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MOVEMENTS, DISTRIBUTION, AND ABUNDANCE OF GREAT ARGUS PHEASANTS (*ARGUSIANUS ARGUS*) IN A SUMATRAN RAINFOREST

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ABSTRACT.—We used radiotelemetry, habitat sampling, camera trapping, and line-transect surveys to explore movement patterns, distribution, and abundance of Great Argus Pheasants (*Argusianus argus*) in Sumatra, Indonesia. We radiotracked six adult and one subadult males. Territories averaged 14.5 ± 8.5 ha, and home-range size did not vary by month or by relative abundance of selected plant foods. Daily travel distance (849 ± 211 m) varied significantly between months but did not reflect changes in plant foods. Territories were used almost exclusively by resident males. Males preferentially used undisturbed forest (habitat I). Vegetation structure at male display sites and random points indicated that display sites were located in undisturbed forest, with few lianas and small leaf size on trees adjacent to the display site. Between 1998 and 2001, we conducted five line-transect surveys in conjunction with camera-trap surveys. Density estimates of calling males varied from 0.4 to 2.5 males km^{-2} , and the total density estimate ranged from 0.9 to 3.7 birds km^{-2} . Density estimates increased substantially between 1998 and 2001, reflecting recovery from depressed densities after the 1997–1998 El Niño drought. Habitat occupancy estimates varied from 25% to 38% but were not significantly different over time. The proportion of occupied habitat was similar to the proportion of habitat I. We conclude that Great Argus Pheasants prefer undisturbed forest and rarely use other habitat even as population density increases. Restricted movements and habitat preference may limit the ability of Great Argus Pheasants to colonize forest fragments. Received 3 October 2007, accepted 23 November 2008.

Key words: *Argusianus argus*, density, distribution, Great Argus Pheasant, habitat preference, male movements.

Movimientos, Distribución y Abundancia de *Argusianus aarhus* en un Bosque Lluvioso de Sumatra

RESUMEN.—Usamos radiotelegrafía, muestreos de hábitat, captura con cámaras fotográficas y transectos lineales para explorar los patrones de movimiento, la distribución y la abundancia de *Argusianus aarhus* en Sumatra, Indonesia. Seguimos a seis machos adultos y a un subadulto con radiotelegrafía. Los territorios fueron en promedio de 14.5 ± 8.5 ha, sin variación en los ámbitos de hogar entre meses o en relación con la abundancia relativa de algunas especies de plantas que sirven como alimento. Las distancias de movimiento diario (849 ± 211 m) variaron significativamente entre meses pero esta variación no se relacionó con los cambios en las plantas que sirven como alimento. Los territorios fueron usados casi exclusivamente por machos residentes. Los machos prefirieron áreas de bosque no intervenido (hábitat I). La estructura de la vegetación en las áreas de exhibición de los machos y en puntos distribuidos al azar indicó que las áreas de exhibición estaban localizadas en bosques sin intervención, con pocas lianas y con árboles de hojas pequeñas en las áreas adyacentes a los sitios de exhibición. Entre 1998 y 2001, realizamos muestreos en cinco transectos lineales y utilizando cámaras fotográficas. Las estimaciones de densidad de machos vocalizando varió entre 0.4 y 2.5 machos km^{-2} , y el estimado de densidad total varió entre 0.9 y 3.7 aves km^{-2} . Las estimaciones de densidad aumentaron considerablemente entre 1998 y 2001, reflejando una recuperación de las densidades bajas que se registraron después de la sequía causada por El Niño entre 1997 y 1998. Las estimaciones de ocupación de hábitat variaron de un 25% a un 38% pero éstas no fueron significativamente diferente entre periodos de tiempo. La proporción de hábitat ocupado fue similar a la proporción de hábitat I. Concluimos que estos faisanes prefieren bosques no intervenidos y que rara vez utilizan otros tipos de hábitat, incluso cuando las densidades poblacionales aumentan. El movimiento restringido y las preferencias de hábitat de esta especie pueden limitar su colonización de fragmentos de bosque.

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THE GREAT ARGUS Pheasant (*Argusianus argus*), one of the world's largest pheasants, is restricted to tropical forests of the Sunda Shelf, including the Malay Peninsula, Sumatra, and Borneo (Smythies 1981, MacKinnon and Phillipps 1993). The species includes two subspecies, the Bornean Great Argus Pheasant (*A. a. grayi*) and the Malay–Sumatra Great Argus Pheasant (*A. a. argus*). The species is sexually dimorphic, with males averaging 2.35 kg and females 1.59 kg. Males have iridescent ocelli on the large secondary feathers and elongate central retrices on the tails, which are ≤ 1.43 m in length (Delacour 1977, Johnsgard 1999). The mating system is polygynous, with males advertising on dancing sites in an exploded-lek system (Davison 1981b, Johnsgard 1999). Davison (1981a) reported, on the basis of vocalizations and foraging observations, that both males and females may defend territories. Little is known about the timing of reproduction in the wild. Beebe reported one recently hatched nest, probably in October (Johnsgard 1999). Davison (1981a) discovered a nest in June and reported a breeding season from February to August (Davison 1981b). In Sumatra, Indonesia, we observed a nest with two eggs in August 1997 (M. F. Kinnaird unpubl. data). Madge and McGowan (2002) concluded that the breeding season was unclear but may occur between March and July. In captivity, females have laid 4–17 clutches of two eggs per year, with clutches in every month (Johnsgard 1999), which suggests the possibility of multiple clutches per year in the wild. The Great Argus Pheasant's omnivorous diet includes fruits, seeds, flowers, leaf buds, and leaf-litter invertebrates. Beebe (1926) reported that the Borneo subspecies consumed primarily ants, but also other invertebrates, leaves, nuts, fallen fruit, and seeds. On Peninsular Malaysia, Davison (1981a) reported that the Malay–Sumatra subspecies' diet was rich in ants but dominated by fruits of the Palmae, Annonaceae, and Fabiaceae.

The species inhabits primary forest but can also be found in old secondary forest and, rarely, in young secondary forest (Nijman 1998). Despite their size and their loud, distinctive call, a penetrating two-note *kwow wow*, the birds are difficult to observe, and there have been only two systematic studies of the species (Davison 1981a, Winarni 2002) and one long-term survey (O'Brien and Kinnaird 2008). Great Argus Pheasants appear to prefer lowland and hill forests below 1,200 m with a low density of undergrowth and presence of climbing vines (Davison 1981a, Nijman 1998). Nijman (1998) found that Great Argus Pheasants on Borneo were less common near villages, but on Sumatra, O'Brien et al. (2003) and O'Brien and Kinnaird (2008) found that Great Argus Pheasant abundance was high in forests adjacent to villages and that distance to forest edge or villages made little difference in the species' occurrence and abundance. The differences between studies may be attributable to higher hunting pressure in Borneo, where Great Argus Pheasant feathers are used in traditional dances. Great Argus Pheasants occur at densities of 0.3–4.5 birds km^{-2} (both sexes) in Malaysia and 0.8–2.0 birds km^{-2} (calling males) in Borneo (Davison and Scriven 1987, Nijman 1998).

The lowland and hill forests of Indonesia have suffered serious deforestation in recent decades. National average annual deforestation is estimated at 1.7 million ha since 1989 (Holmes 2002). The island of Sumatra has experienced the highest rates of deforestation in Indonesia; between 1990 and 2002, Sumatra lost nearly a third of its forest cover (Kinnaird et al. 2003). Lowland and hill forests that support the highest biodiversity have experienced the

most loss. Today, <13% of the original lowland forest area remains, and much of that is fragmented. Most Sumatran galliforms are forest interior specialists and are believed to be sensitive to the effects of forest fragmentation (McGowan and Gillman 1997, Winarni et al. 2005). The Great Argus Pheasant is considered "near threatened" by IUCN (Fuller and Garson 2000), and it is protected by law in Indonesia. However, other than records of occurrence and the surveys by Nijman (1998) and Winarni et al. (2005), little information is available on this threat classification or on the effects of habitat disturbance on pheasants.

Here, we report on the ecology of Great Argus Pheasants in a national park in southern Sumatra. We combine radiotelemetry, habitat analysis, occupancy analysis, and population estimation to explore the characteristics and spatial distribution of home ranges of males and to estimate the density and distribution of this lowland-forest population.

METHODS

Study area.—This research was conducted in Bukit Barisan Selatan National Park (BBSNP), Sumatra (Fig. 1), in the southwestern part of the island ($4^{\circ}31'–5^{\circ}57'S$ and $103^{\circ}34'–104^{\circ}43'E$). The third-largest protected area in Sumatra (3,568 km^2 ; O'Brien and Kinnaird 1996), BBSNP contains some of the largest remaining tracts of lowland rainforest in Sumatra and functions as the primary watershed for southwest Sumatra (Kinnaird et al. 2003). It is bordered by villages, agriculture, and plantation forestry and suffers from encroachment for logging and agriculture, as well as from illegal hunting (Kinnaird et al. 2003, O'Brien et al. 2003). The park covers an altitudinal gradient from sea level to 1,800 m, and forest habitats include lowland, hill, and montane forests. Rainfall is slightly seasonal, averaging 276 mm month^{-1} (3,400 mm year^{-1}) during the present study. Temperatures normally fluctuate between 22° and 35°C . The region is subject to droughts during El Niño–Southern Oscillation (ENSO) events, when monthly rainfall may drop to 0 mm. The present study was initiated in the year following an especially severe ENSO drought that included forest fires in part of the study area.

The research was conducted in the surroundings of the Way Cangkuk Research Station ($5^{\circ}39'32"S$, $104^{\circ}24'21"E$), in the southwestern part of BBSNP (Fig. 1). The station is located in lowland forest and hosts a high diversity of wildlife, including several endangered large mammals, such as Sumatran Tiger (*Panthera tigris*), Sumatran Elephant (*Elephas maximus*), Sumatran Rhinoceros (*Dicerorhinus sumatrensis*), and 221 species of birds, including 3 pheasant species (Winarni 1999). The study area encompasses a 1,000-ha forest block within a larger forest matrix and includes a grid of trails at 200-m intervals. This gridded area is bisected by the Cangkuk River, and the two sub-areas are referred to as "north side" and "south side." All trails are permanently marked at 50-m intervals. The study area contains a mosaic of lowland habitat types, including primary forest, lightly disturbed forest, and previously burned forest (D. S. Busch et al. unpubl. data, Sunarto 2000). The last category resulted from fires during the 1992–1993 and 1997–1998 ENSO droughts (Kinnaird and O'Brien 1998).

Radiotelemetry.—Male Great Argus Pheasants were captured using a modification of a traditional leg-snare device, consisting of a thin platform of twigs attached to a triggered snare,

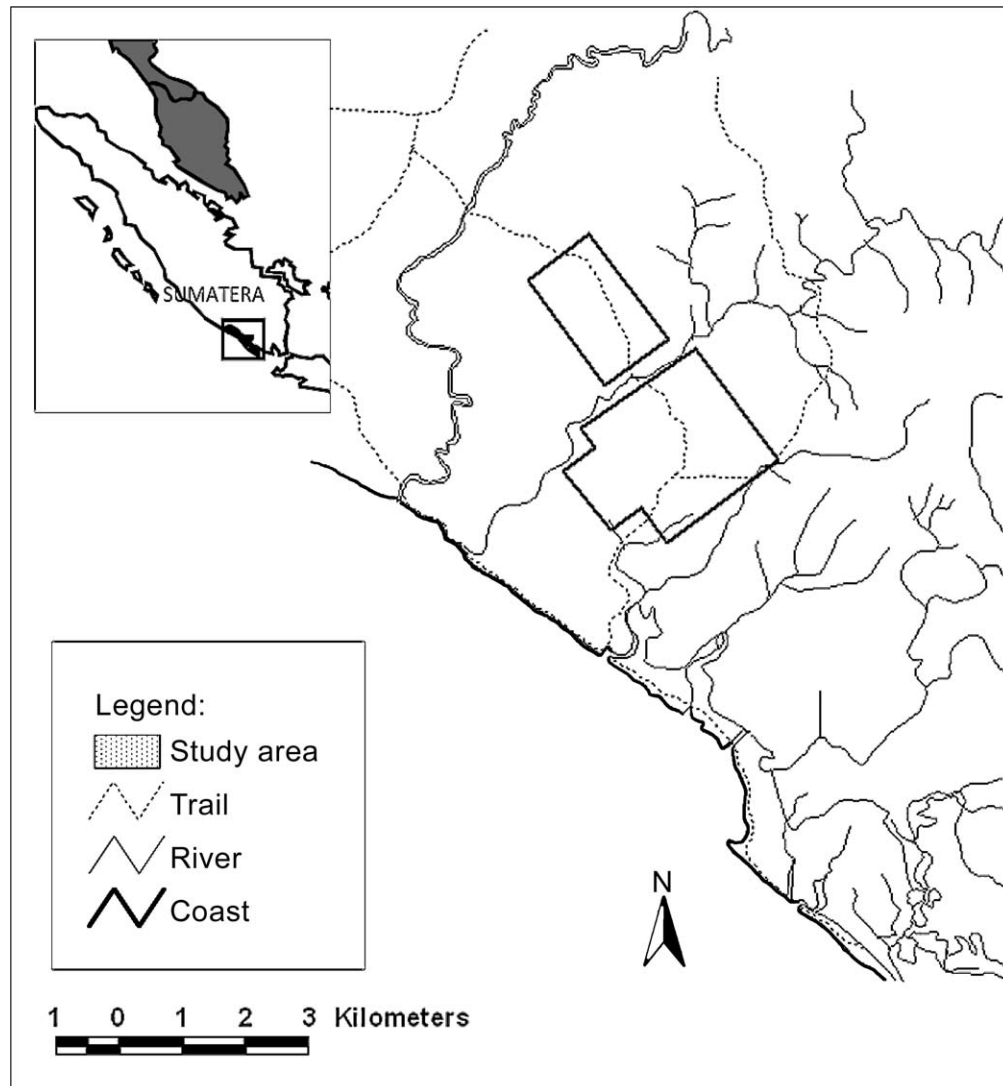


FIG. 1. Location of the Way Canguk study area, Sumatra, Indonesia.

which was anchored to a flexible fiberglass fishing-rod tip. As the bird stepped on the platform, the twigs collapsed, triggering the snare, which was tightened by a quick tug of the fishing-rod tip. Capture attempts were focused on males with active dancing grounds. Typically, males with dancing grounds use two or three entrances (Davison 1981b, N. Winarni pers. obs.), so we set five to seven snares at or near entry points. We also set snares along the trail system in the vicinity of dancing grounds. Snares were constructed the day before deployment and set before dawn. We checked the snares on the basis of the birds' calling behavior. During preliminary observation, we found that birds usually call from a branch adjacent to the dancing ground before entering it. We let the bird perform its first morning call before checking snares and then checked at two-hour intervals until 1200 hours.

Each captured bird was fitted with a 164-MHz necklace-type radiotransmitter (model A3960, Advanced Telemetry Systems, Isanti, Minnesota), leg band, and numbered collar. We collected

standard measurements and released the bird near the capture site. After capture, to reduce stress on the birds, all snares were removed from the site and human activity was reduced in the area for several days before tracking began.

Birds were tracked for three months during September–November 2001, depending on date of capture. We assume that this was late in the breeding season on the basis of observations by Davison (1981b) and because males actively maintained display sites throughout the study. Radio signals were monitored using Wildlife Materials TRX-2000S (164–165 MHz) receivers and three-element Yagi antennae. Individuals were first located within a 4-ha block delineated by the trail grid. We used triangulation by two teams of observers spaced 100–200 m apart to collect pairs of bearings of the individual simultaneously from the grid transect system. Usually, triangulation bearings were taken from distances <150 m from the bird, which minimized the chance of signal bounce and produced 90% error polygons <160 m²

(White and Garrott 1990). To determine daily home range and movements, we conducted intensive daily tracking twice a month for each bird from 0600 to 1700 hours, with locations taken at 1-h intervals. In addition to intensive tracking, we obtained a location for each bird on 12 days each month. Home-range size was calculated from tracking data using 100% minimum convex polygon (MCP; White and Garrott 1990). Kernel home range (White and Garrott 1990) was used to determine utilization distribution within home ranges and centers of activities based on a 50% probability of use. We performed repeated-measures analyses of variance to test whether there is a significant effect of time on home ranges, daily travel, and mean distances of radiolocations to dancing ground. All home ranges, movement patterns, and distance of travel were calculated using ARCVIEW, version 3.2, with Animal Movement extensions (Hooge and Eichenlaub 1997).

Food abundance.—Because Great Argus Pheasants consume primarily fruits and other plant materials (Davison 1981a), we attempted to measure availability of fruits, flowers, seeds, and fungi. In the vicinity of each dancing ground, we placed two to sixteen 100-m transects spaced 50 m apart. We used the existing grid trails as the starting points of transects. We attached a 1-m stick on a 100-m measuring tape along each transect, and at 1-m intervals we recorded the number of fallen fruits, flowers, seeds, and mushrooms present beneath the stick. This process was repeated monthly to develop an index of abundance for plant food types. We used multiple regressions to test whether monthly home-range size fluctuated as a function of changes in the abundance index for flowers, fruits, seeds, and mushrooms considered separately or as the summed food abundance index. Similarly, we tested the effect of plant food abundance index on daily ranging patterns and distance moved from the dancing ground. All statistical analyses were performed using SPSS, version 10.0.05 (SPSS, Chicago, Illinois).

Habitat use.—Macrohabitat classification followed the structural classification of D. S. Busch et al. (unpubl. data), modified to incorporate changes attributable to the 1997 ENSO fire (Kinnaird and O'Brien 1998, T. O'Brien unpubl. data). Data were collected in 240 circular plots of radius 5 m placed systematically along the trail system throughout the study area. The classification of habitats was based on size distribution, height, and density of trees with diameter at breast height [DBH] ≥ 10 cm, sapling density and size distribution, understory density, and canopy openness. Disturbance was indicated by the presence of rattan and other palms (Palmae), lianas, bamboo (Poaceae), and wild ginger (Zingiberaceae; Whitten et al. 2000). The macrohabitats of the study area were classified at the scale of 1 ha and divided into four habitat types: (I) undisturbed forest with large trees (39.1%), (II) undisturbed forest with small trees (17.1%), (III) disturbed forest with large trees (22.4%), and (IV) disturbed forest with small trees (21.4%).

Locations of radiotagged Great Argus Pheasants and 100% MCP were overlaid on a habitat classification map and classified by habitat type using ARCVIEW and the Spatial Analyst extension. Habitat use by radiotagged Great Argus Pheasants was compared with habitat availability using compositional analysis (Aebischer et al. 1993). The MCP home range of each individual was analyzed using ARCVIEW with Animal Movement extensions (Hooge and Eichenlaub 1997). In addition, we also analyzed

kernel home ranges based on 30%, 50%, and 70% probability of use (Hooge and Eichenlaub 1997). Compositional analysis was conducted in two steps, following Aebischer et al. (1993). We analyzed (1) the proportion of MCP versus study area and (2) proportions of radiolocations within the home ranges. We used MACOMP.SAS (Ott and Hovey 1997) to conduct compositional analysis of pooled data from the south and north study areas. Zero values, which are unutilized habitat, were replaced by 0.001%.

We attempted to locate all dancing grounds throughout the study site. We compared macrohabitat classification of display sites with expected values based on the proportion of each habitat category in the study area. Next, we paired active dancing grounds and random sites within delineated home ranges for microhabitat comparisons. On each of the active dancing grounds and random sites, a 10-m-radius circular plot was laid out. Within this circular plot, we counted number of trees and measured the DBH of five nearest trees with DBH ≥ 10 cm, measured the distance to the center of the dancing ground, and recorded the size of five leaves for each of these five trees. Size of leaves was divided into three types: small (length ≤ 20 cm, width ≤ 10 cm), medium (length 20–35 cm, width ≤ 15 cm), and large (length > 35 cm, width > 15 cm). We also counted the number of fallen logs and the distance to the center of the dancing ground. At four different bearings, we measured understory density, canopy openness, and litter thickness. Understory density was estimated using coverage of a 1 \times 1 m sheet divided into 25 \times 25 cm grids. We used a spherical densiometer to measure canopy openness at the center and at four random locations within the plot. We also recorded position of dancing ground as on or off a human trail, presence or absence of a game trail, whether the site was on level ground or on a ridge, and the relative density score of dominant understory plant types (seedlings and saplings, lianas or climbers, grass herbs, gingers). Scoring of understory plant density was divided into a four-point scale based on percent coverage of each type of plant within the plot: score 1 (0–25%), score 2 (26–50%), score 3 (51–75%), and score 4 (76–100%).

Camera trapping and line transects.—We conducted camera-trap sampling in the south Way Canguk research area on five occasions between August 1998 and November 2001 to estimate the proportion of occupied habitat in the study area. We used passive infrared camera traps (CamTrak South, Watkinsville, Georgia) with data packs that stamp each photograph with time and date of the event. We deployed 38 camera traps in a systematic arrangement throughout the study area. Cameras were left in place for ~ 30 days and then retrieved. After films were processed, we scored each photograph for number of birds in the frame and sex of each bird, when possible. Adult Great Argus Pheasants are easily sexed, but chicks resemble females until first molt, when male characteristics become apparent (Madge and McGowan 2002). We also scored each photograph as an independent event on the basis of O'Brien et al.'s (2003) criteria to minimize the possibility of counting individuals twice and used only independent photographs for analysis. We scored each day of sampling at each sample point for presence of pheasants.

To estimate the proportion of the study area occupied by Great Argus Pheasants, we used occupancy analysis (MacKenzie et al. 2002, 2006). Eight-day sampling intervals were combined into four sampling replicates, and we used methods described by

MacKenzie et al. (2002) to estimate site occupancy (ψ) and detection probability (p) for each survey. We considered three possible outcomes: (1) the site is occupied and Great Argus Pheasants are detected, $\psi \times p$; (2) the site is occupied but Great Argus Pheasants are not detected, $\psi \times (1 - p)$; and (3) the site is unoccupied, $1 - \psi$. In these analyses, we assumed that detection probabilities and site occupancy were constant across time and space within each sample period (model $\psi(\cdot)p(\cdot)$). Although there are alternative multiseason models and covariate models that might better represent the data, we used this model as a basic description for between-sample comparisons and for comparison to density estimates. All analyses were conducted using PRESENCE, version 2.0 (MacKenzie et al. 2002).

We estimated densities of Great Argus Pheasants using line-transect sampling methods (Burnham et al. 1980, Buckland et al. 1993). Each month, from June 1998 to January 2002, three pairs of observers walked 18 transects in the Way Canguk research area over a three-day period for a total of 38.4 km month⁻¹. Transects were walked each day by observer pairs spaced at 400-m intervals, beginning at 0600 hours and ending at ~0930 hours. We recorded the total length of transect walked and the number of clusters (consisting of one or more birds) detected. For each cluster, we noted the time of observation, detection cue (audio, visual), number of individuals, sex when possible, distance to cluster, and angle from transect to cluster. All surveys were evaluated for the possibility of duplicate observations that might arise from more than one observer recording a loud call. Duplicate records were eliminated. We calculated density estimates for each of five samples by combining census data for a three-month period that centered on the month of camera trapping in the study area using DISTANCE, version 5.0 (Burnham et al. 1980; Buckland et al. 1993, 2001). We initially calculated detection probabilities for each sample separately, but, because of limited sample sizes, we pooled observations to obtain a single detection function and applied this to each sample to obtain final density estimates. We made separate density calculations for males detected by calls and an overall density based on combined visual and call cues.

RESULTS

Male home-range and movement patterns.—In 2001, between July and mid-September, we captured nine male Great Argus Pheasants during a total of 410 trap-hours of effort. There was no indication that the birds were injured by the snares, and no bird died as a result of capture stress. One bird, however, was killed by an unknown

predator while in the snare. Eight birds were fitted with radiotransmitters, but one of these died soon afterward and was presumed to have been killed by a predator. One adult male's radio failed in the final month of the study. We analyzed data for six adult males that maintained dancing grounds and one sub-adult male without a dancing ground. We recorded 82–122 radiolocations bird⁻¹ (Table 1).

Total home-range sizes varied, ranging from 7 to 32 ha ($\bar{x} = 14.5 \pm 8.5$; Table 1). The sub-adult male's home range was twice as large as that of the largest adult male. Home-range overlap among neighboring territories was low, averaging 9.5% (range: 0.83–30%). The sub-adult male's home range overlapped with that of another male that occupied a dancing ground. Mean daily home ranges were approximately 1–4 ha and did not differ significantly among birds. Home-range sizes did not differ significantly by month ($F = 2.15$, $df = 2$ and 4 , $P = 0.17$; Table 1).

The distribution of radiolocations within home ranges of adult males was concentrated around the birds' dancing grounds. Kernel analysis showed that core areas (50% of use) of male Great Argus Pheasants were very small, at 6–12% of total home-range size. All males had multiple centers of activity. Three of the six adult males centered their activities close to dancing grounds that were located near the boundaries of the home range. Dancing grounds of the other three adult males were in the middle of the home range. These individuals moved throughout their home ranges more uniformly.

Daily movements of male Great Argus Pheasants ranged between 412 and 1,145 m ($\bar{x} = 849 \pm 211$ m; Table 2) with significant differences among months ($F = 5.23$, $df = 2$ and 4 , $P = 0.028$). Daily movements were significantly shorter in September ($\bar{x} = 705$ m) than in October ($\bar{x} = 995$ m). Although there were differences in the number of locations near dancing grounds, we found no significant monthly differences in distances to dancing grounds ($F = 2.065$, $df = 2$ and 3 , $P = 0.19$). Adult male Great Argus Pheasants' mean distances to the dancing ground varied from 67 to 199 m ($\bar{x} = 139 \pm 37.8$) and showed an increasing trend over time ($\bar{x}_{\text{Sept.}} = 124$ m, $\bar{x}_{\text{Oct.}} = 145$ m, $\bar{x}_{\text{Nov.}} = 150$ m).

Correlation of food abundance and home range.—The index of plant food abundance (fruits, flowers, seeds, and fungi) was generally low and did not show any particular pattern or trend over the three months of the study. We found that home-range size was not related to availability of plant food for the food types measured. Also, daily ranging patterns and distance moved from dancing grounds were unrelated to availability of plant food.

Habitat characteristics of home range.—Home ranges and point locations were divided among macrohabitat types.

TABLE 1. Minimum convex polygon (MCP) monthly and three-month total home ranges (ha) of male Great Argus Pheasants during September–November 2001, in Bukit Barisan Selatan National Park, Sumatra, Indonesia.

Individual	Age	Number of locations	Number of locations			Total
			September	October	November	
A	Adult	122	9.2	8.0	6.6	16.1
B	Adult	112	7.4	9.4	7.0	12.6
C	Adult	116	4.6	9.5	7.5	14.5
D	Adult	113	2.9	4.9	1.8	7.6
E	Adult	82	6.3	5.9	No data	8.3
G	Adult	86	2.7	9.5	2.2	10.0
F	Subadult	105	13.8	8.4	7.6	32.3

TABLE 2. Means (\pm SE) of daily travel (m) of male Great Argus Pheasants during September–November 2001, in Bukit Barisan Selatan National Park, Sumatra. Daily tracking was conducted twice a month for each bird (an asterisk indicates that only one daily tracking was conducted).

Individual	September	October	November
A	1,145.1 \pm 127.0	1,084.5 \pm 253.2	907.1 \pm 484.1
B	649.0 \pm 70.0	1,001.5 \pm 139.3	821.7 \pm 119.8
C	412.7 \pm 86.8	1,024.2 \pm 85.0	924.2 \pm 327.0
D	629.2 \pm 122.9	733.7 \pm 26.8	626.4 \pm 86.9
E	979.0 \pm 184.8	847.1 \pm 240.7	No data
G	578.4*	1,042.0 \pm 422.1	595.3 \pm 5.5
F	815.8 \pm 24.3	1,087.4 \pm 170.1	1,073.4 \pm 25.6

Compositional analysis indicated the same rank order of habitats in the study area and in the MCP ranges. Home ranges were located primarily in habitat I, and home ranges contained more of habitat II and less of habitat IV than the study area. Only two home ranges contained more disturbed than undisturbed habitat. Overall, however, there were no significant differences between availability of habitats and occurrence of habitats in the MCP ranges. Although MCP ranges included all habitat types, radiolocations of male Great Argus Pheasants occurred primarily in undisturbed habitats I (\bar{x} = 54%) and II (\bar{x} = 22.7%). Compositional analysis also identified different rank order in radiolocations compared with proportion to habitat available within the home range. Use of habitat I was significantly higher than use of habitat III (T = 2.71, df = 3, P = 0.04) or habitat IV (T = 2.73, df = 3, P = 0.02). Use of habitat I was greater than use of habitat II, and use of habitat II was greater than use of habitats III and IV, but these differences were not significant. Comparison of percentage of use of the 100% MCP home ranges with probabilistic kernel home ranges indicated that male Great Argus Pheasants were most likely to use habitat I and avoid habitat IV. Habitat IV is represented as 1% of habitat use in the 70% kernel and 0% of habitat use in the 50% kernel representing the core range. By contrast, habitat I is represented as 66% and 70% of habitat use in the 70% kernel and 50% kernel, respectively. Use of habitats II and III appears to be similar to availability.

Habitat characteristics of display sites.—We classified 15 active dancing grounds to macrohabitat and measured microhabitat characteristics of the dancing grounds and 15 random sites within home ranges of male Great Argus Pheasants. Most dancing grounds were located in undisturbed forest (habitat I, n = 6; habitat II, n = 6; habitat III, n = 3). The difference between the observed and expected distributions of dancing grounds among the four habitat types was marginally significant (χ^2 = 7.08, df = 3, P = 0.049). A forward-stepwise binary logistic regression of microhabitat variables at the display sites and random points resulted in a model that retained lianas (χ^2 = 24.375, df = 3, P < 0.005) and leaf size (χ^2 = 38.816, df = 4, P < 0.005) as significant explanatory variables. Display sites were characterized by having fewer lianas nearby and smaller leaf sizes on adjacent trees, compared with random points. The model then correctly classified 29 of the 30 sites used to create the model.

Abundance and distribution.—We used 15 line-transect surveys, grouped in three-month intervals centered on five camera-trap surveys between August 1998 and January 2001 in the Way

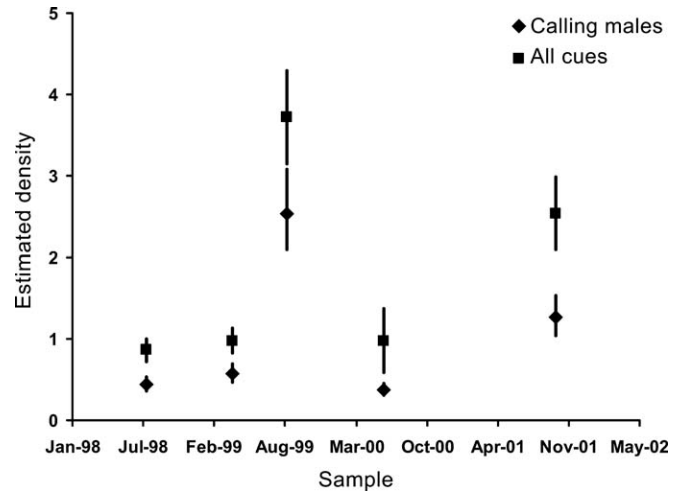


FIG. 2. Density estimates with 95% confidence intervals for calling males and all Great Argus Pheasants between July 1998 and November 2001.

Canguk research area. Observations were truncated at 100 m. Great Argus Pheasants were detected 114 times during line-transect surveys, and 75% of these detections were of calling males. We rarely distinguished sex during visual encounters and could not analyze male and female density separately using visual encounters. We calculated detection probability for each of the five calling-male samples and found no significant differences (range: 0.4–0.75) among detection probabilities, so we combined data sets to estimate the detection function by fitting a half-normal distribution with cosine adjustment terms. The detection probability (\pm SE) of calling males was 0.821 ± 0.081 , and effective strip width was 82.0 ± 8.1 m. Densities of calling males increased from 0.44 km^{-2} to a maximum of 2.54 km^{-2} and then declined to 1.27 km^{-2} in the final survey (Fig. 2). Overall male density showed an increasing trend over time, with a geometric mean increase of $16\% \text{ year}^{-1}$ between the first and last surveys.

We estimated the detection function for males and females by combining calling and visual observations and fitting a half-normal distribution with cosine adjustment terms. Birds were detected with an average probability of 0.665 ± 0.049 , and the effective strip width was 66.0 ± 4.9 m. The total density estimate increased from 0.86 km^{-2} to a maximum of 3.72 km^{-2} and declined to 2.54 km^{-2} in the final survey. Total population increased at a rate similar to that of calling males, with a geometric mean of $13\% \text{ year}^{-1}$ between the first and last surveys.

Camera-trap surveys resulted in 149 independent photographs of single birds, 25 photographs of two birds, and three photographs of three birds. Birds were photographed throughout the day (0500–1800 hours) but were most active between 0600 and 1000 hours (54% of photographs). Great Argus Pheasants were detected at least once at 10 locations in each survey in Way Canguk, for an average observed or naïve occupancy estimate (assuming detection probability = 1) of Great Argus Pheasant occurrence equal to 29% (range: 24–38%) of camera locations. Occupancy estimates were 4% higher, on average (\bar{x} = 33%, range: 25–38%), and more consistent than the naïve estimates. Naïve estimates were consistently lower, and in the April 1999 sample fell below the 95%

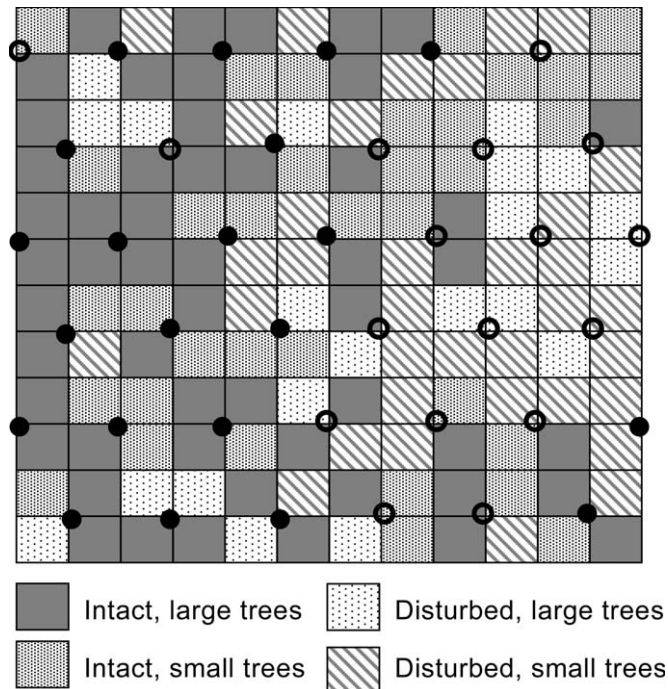


FIG. 3. Locations of camera traps in the south study area of Way Canguk in relation to the four dominant habitat types. Filled circles indicate locations where Great Argus Pheasants were photographed at least once during five surveys between 1998 and 2001.

confidence interval (CI) for estimated occupancy. As was observed for males in the radiotelemetry study, Great Argus Pheasants occurred more often at cameras that were adjacent to or surrounded by intact habitat (habitats I and II; $\chi^2 = 6.63$, $df = 2$, $P = 0.03$; Fig. 3), and no individuals were photographed by cameras in highly disturbed forest. Only one photograph was obtained at a trap site that was not adjacent to intact habitat.

To test for possible habitat separation between males and females, we examined the distribution of males and females across films at locations where they were photographed. For each sample period, camera points were scored as “only males photographed” ($n = 15$), “only females photographed” ($n = 13$), and “both sexes photographed in the same sample” ($n = 21$). If the sexes were segregated spatially in Way Canguk, we expected a preponderance of camera points with one sex and few points with both sexes. We found no evidence that sexes were segregated among the camera-trap locations ($\chi^2 = 1.96$, $df = 2$, $P = 0.375$).

DISCUSSION

Our telemetry results indicate that male Great Argus Pheasants are highly territorial during the breeding season and that male movements appear to be constrained more by the need to attend and possibly defend the display site than by foraging needs. Our results also show that Great Argus Pheasants, males and females, are habitat specialists, preferring intact forest with large trees and open understory, and show no evidence of habitat separation. Increases in the abundance of Great Argus Pheasants over 3.3 years

were not accompanied by expansion into unoccupied habitat. Our results also indicate that populations of Great Argus Pheasant are subject to rapid changes in abundance over a short period. Habitat specificity and rapid population fluctuations may make Great Argus Pheasants especially vulnerable to the effects of forest loss and degradation, as well to the increasing frequency of ENSO events.

Movement patterns, display sites, and food abundance.—The average male home ranges in our study site, both monthly (6.80 ± 2.98 ha) and over three months (14.50 ± 8.46 ha), are considerably larger than home-range estimates collected over five months from peninsular Malaysia (1.09 – 2.50 ha; Davison 1981a). Core-area use averaged <10% of the MCP in Sumatra and consistently covered larger areas than observed in Malaysia (0.4 – 4.4 ha and 0.1 – 0.5 ha, respectively). Daily movements of Great Argus Pheasants were also larger in Sumatra than in Malaysia. In Sumatra, birds traveled an average of 849 ± 211 m daily, whereas in Malaysia, the maximum distance traveled in a day was 800 m and 910 m for each of two birds. There are some temporal and habitat differences between the two studies. Whereas our study was conducted at the end of the presumed breeding season, Davison’s (1981a, b) spanned the pre-breeding and breeding seasons, as determined by maintenance of display sites and calling. The Malaysian site was hilly, the forest was dominated by the tree family Dipterocarpaceae, and both birds maintained their display site on the tops of ridges and moved about on the hillside below. In Way Canguk, the site was flat, and although Dipterocarpaceae was the most numerous family in the canopy, this family did not dominate the forest. Davison and Scriven (1987) reported that display sites were spaced more widely on flat, lowland sites than on hilly sites and that densities of calling males were lower at flat sites. Both results imply either larger territories or a patchier distribution of territories on flat terrain in Malaysia.

Movements and territory size of male Great Argus Pheasants may be affected by food abundance (Davison 1981a, Johnsgard 1999) as well as by the need to stay close to a display site during the breeding season. We found that our index of plant-food abundance was unrelated to male territory size or daily movement patterns. However, Great Argus Pheasants are omnivorous, and we did not measure leaf-litter invertebrates in the present study. We observed that daily distance traveled increased over time, possibly coinciding with the end of the breeding season. We know very little about the breeding season of Great Argus Pheasant (Madge and McGowan 2002, present study), however, except that nests have been found in May, June, July, August, and October (Davison 1981a, Johnsgard 1999, M. F. Kinnaird pers. obs.). If display sites are a limited and defended resource, as they are in many lekking species (Davison 1981b, Madge and McGowan 2002), there should be a tradeoff between foraging and defending a territory. Davison (1981a) suggested that during the breeding season, possession of a display site and the amount of time spent there are critical to a male’s fitness. He also suggested that Great Argus Pheasants are able to minimize their energy expenditure during low food availability by limiting movements and spending 80–90% of the day resting (Davison 1981a). In Bukit Barisan Selatan National Park, birds were active throughout the day, though 54% of activity occurred between 0600 and 1000 hours (O’Brien and Kinnaird 2008).

Forests dominated by Dipterocarpaceae are usually characterized as fruit-poor during non-masting years (Leighton and

Leighton 1983, Wich and Van Schaik 2000). Fruit specialists in Dipterocarpaceae-dominated forests must be able to move widely over the landscape (Kinnaird and O'Brien 2007) to secure sufficient resources. Although Way Canguk is not dominated by Dipterocarpaceae, only 5% of all tree species were in fruit (at all stages of ripeness) in any month during the study. Given the small male territory size, constrained movements, and low plant-food index values, it is possible that males relied more heavily on invertebrates as a food supply during this study period. Beebe (1926) reported that the Bornean subspecies inhabiting Dipterocarpaceae-dominated forests ate primarily ants but also leaves, fruits, and seeds. Davison (1981a) analyzed droppings and reported that solitary leaf-litter ants were the primary invertebrate food of the Malay-Sumatra subspecies but that fruits were predominant in the diet. Ants and other leaf-litter invertebrates are usually exploited by systematically exploring small patches, a description that fits the meandering foraging behavior of Great Argus Pheasants (Davison 1981a). Davison (1981a) concluded that the most likely changes in the foraging patterns of Great Argus Pheasants would be related to changes in diet and changes in the speed and amount of time spent searching for food. If plant food resources were, in fact, scarce during the present study, the increases in movements over a restricted area we recorded might be explained by invertebrate foraging. However, the short duration of our study and the lack of data on leaf-litter invertebrates preclude firm conclusions.

Habitat preference.—Several lines of evidence point to strict habitat specificity in Great Argus Pheasants. First, male display sites tend to be located in undisturbed forest with large trees (habitat I, $P = 0.049$), and 12 of the 15 dancing grounds were found in the undisturbed habitats. Display-site characteristics included animal trails, presence of low branches, and low density of seedlings, saplings, lianas, herbs, and gingers. Lianas, herbs, and gingers are characteristic of disturbed sites at Way Canguk. Nijman (1998) reported that of six active display sites located during surveys in Borneo, five occurred in primary forest and one in old secondary forest. Davison (1981b) reported that 19 display sites were found in primary and tall secondary forest.

Second, radiotelemetry suggests that home ranges of male Great Argus Pheasants were centered on undisturbed forest, habitat I in particular. Although MCP home ranges incorporated habitats I–IV in similar order to their representation at the site, radio locations placed male Great Argus Pheasants firmly in habitat I (54% of locations) and habitat II (23% of locations). Habitat I was used significantly more than all other habitats and constituted 70% of the habitat in the core area. Other habitats were either avoided (habitat IV) or used in proportion to occurrence.

Third, camera-trap surveys confirmed that male and female Great Argus Pheasants were associated with undisturbed habitat, with no evidence of spatial segregation between sexes. In Way Canguk, individuals were photographed at a camera site surrounded by disturbed forest only once over a 3.3-year period (4,943 camera-trap days of effort). As the Great Argus Pheasant population increased in Way Canguk, the estimated proportion of occupied habitat did not increase, which indicates that the species used only a subset of the total study area.

Most authors agree that Great Argus Pheasants prefer primary forest and old secondary forest (Davison 1981a, Nijman 1998, Johnsgard 1999). Use of secondary forest appears to be

closely linked to time since disturbance, with old secondary forest preferred over young secondary forest. In the present study, undisturbed forest with large trees was preferred; this forest type has a less dense understory, preferred for display sites, and a well-developed litter layer, which is critical as a foraging substrate (Davison 1981a, b).

Abundance and distribution.—The estimated density of calling males at Way Canguk increased from 0.4 to a peak of 2.5 males km^{-2} and then declined to 1.27 males km^{-2} over a 3.3-year period following a major ENSO drought and fire (Kinnaird and O'Brien 1998). At the same time, density of all Great Argus Pheasants increased from 0.9 birds km^{-2} to a peak of 3.7 birds km^{-2} and declined to 2.54 birds km^{-2} . Both data sets indicate a three-fold increase in Great Argus Pheasants between 1998 and 2001. Three potential problems regarding the density results should be considered. (1) Detection probabilities, rather than density, varies over time, and use of pooled data obscures that relationship. (2) Sampling error inflated results for September 1999. And (3) overall densities were underestimated because of sex-specific differences in detectability between males and females.

Detection probabilities ranged from 0.4 to 0.75 across samples, but these differences were not significant. Maximum and minimum detection probabilities did not correspond to maximum and minimum density estimates, and the correlation between detection probability and density was not significant ($P = 0.28$). In 2001, we recorded 15 active display sites and estimated 13 calling males (95% CI: 10.4–15.4) from the line-transect data, which is consistent with results of independent surveys. Sampling error could explain the apparent outlier density recorded in September 1999. However, during larger camera-trap surveys of the 3,568- km^2 national park (O'Brien and Kinnaird 2008), we recorded a similar pattern of abundance between 1998 and 2002, with point abundance estimates tripling in BBSNP between 1998 and 2000, followed by a decline.

The final problem of possible sex bias in detection probabilities is more complex. If the sex ratio is skewed (often the case for polygamous species) and there are sex-specific detection probabilities (males detected more often), density estimates based on pooled samples might be biased. Davison (1981a) suggested that both sexes of Great Argus Pheasant maintain exclusive feeding territories during and immediately after the breeding season. He based this conclusion on observations of solitary foraging, dispersion of invertebrate prey, and optimal-foraging considerations (Pyke et al. 1977). If Davison's (1981a) hypothesis is supported, and discrete female territories overlap discrete male territories, we would expect a sex ratio similar to the ratio of respective territory sizes, because males and females would space themselves across the landscape in discrete territory patches. In addition, point samples should record a 1:1 sex ratio, given that, on average, any point would fall in just one male and one female territory. We estimated the sex ratio of Great Argus Pheasants from camera-trap data for Way Canguk and BBSNP in two ways. First, we counted the number of male and female Great Argus Pheasants in 508 independent photographs (T. O'Brien unpubl. data), excluding photographs of unsexed birds. If we assume no habitat separation and that males and females pass through the camera at the same rate, the ratio of birds in photographs should reflect the sex ratio. We estimated a sex ratio of 1.07 males to 1.00 females. Next we assumed that a

camera-trap point was within, at most, one male and one female territory. The ratio of males to females appearing at least once at a camera-trap point was 1.00:1.01. These sex ratios support Davison's (1981a) hypothesis of female and male territories. Finally, if there are sex differences in detection probabilities, we would expect the sex ratio of male density to female density to differ from 1:1. We can derive the sex ratio for each line-transect survey as the ratio of the male density estimate to the total density estimate minus the male density estimate. In line-transect surveys 1 and 5, estimated sex ratios are 1:1; in surveys 2 and 3, sex ratios are male-biased (males:females = 1.4:1.0 and 2.2:1.0, respectively); but in survey 3, the sex ratio is female-biased (1.0:1.6). We conclude that there is no consistent evidence of sex bias in detection probabilities using line-transect sampling.

Density estimates indicate that populations of Great Argus Pheasant may fluctuate considerably over a relatively short time-scale and that timing of surveys can have a large effect on the results observed. We suspect that the populations in the study area and BBSNP were depressed following one of the most severe ENSO droughts of the 20th century (Kinnaird and O'Brien 1998), and the steep increase between 1998 and 2001 may represent a population recovery. Alternatively, density differences may represent annual fluctuations in population size resulting from birth, recruitment and mortality. Data on reproductive patterns in Great Argus Pheasants are scarce: we observed only a single nest in August 1997, and chicks in November 1999, January 2000, and November 2001. This suggests that most recruitment occurs later in the year. Clutch size is two eggs, but multiple clutches in a year are possible (Johnsgard 1999).

The density estimates at Way Canguk are similar to estimates for primary and old secondary forests from other published studies (Davison 1981a, Davison and Scriven 1987, Nijman 1998). These studies, however, reported consistently higher densities on hilly slopes (males: 1.5–2.3 km⁻², total: 3.0–4.5 km⁻²) than on flat areas (males: 0.15–0.54 km⁻², total: 0.54–1.00 km⁻²). Wells (1985) considered Great Argus Pheasants slope specialists, though with little supporting data. Our data suggest that Great Argus Pheasants may reach high densities in flat forest, so long as the forest is not inundated or heavily disturbed. Such forest conditions are becoming increasingly rare in Southeast Asia (Kinnaird et al. 2003, Kinnaird and O'Brien 2007, Sodhi et al. 2008).

Although density in Way Canguk fluctuated considerably between surveys, the overall trend in numbers of Great Argus Pheasants was an increase over time. The proportion of occupied habitat in Way Canguk remained relatively constant and approximated the proportion of undisturbed habitat with large trees. Way Canguk did not experience fires or forest loss during the study period, so proportions of habitat remained relatively unchanged. As their abundance increased, Great Argus Pheasants did not expand their foraging areas or breeding territories to disturbed habitats. These results agree well with the core-area results from the telemetry study of males that show overwhelming use of undisturbed forest, particularly habitat I. Avoidance of disturbed forest may explain why Thiollay (1995) recorded no Great Argus Pheasants in traditional rubber, dammar (resin), or durian agroforests adjacent to primary forest in BBSNP.

As sedentary habitat-specialists, Great Argus Pheasants are not likely to move long distances across unsuitable habitat.

Winarni et al. (2005) found Great Argus Pheasants in only 2 of 13 forest fragments (ranging in size from 2.5 to 50 km²), with varying degrees of isolation. All forest areas >50 km² contained Great Argus Pheasants. As deforestation continues across Peninsular Malaysia, Sumatra, and Borneo, large undisturbed tracts of lowland forest will become a limiting resource for Great Argus Pheasants and other species that depend on high-quality lowland forest, such as peacock pheasants (*Polyplectron* spp.), Wrinkled Hornbill (*Rhyticeros corrugatus*), and Black Hornbill (*Anthracoceros malayanus*). Strict habitat-specificity reduces the likelihood that Great Argus Pheasants will recolonize empty forest fragments.

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