorial defence should increase with increasing territory size (López-Sepulcre & Kokko, 2005), and

theoretical models predicting the maximum size of an economically defendable territory have some empirical support (Lowen & Dunbar, 1994; Mitani & Rodman, 1979; Pasinelli, 2000; Tufto, Andersen, & Linnell, 1996), despite the difficulty of estimating habitat quality and controlling for the effects of group size (Koenig, Scarry, Wheeler, & Borries, 2013), individual quality (Germain & Arcese, 2014) and population density (Dhondt, 2010). On the opposite extreme, the need to access adequate resources throughout the year should place a lower limit on territory size (Brockelman, Nathalang, & Suwanvecho, 2014; Carr & MacDonald, 1986). Groups may be able to defend sufficient resources in a relatively small area of high-quality habitat, while in low-quality habitat, large home ranges or territories may be required.

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Ranging behaviour should also be related to social organization, because larger groups require more resources and may have higher resource-holding potential, but most research on this relationship has focused on species where females associate spatially (Kappeler & van Schaik, 2002; Koenig et al., 2013). When adult females range separately from other females, males are expected either to range with a single female, or to range over an area containing the home ranges of one or more females (Koenig et al., 2013; Komers & Brotherton, 1997; Port & Kappeler, 2010). The formation of social groups containing two or more adult males and one adult female should be rare, as sharing access to a single female should usually be a worse strategy than forming a pair (Shuster & Wade, 2003). Nevertheless, in some cases, cooperation between males may yield benefits that can exceed the costs (Diaz-Muñoz, DuVal, Krakauer, & Lacey, 2014; Shuster & Wade, 2003). Multimale–unifemale (socially polyandrous) groups have been reported in several bird (Riehl, 2013; Santos, Santos, Lagisz, & Nakagawa, 2015) and primate (Diaz-Muñoz et al., 2014; Erb & Porter, 2017) species where males cooperate to care for offspring. Cooperative care of offspring may benefit males through multiple mechanisms, including inclusive fitness, group augmentation and increased survivorship or mating success (Erb & Porter, 2017). However, the formation of socially polyandrous groups has also been reported in species without direct male parental care (Reichard, 2009; Savini, Boesch, & Reichard, 2009) or where males in multimale groups provide little care (Lappan, 2008). In these cases, tolerance between males is more difficult to explain.

In most species with socially polyandrous groups, these groups occur alongside other types of groups (Shuster & Wade, 2003), which suggests that the benefits of multimale grouping vary across ecological contexts. The ecological constraints hypothesis proposes that ecological and demographic conditions shape animal dispersal decisions, resulting in social polyandry under some conditions (Emlen, 1982, 1994). In species where males defend territories, local costs and benefits of territorial defence may affect male behavioural decisions (Koenig et al., 2013; Mosser & Packer, 2009; Scarry, 2013). Where the costs of territorial defence are high, a territorial male may benefit from help with territorial defence from a second male. For example, in facultatively polyandrous dunnocks, *Prunella modularis*, the probability of polyandry is positively related to home range size (Davies, 1992; Davies & Lundberg, 1984). While social polyandry may reduce certainty of paternity for both males, this potential cost may not always reduce male reproductive success. For example, in white-browed scrubwrens, *Sericornis frontalis*, where two unrelated males reside with a single female, alpha males lose some paternity to beta males, but pair-living males experience substantially greater loss of paternity to extragroup males (Santos et al., 2015; Wittingham, Dunn, & Magrath, 1997). As a result, the percentage of group offspring sired by the alpha male is identical in pairs and multimale groups (Wittingham et al., 1997). A similar pattern has recently been reported in dunnocks (Santos et al., 2015).

Dominant males may benefit if social polyandry increases group reproductive success or extends the tenure of the dominant male. For example, while geladas, *Theropithecus gelada*, typically form one-male units, dominant males that concede some paternity to 'follower' males have longer tenures and greater reproductive success than males in one-male units (Snyder-Mackler, Alberts, & Bergman, 2012). Similarly, dominant male golden lion tamarins, *Leontopithecus rosalia*, with more helpers have longer tenures than those with fewer helpers (Bales, Dietz, Baker, Miller, & Tardif, 2000).

Potential benefits of social polyandry to a beta male depend on the beta male's genetic relationship with other group adults.

Beta males not related to the group female may have the opportunity to obtain some paternity, and beta males may gain inclusive fitness benefits if they are related to at least one dominant adult (Green, Freckleton, & Hatchwell, 2016). Beta males can also avoid or defer the costs of dispersal if they remain in their natal group, or avoid the costs of being solitary if they join an established group. However, information about the actual fitness costs and benefits of social polyandry is unavailable for most species.

Gibbon (Hylobatidae) groups usually contain one adult male and one adult female with zero to four immature individuals. However, some variation has been reported. For example, stable groups containing at least two adult females occur in some crested gibbon (*Nomascus* spp.) populations (Fan, Fei, Xiang, Ma, & Huang, 2010; Fan, Jiang, Liu, & Luo, 2006). In addition, some white-handed gibbons, *Hylobates lar* (Reichard, 2009; Savini et al., 2009) and siamangs (Lappan, 2007; Morino, 2015) form long-term (>>1 year) associations between two or more males and one female. Groups are usually territorial, defending most or all of a ~5–40 ha home range (Bartlett, 2011), resulting in home ranges that contain a core area of exclusive use surrounded by areas of overlap with neighbouring groups. Areas of overlap are often defended using vocal displays and chases by both groups. White-handed gibbon groups living in areas with lower monthly fruit production have larger home ranges and a higher probability of polyandry, which is consistent with the interpretation that polyandrous males may cooperate to defend territories where costs of territorial defence are high (Savini et al., 2009). However, siamangs show more dietary flexibility than white-handed gibbons (Palombit, 1997), so it is unclear whether they should respond in the same way to variation in fruit availability. Siamang group members are also more spatially cohesive than white-handed gibbons (Palombit, 1996), which may affect the dynamics of cooperative resource defence by males.

In this study, we examined an ecological constraints model for the occurrence of social polyandry in siamangs in Way Canguk Research Area (WCRA). If variation in habitat quality affects siamang grouping patterns, this relationship is probably mediated by an underlying relationship between habitat quality and the costs and benefits of resource defence. To meet their nutritional needs, siamangs must have access to an adequate number of food patches. While siamangs consume parts of a variety of plant species, a few important species comprise a substantial part (>10% each) of their annual diet. Accordingly, we first tested predictions of the hypothesis that variation in the size and density of important food trees affects the size of siamang home ranges and areas of exclusive use (Hypothesis 1; Table 1). In saturated habitats, siamang groups should compete with neighbouring groups for access to food resources, and two males may be able to cooperate to economically defend a larger home range or area of exclusive use than a single male. In WCRA, two-male (2M) groups are more likely to 'win' in intergroup encounters with a decided outcome than one-male (1M) groups (Elder, 2013; Kinnaird, O'Brien, Nurcahyo, & Prasetyaningrum, 2002). Accordingly, we subsequently tested the hypothesis that 2M groups benefit from cooperative defence of the home range and the area of exclusive use (Hypothesis 2; Table 1). This benefit may come via reduced costs of territorial defence, increased benefits of territorial defence, or both. The presence of a second male may reduce the costs for each male, either because costs are shared between two males or because coordinated defence by two males results in reduced resistance from neighbours. The benefits of territorial defence, on the other hand, depend on the quantity of food that can be effectively defended. Testable predictions generated by each of these hypotheses are shown in Table 1.

Table 1
Hypotheses and predictions

Hypothesis	Prediction
H1: Variation in the size and density of important food trees[a] affects the size of siamang HR and AEU	(1) Fig and rao density are negatively related to HR and AEU size
	(2) Fig and rao crown volume per ha are negatively related to HR and AEU size
H2: 2M groups benefit from cooperative defence of the HR and AEU	(3) 2M groups have larger mean HR and AEU size than 1M groups
	(4) HR or AEU of 2M groups contain more fig or rao trees or a greater fig or rao crown volume than those of 1M groups
	(5) Models of HR size including plant density or crown volume/ha and the number of males explain variation in HR size better than models including only plant density or crown volume/ha

HR: home range; AEU: area of exclusive use; 2M groups: groups with two adult males; 1M groups: groups with one adult male; Fig: *Ficus* spp.; rao: *Dracontomelon dao*.
[a] Trees with parts comprising >10% of siamang annual diet.

METHODS

Study Site

WCRA (5°39″S, 104°24″E) is located in the Bukit Barisan Selatan National Park in southern Sumatra, Indonesia, and contains ~900 ha of lowland wet forest (0−50 m above sea level). The habitat includes primary forest interspersed with light gaps and areas of secondary forest created by wind, elephants or fire. The research area contains forest on the north and south banks of the Canguk River and is crossed by a grid of trails at 200 m intervals. See Kinnaird and O'Brien (1998, 2005) and O'Brien, Kinnaird, Anton, Prasetyaningrum, and Iqbal (2003) for a detailed site description.

Study Groups

We collected ranging and group composition data from 11 siamang groups that did not respond visibly to the presence of human observers. Group compositions were monitored during behavioural studies conducted throughout two sampling periods (2000−2002 and 2007−2009; Table 2) and were recorded concurrently with ranging and feeding data. All individuals in the study groups were recognizable based on their physical features. Males were classified as adult if they were of full adult body size and shape. Each group contained a single adult parous female.

Ranging Data Collection

Ranging data were collected during sleeping-tree to sleeping-tree follows of focal siamang groups conducted during other behavioural research projects conducted by three research teams (Table 2). Group or individual locations within a set of *x,y* co-ordinates framed by the WCRA trail system were estimated along each axis to the nearest metre using a rangefinder and compass and recorded at specified intervals throughout the day on each sampling day. Three of us (A.N., T.G.O., M.F.K.) collected ranging data from five groups (B, C, F, G, S) 5 days/month and recorded the location of each

individual at 30 min intervals from 0530 hours to 1730 hours. As group members ranged <20 m apart most (>75%) of the time, only data from adult females were included in this study to avoid pseudoreplication. One of us (S.L.) collected location data from a focal adult in six groups (A, B, C, F, G, S) during sleeping-tree-to-sleeping-tree follows at 15 min intervals for 4−6 consecutive days/month. One of us (L.M.) recorded the location of a focal adult in 11 groups (A, B, C, E, F, G, H, L, M, S, U) at 10 min intervals during sleeping-tree-to-sleeping-tree follows for 3−4 consecutive days/month.

Estimation of Density and Crown Volume of Important Food Trees

We estimated home range quality by quantifying the number and size of trees of two plant taxa that were identified in previous studies (Lappan, 2010; O'Brien et al., 2003) as being the two most important siamang foods in WCRA: *Ficus* spp. ('figs') and *Dracontomelon dao* ('rao'). Figs, in particular, are known to be of central importance in the diets of tropical frugivores (Shanahan, So, Gompton, & Gorlett, 2001), including gibbons (Bartlett, 2011), and fig density has been shown to predict gibbon densities on Borneo (Marshall & Leighton, 2006). Siamangs in the WCRA include a large number of plant species in their diets (Elder, 2013), but in a 2000−2002 study of five siamang groups, adults spent an average of 44% of feeding time eating parts (mostly fruits, but also including fig leaves and flowers) of these two species (Lappan, 2010). Estimates of siamang fruit intake (dry matter/min) during fig (5.5 g) and rao (1.4 g) feeding are similar to estimates for the top 18 nonfig fruit species in the WCRA (mean = 2.6 g, range 0.2−9.7 g; Elder, 2013), which suggests that the high feeding times for these food items reflect their importance in the siamang annual diet. From July to December 2012, we recorded the number of fig and rao trees in the home ranges of groups A, B, C, F, G, L, S and U by walking parallel transects at approximately 20 m intervals across the home range of each group and identifying and marking all rao trees with diameter at breast height (dbh) >10 cm and all freestanding or strangler figs. Mapping of food trees (figs and rao) in the home ranges of groups M and H was incomplete, so they are excluded from the analyses of

Table 2
Sampling periods and sample sizes

Group	Sampling periods and research teams (in parentheses)	Sample days	Location points
A	Oct 2007−Apr 2009 (L.M.)	78	3232
B	Feb−Apr 2000 (A.N., M.F.K., T.G.O.), Jan−Aug 2002 (S.L.), Sep 2007−Jun 2008 (L.M.)	70	2858
C	Feb−Aug 2002 (S.L.); Feb 2008−Apr 2009 (L.M.)	55	2130
E	Sep 2007−Apr 2009 (L.M.)	72	3221
F	Apr 2000−Jan 2001 (A.N., M.F.K., T.G.O.), Jan−Aug 2002 (S.L.); Oct 2007−Apr 2009 (L.M.)	127	5141
G	Feb 2000−Jan 2001 (A.N., M.F.K., T.G.O.), Jan−Aug 2002 (S.L.); Feb 2008−Apr 2009 (L.M.)	139	4742
H	Feb 2008−Apr 2009 (L.M.)	57	2736
L	Jan 2008−Mar 2009 (L.M.)	36	1222
M	Oct 2007−Mar 2009 (L.M.)	57	3068
S	May 2001−Aug 2002 (A.N., M.F.K., T.G.O., S.L.); Oct 2007−Mar 2009 (L.M.)	52	2213
U	Jan 2008−Mar 2009 (L.M.)	36	1526

food tree density and crown volume. The estimated location of each tree was recorded using the same coordinate system used for the mapping of home range. Tree height, crown diameter and crown height (the distance from the lowest branch on the tree to the top of the tree) were measured in metres using a laser rangefinder. The tree survey was conducted several years after the collection of ranging and group composition data, such that some large food trees may have died and new large trees may have been recruited into the population. However, turnover for rao in the WCRA is very slow (<<1% of trees died annually during 1997–2016; Kinnaird & O'Brien, n.d.), so little error should result from the delay in measurement for this taxon. Death rates are somewhat higher for figs (~2% of trees died annually during 1997–2016; Kinnaird & O'Brien, n.d.), but we assume that the error introduced by tree death during the relatively short interval between collection of ranging and food availability data did not substantially undermine our estimates of food availability, because rates of fig recruitment into the 10 cm dbh size class are approximately equal to rates of death (Kinnaird & O'Brien, n.d.). We also collected data from males of the dioecious species *Hydnocarpus gracilis*, which was the third most important food tree for this population in 2000–2002, but we excluded them from the analysis due to their relatively low density in 2012, and our inability to estimate turnover rates for this taxon.

Data Analysis

Groups that contained one male in most study months were classified as one-male (1M) groups, and groups that contained two males in most study months were classified as two-male (2M) groups. For the four groups that were 1M during some parts of the sampling period and 2M at other times (groups A, B, C, U), we then excluded all ranging data collected during periods when the group composition was not consistent with their assignment as 1M or 2M. The resulting sample sizes for the study groups ranged from 36 to 139 observation days (mean $\pm$ SD $= 70 \pm 34$ days) and from 1222 to 5141 scans (mean $\pm$ SD $= 2917 \pm 1202$ scans; Table 2). To verify our assumption that home range locations did not change substantially across the sampling period, we mapped the home range centroids using data from the 2000–2002 and 2007–2009 samples and confirmed that there was little change in centroid location (estimated distance between centroids 33 ± 13 m, $N = 5$ groups) between sampling periods. To verify our assumption that within the range of sample sizes in this study, sample size did not substantially affect the estimate of home range size, we selected five random subsamples of 30 days of data from the sample for group G, which was the group with the largest sample. Estimates of home range size derived from these subsamples differed from each other and from the estimate derived from the whole 139-day sample by a mean ($\pm$SD) of only $5 \pm 2\%$.

We used the ranging data to estimate 95% kernel density home range for all 11 groups in Geospatial Modeling Environment 0.7.2.0 (Beyer, 2012) with R (R Development Core Team, 2012) using Gaussian kernels and smoothed cross-validation with cell size set at 25. The resulting 95% kernel density home ranges were then projected in ArcMap 10.0 (Environmental Systems Research Institute (ESRI), Redlands, CA, U.S.A.) for estimation of home range size and overlap. The area of exclusive use was calculated as the component of the home range that did not overlap with the home range of any other group. For groups C, F, G and S, ranging data were available from all neighbouring groups, so areas of exclusive use and areas of overlap could be directly calculated. For groups A, B, E, H, L, M and U, however, the home range of at least one neighbouring group had not been mapped. In cases where the home range of $\geq 50\%$ of neighbouring groups were mapped, we extrapolated from the area of overlap from neighbours with known home ranges to estimate a

total area of overlap for the group. For groups A and M, the home range of <50% of neighbouring groups had been mapped, so these groups were excluded from analyses of areas of exclusive use and home range overlap.

We mapped tree locations in the WCRA coordinate system using ArcMap 10.0 and calculated the number of individuals of each tree taxon in the home range, area of exclusive use and area of overlap for each siamang group to estimate the number of food patches available to each group. Since dbh is not a meaningful measurement for strangling figs, we used crown volumes to estimate the size of each food plant. Crown volumes were estimated as ellipsoids, using the equation: $\frac{\pi}{6} \times$ crown height $\times$ crown diameter^2. We then estimated the total crown volume (sum of individual crown volumes, in m^3) for each plant taxon in the home range, area of exclusive use and area of overlap for each siamang group. Tree density in the home range and area of exclusive use were calculated as the total number of individuals in the home range divided by the home range area (in ha) and the total number of trees in the area of exclusive use divided by the size of the area of exclusive use (in ha), respectively. We estimated crown volume/ha for each plant taxon as the total crown volume in the home range divided by the home range area or the total crown volume in the area of exclusive use divided by the size of the area of exclusive use.

Testing of Predictions

We used four general linear models (GLM; Fox, 1997) to examine the relationships between estimated density (trees/ha) of figs and rao and an interaction term for fig and rao (predictor variables for models 1 and 3) and siamang home range (response variable for model 1) or area of exclusive use (response variable for model 3) and estimated crown volume/ha (1000 m^3/ha) of figs and rao and an interaction term for fig and rao (predictor variables for models 2 and 4) and siamang home range (response variable for model 2) or area of exclusive use (response variable for model 4; H1 Predictions 1–2; Table 1). The interaction terms were not significant ($P > 0.05$) for any model, so they were excluded from the final models (Lowry, 1992). We used one-tailed t tests to examine the directional predictions that 2M groups had larger home ranges and areas of exclusive use than 1M groups (H2 Prediction 3; Table 1). We also used one-tailed t tests to assess the directional predictions that home ranges or areas of exclusive use of 2M groups contain more important food trees or a greater total crown volume of food trees than those of 1M groups (H2 Prediction 4; Table 1). Because variation between groups in food availability may be associated with either differences in per capita food availability or differences in group size, or both, we used two-tailed t tests to compare the per capita number of food trees and per capita crown volume of food trees in the home ranges and areas of exclusive use of 1M and 2M groups and to compare group sizes and the number of immature individuals in 1M and 2M groups. Finally, after determining which plant food variables were related to home range size, we evaluated whether the number of males in a group influenced the relationship between the plant food variables and home range size (H2 Prediction 5; Table 1). We used likelihood ratio tests to compare GLM with home range size as the response variable and the plant food variable (fig density for model 5 and fig crown volume/ha for model 6) and the number of males as predictor variables to models with home range size as the response variable and only the plant food variable (fig density for model 5 and fig crown volume/ha for model 6) as a predictor variable to determine whether adding the number of males as a predictor variable significantly improves model fit. To validate the assumptions of normality and homoscedasticity, we visually examined Q–Q plots and residuals plotted against fitted values. We did not detect substantial violation of any

model assumptions. The highest variance inflation factor (VIF) was low (1.142), which indicates that collinearity was not a problem.

Ethical Considerations

All research reported here was in compliance with ASAB/ABS Guidelines for the use of animals in research, the laws of the Republic of Indonesia and the institutional guidelines of New York University (approved by University Animal Welfare Committee without full review as a noninvasive field study), Rutgers University (IACUC protocol 07-023) and Wildlife Conservation Society. S.L. conducted research with permission from Lembaga Ilmu Pengetahuan Indonesia (LIPI) during 2000—2002 and from the Indonesian Ministry of Research and Technology (RISTEK) in 2012. L.M. conducted research with permission from RISTEK during 2007—2009. M.F.K., T.G.O. and A.N. were permitted to conduct research in Indonesia under a memorandum of agreement between Wildlife Conservation Society—Indonesia Program and the Indonesian Ministry of Forestry's Department of Forest Protection and Nature Conservation (PHKA).

RESULTS

Predictions 1 and 2

Stem densities of figs and rao were not related to home range size (Table 3). However, home range size decreased with increasing fig crown volume/ha (Table 3). Each additional 1000 m^3 of fig crown/ha in the home range was associated with a 2.2 ha reduction in home range size (Table 3, Fig. 1). None of the estimates of fig or rao abundance were related to the size of the area of exclusive use (Table 3).

Predictions 3 and 4

2M groups had substantially larger home ranges (mean ± SE: 2M = 24.1 ± 2.5 ha, 1M = 12.3 ± 3.4 ha; t test: t_9 = 2.852, P = 0.010) and areas of exclusive use (mean ± SE: 2M = 19.0 ± 2.9 ha; 1M = 10.0 ± 3.0 ha; t_7 = 2.093, P = 0.038) than 1M groups. The home ranges and areas of exclusive use of 2M groups also contained more freestanding or strangling figs (Table 4) than those of 1M groups. The total crown volume of figs or rao and the number of rao trees did not differ significantly between the home ranges and areas of exclusive use of 1M and 2M groups (Table 4).

The per capita number and crown volume of figs and rao in the home range did not differ between 1M and 2M groups (Table 4).
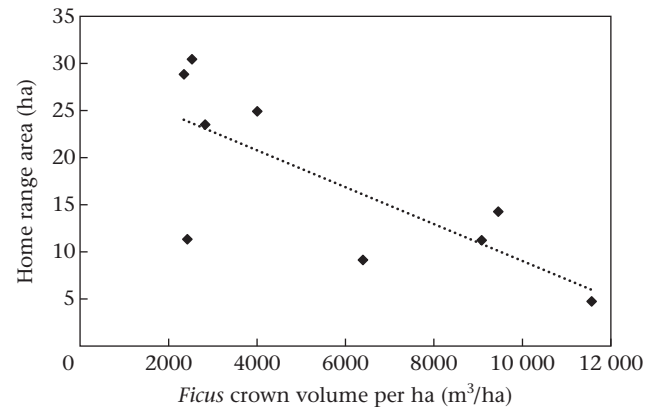

Figure 1. Relationship between estimated *Ficus* crown volume/ha and home range size for siamangs at Way Canguk Research Station in southern Sumatra.

Rather, 2M groups were larger (mean ± SD = 5.3 ± 0.41 individuals; t test: t_9 = 7.627, P < 0.001) and contained more immature individuals (mean ± SD = 2.3 ± 0.41 immatures; t test: t_9 = 4.163, P = 0.002) than 1M groups (mean ± SD = 3.1 ± 0.6 individuals and 1.1 ± 0.5 immatures).

Prediction 5

Inclusion of the number of males as a predictor variable resulted in significant improvement of model fit for the GLM including fig density as a predictor variable and home range size as a response variable (model 5; likelihood ratio: $-2\log\Lambda_1$ = 10.39, P = 0.001; Table 5) and the GLM including fig crown volume/ha as a predictor variable and home range size as a response variable (model 6; likelihood ratio: $-2\log\Lambda_1$ = 8.448, P = 0.004; Table 5). In model 5, each additional fig plant was associated with a 6.28 ha reduction of home range size, and adding a second male to a group was associated with an 11.33 ha increase in home range size (Table 5). In model 6, each additional 1000 m of fig crown was associated with a reduction in home range size of 1.53 ha, and the addition of a second male was associated with an increase in home range size of 8.32 ha (Table 5).

DISCUSSION

While previous studies of facultatively polyandrous species have supported the hypothesis that territories are larger in areas of poor

Table 3
Results of general linear models (GLM) of the relationship between fig (*Ficus*) and rao (*D. dao*) stem density (individuals/ha) or crown volume per ha (1000 m^3/ha) and size of the home range (HR) or area of exclusive use (AEU) (ha)

Model	Model variables		Est.	SE	t	P	95% CI	
	Response	Predictor					Lower	Upper
1	HR	Intercept	28.58	12.50	2.285	0.062†	−2.03	59.13
		Fig density	−6.75	4.47	−1.510	0.182	−17.69	4.19
		Rao density	0.57	3.26	0.174	0.868	−7.40	8.54
2	HR	Intercept	35.56	8.46	4.203	0.006*	14.86	56.25
		Fig crown volume/ha	−2.18	0.70	−3.118	0.021*	−3.88	−0.468
		Rao crown volume/ha	−2.08	2.18	−0.955	0.377	−7.40	3.25
3	AEU	Intercept	19.90	13.78	1.444	0.208	−15.53	55.34
		Fig density	−3.58	5.65	−0.635	0.554	−18.11	10.94
		Rao density	−0.17	2.78	−0.06	0.954	−7.34	7.00
4	AEU	Intercept	27.10	8.58	3.159	0.025*	5.05	49.15
		Fig crown volume/ha	-1.7	0.97	−1.727	0.145	−4.16	0.82
		Rao crown volume/ha	-1.9	1.7	−1.152	0.301	−6.25	2.38

†P < 0.10; *P < 0.05.

Table 4
Results for analysis of the relationship between the number of males in a siamang group and the number of trees or the total crown volume for figs (*Ficus* spp.) and rao (*D. dao*) in the home range (HR, $df = 7$) and area of exclusive use (AEU, $df = 6$)

		t	P	Mean±SD		Mean difference (2M − 1M)
				1M	2M	
Trees (HR)	Fig	2.932	0.011*	19.6±8.6	40±12.4	20.4
	Rao	1.817	0.056†	29.0±16.9	59.0±32.1	30.0
Crown volume (HR)	Fig	0.834	0.216	69.5±31.9	86.5±32.6	18.0
	Rao	0.823	0.225	40.9±28.7	58.0±33.5	16.7
Trees (AEU)	Fig	3.001	0.012*	13.7±7.6	33.3±11.1	19.6
	Rao	1.330	0.116	23.9±12.7	48.8±40.5	24.9
Crown volume (AEU)	Fig	1.577	0.083†	40.9±28.7	72.8±25.5	31.8
	Rao	0.232	0.412	35.9±21.7	41.1±43.2	5.2
Trees per capita (HR)	Fig	0.872	0.412	6.3±2.4	7.7±2.6	1.5
	Rao	0.475	0.649	9.6±5.7	11.5±6.5	1.9
Crown volume per capita (HR)	Fig	−1.084	0.314	21.4±7.6	16.5±5.4	−4.9
	Rao	−0.369	0.723	13.3±9.0	11.3±6.6	−2.0
Trees per capita (AEU)	Fig	1.336	0.115	4.3±2.1	6.5±2.4	2.2
	Rao	0.444	0.337	7.9±4.3	9.8±8.2	1.9
Crown volume per capita (AEU)	Fig	0.306	0.385	12.4±8.1	14.0±4.0	1.6
	Rao	−0.615	0.561	11.7±6.9	8.3±8.6	−3.4

1M: groups with one adult male; 2M: groups with two adult males. Crown volumes are reported in units of 1000 m³. Analyses of group values used one-tailed t tests, whereas per capita analyses used two-tailed t tests.
†$P < 0.10$; *$P < 0.05$.

Table 5
GLM models of home range (HR) size with density (model 5, individuals/ha) or fig crown volume/ha (model 6, units of 1000 m³/ha) and number of males (two-male group (2M) as reference category) as predictor variables

Model	Model variables		Estimate	SE	t_6	P	95% CI	
	Response	Predictor					Lower	Upper
5	HR size	Intercept	35.32	5.94	5.947	0.001*	20.79	49.85
		Fig density	−6.28	2.91	−2.160	0.074†	−13.41	0.84
		Males	−11.33	4.06	−2.792	0.031*	−21.27	−1.40
6	HR size	Intercept	30.83	3.65	8.449	<0.001*	21.90	39.76
		Fig crown vol./ha	−1.53	0.57	−2.685	0.036*	−2.92	−0.14
		Males	−8.32	3.86	−2.14	0.076†	−17.83	1.19

†$P < 0.10$; *$P < 0.05$.

habitat quality (Davies, 1992; Savini et al., 2009), our results showed fairly weak support for this hypothesis. Specifically, while we found that siamang home ranges were smaller when they contained larger fig trees (measured as fig crown volume/ha), our results did not show relationships between fig stem density and home range size, between fig density or tree size and the size of the area of exclusive use, or between rao density or tree size and home range or the size of the area of exclusive use. This difference may result from differences in methods, as Savini et al. (2009) estimated total biomass of 31 important food species produced in each home range each month, whereas we considered stem density and tree size for the top two food species separately, and we did not estimate biomass. Our results may also reflect the central importance of figs in siamang diets in WCRA. During 1997–2002, fig fruits were available in every month, and figs produced approximately 64% of the total fruit crop and 41% of the fruit biomass in WCRA (Kinnaird & O'Brien, 2005). Our results may therefore reflect a tendency for siamang ranging and territorial behaviour in WCRA to have a strong relationship with the distribution of large figs, but to be weakly related or unrelated to the distribution or abundance of other individual plant species, even species that comprise a substantial proportion of their diets. Figs also predict gibbon densities on Borneo (Marshall & Leighton, 2006), and other specific food resources are more important determinants of population density and ranging behaviour than overall food abundance for many primate taxa (Hanya & Chapman, 2013). However, if siamang ranging and territorial behaviour is oriented around figs, it is less clear why

fig tree size (measured as crown volume/ha) should be related to home range size, but not to the size of areas of exclusive use. The vast majority (ca. 90%) of siamang intergroup encounters in the WCRA occur around large fruiting figs (Kinnaird & O'Brien, 2005), which indicates the centrality of figs for intergroup relationships. One possibility, therefore, is that because of their high value, figs are more likely to be contested than other food sources, and that as a result, home range overlap occurs primarily in areas where large figs are concentrated. Indeed, the mean density of figs in the areas of overlap for groups in this study (3.6 individuals/ha) was higher than the mean density in the areas of exclusive use (1.6 individuals/ha), which is consistent with this interpretation. Alternatively, given our small sample of groups and the fact that our estimates of food production were based on stem densities and crown volumes rather than estimates of actual fruit biomass, these inconsistencies may simply reflect low statistical power. Studies including larger samples or more precise measurements of fruit production may reveal negative relationships between fruit production/ha and the sizes of both the home range and the area of exclusive use for figs and other important species.

In WCRA, 2M groups range over larger areas and have larger areas of exclusive use than 1M groups, which is consistent with patterns observed in other facultatively polyandrous species (Davies, 1992; Davies & Lundberg, 1984; Savini et al., 2009). The ecological constraints model supposes that in areas of poorer habitat quality, groups may require a larger home range to obtain sufficient resources, and that the larger home range size creates

opportunities for the formation of 2M groups to spread the costs of territorial defence across two males. However, it is also possible that groups with larger home ranges have access to more food than groups in smaller home ranges, and that they may therefore be more likely to become 2M due to the retention of adult offspring or the acceptance of male immigrants. Longitudinal data showing changes in group composition and home range size over time will be necessary to distinguish between these possibilities.

While male aggression is usually interpreted as a form of intrasexual mating competition, males of several mammalian species cooperate to defend food resources, resulting in some cases in greater access to food resources for members of groups containing more males (Crofoot, 2007; Fashing, 2001; Mosser & Packer, 2009; Scarry, 2013). Where outcomes of intergroup interactions in the WCRA were decided, larger groups were more likely to 'win' than smaller groups (Elder, 2013; Kinnaird et al., 2002). 2M groups may therefore enjoy a competitive advantage over 1M groups beyond the benefits that may come from sharing the costs of territorial defence. Indeed, since siamang group members are very spatially cohesive, the presence of a second male may not substantially reduce the energy costs associated with territorial defence for each male, as the entire group will still need to visit all areas of the territory regularly to monitor territorial boundaries and expel intruders. Therefore, 2M grouping may offer territorial benefits not (or not only) because of reduced costs of territorial defence, but instead because of the ability of a 2M group to expand the home range and area of exclusive use and thereby to access more resources than 1M groups. The results of our analyses offer tentative support for this interpretation, as the home ranges and areas of exclusive use of 2M siamang groups contained more freestanding or strangling figs than the home ranges and areas of exclusive use of 1M groups, despite the negative relationship between fig size (crown volume/ha) and home range size. While none of the other food variables showed significant differences between 1M and 2M groups, several of the results approached significance ($P < 0.10$), and the pattern of differences between 1M and 2M groups was consistent. For all food variables measured, 2M groups had mean values that were higher than those for 1M groups, despite the small sample sizes and substantial variability within each category. This pattern suggests that home range sizes in the WCRA may be determined not by overall food availability, but rather by the distribution of very large figs, such that larger home ranges may contain substantially more food of other important plant species and more fig plants than smaller home ranges. This pattern may then be self-reinforcing if siamang groups living in larger home ranges tend to become 2M, and 2M groups have a competitive advantage in intergroup feeding competition over 1M groups, allowing them to further expand their home range size and to outcompete 1M groups for access to food resources in the area of overlap. The improved fit of the GLM of the relationship between fig crown volume/ha and home range size or fig density and home range size when the number of males was added to the models adds support for this interpretation. Additional studies including more refined estimates of actual food availability and larger sample sizes and considering temporal variation in food availability will be necessary to better understand the relationships among food availability, ranging variables and grouping patterns in siamangs.

2M groups in the WCRA were larger than 1M groups, not only because of the presence of a third adult but also because they contained approximately twice as many immature individuals. Per capita abundance of food trees and food tree crown in the home range and area of exclusive use did not differ between 1M and 2M groups. These results suggest that if males in 2M groups benefit from greater access to food resources, it is via the conversion of

those food resources into surviving offspring, rather than via somatic investment. Siamangs in lower-quality habitat in WCRA have fewer surviving offspring (1.1–1.3 surviving offspring per female) than those in higher-quality habitat (3.1–3.7 surviving offspring per female; O'Brien et al., 2003). The same pattern is seen in white-bearded gibbons, *Hylobates albibarbis*, in Gunung Palung National Park (Marshall, 2009), which is consistent with the interpretation that variation in habitat quality primarily affects reproductive success rather than adult survivorship for gibbons. Female chimpanzees, *Pan troglodytes*, with larger ranges also have reduced interbirth intervals relative to those in smaller ranges (Williams et al., 2004), which suggests that, among primates more broadly, cooperative male resource defence may function to increase group reproductive rates.

Our study included a relatively small sample of groups, and we were not able to compare male survivorship or tenure in 1M and 2M groups, or to directly measure reproductive success. Therefore, while our results suggest that 2M siamang groups may benefit from their ability to obtain and defend a larger home range than 1M groups, this may not be the only or the most important reason for the formation of 2M groups in this population. In saturated habitat, subordinate males in 2M groups may also benefit from avoiding the costs of dispersal or becoming solitary, and may obtain inclusive fitness benefits by helping the dominant pair with territorial defence, mate defence, antipredator defence or infant care if they are related to the dominant male or female. Infants in this population that are cared for by two males do not receive more male care or more care overall than infants cared for by a single male (Lappan, 2008). However, infants and their parents may benefit in other ways from the presence of a second male. For example, 2M groups appear to be less vulnerable to take-overs, which may reduce the risk of infant and juvenile mortality and extend male tenure in 2M groups. Infants and juveniles in 2M groups may also have a higher chance of surviving the death of a group male than those in 1M groups (Morino & Borries, 2015). The actual composition of any group is therefore likely to result from a complex interaction of social, demographic and ecological factors. To better understand the factors promoting facultative polyandry in siamangs, future studies should measure components of inclusive fitness, including number of surviving offspring, indirect fitness and tenure of each adult in 1M and 2M groups.

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