RESEARCH ARTICLE

Habitat-Specific Ranging Patterns of Dian's Tarsiers (*Tarsius dianae*) as Revealed by Radiotracking

STEFAN MERKER*
Institute of Anthropology, Johannes Gutenberg University Mainz, Mainz, Germany

Dian's tarsier *Tarsius dianae*, one of the smallest primates on earth, is endemic to the central regions of Sulawesi, Indonesia. To evaluate the effects of increasing land use by humans on the ranging patterns of this nocturnal insect hunter, four study plots along a gradient of anthropogenic disturbance were selected for this study. In these plots, 71 tarsiers were captured with mist nets, and 30 of these were fitted with 3.9 g radiotransmitters and subsequently tracked over the course of 2 weeks per animal. The average home ranges were 1.1–1.8 ha in size, with the smallest ranges in slightly disturbed habitat and the largest ranges in a heavily disturbed plantation. These findings coincide with different estimates of insect abundance in the study plots. Nightly travel distances were smallest in undisturbed old-growth forest and slightly increased along a gradient of human disturbance. The tarsiers were most active shortly after dusk and just before dawn. The results of this comprehensive radiotracking study on tarsiers show that *T. dianae* adapts its ranging behavior to the degree and type of human land use. Integrated data on home range size and travel distance indicate that slightly disturbed forest is as favorable to these animals as undisturbed habitat. However, with increasing anthropogenic effects, the living conditions of the tarsiers appear to deteriorate, resulting in the necessity for larger home and night ranges. The results of this study provide an important tool for directing conservation efforts targeted at the survival of this primate in central Sulawesi. Am. J. Primatol. 68:111–125, 2006. © 2006 Wiley-Liss, Inc.

Key words: home range; path length; activity rhythm; Lore-Lindu; Sulawesi

WILEY
InterScience®
DISCOVER SOMETHING GREAT

INTRODUCTION

With *Macaca* and *Tarsius*, two primate genera have crossed Wallace's line into Sulawesi, an island in the midst of the Malay archipelago. Known for its unique and highly endemic fauna, Indonesia's fourth-largest island has experienced a dramatic loss of pristine forest [Whitten et al., 2001] and a subsequent decline in primate population densities [Gursky, 1998a; Merker et al., 2004]. National and international conservation organizations are struggling to protect the remaining forests and keep the wildlife from becoming locally or regionally extinct. Nevertheless, scientific data on Sulawesi's primates are rare, and most conservation efforts have to be based on assumptions rather than insights. In the case of Dian's tarsiers, however, it is possible to test the effects of habitat structure and disturbance on these animals because they are still reasonably abundant in a variety of habitats [Merker, 2003; Merker et al., 2004].

Over the past 20 years, the results from radiotracking have amended studies on primates and greatly increased our knowledge regarding their ranging behavior and social interactions. In tarsier research, Crompton and Andau [1986, 1987] were the first to use (and report using) radiotelemetry to estimate home range sizes of Western tarsiers (*Tarsius bancanus*) in Borneo. Dagosto and Gebo [1997] and Neri-Arboleda et al. [2002] radiotracked Philippine tarsiers (*T. syrichta*). In Sulawesi, Tremble et al. [1993] radiotagged and tracked four Dian's tarsiers (*T. dianae*), and Gursky [1998a,b, 2000a–c, 2002a,b] used this methodology to determine home and night ranges, and observe behavior in spectral tarsiers (*T. spectrum*). Although a number of studies have addressed the influence of anthropogenic effects on primate densities [e.g., Chapman, 1987; Ganzhorn, 1999; Johns & Skorupa, 1987; Chapman & Lambert, 2000; Merker & Mühlenberg, 2000], few authors have examined ranging patterns under various types of human disturbance [Heiduck, 2002; Nijssen & Sterck, 2000].

Merker et al. [2005] estimated habitat suitability for Dian's tarsiers based on population densities, group sizes, female home range sizes, and path lengths.

To better elucidate the social and ecological factors that influence the habitat use and distribution of this species, the present study explicitly focuses on the ranging patterns of *T. dianae*. Based on previous findings that population densities vary with the degree of human interference [Merker & Mühlenberg, 2000], it was hypothesized that these tarsiers would also adapt their patterns of range use to different degrees of disturbance. In this study, the home range sizes and nightly path lengths of Dian's tarsiers were investigated in the light of sexual differences and habitat disturbance. Additional objectives were to evaluate the effects of seasonality on prey densities and tarsier home range sizes, and to outline the activity rhythm of *T. dianae*.

MATERIALS AND METHODS

Study Species

With head–body lengths of ca. 12 cm and body weights of 100–140 g, tarsiers are among the world's smallest primates. These nocturnal clingers and leapers [Napier & Napier, 1967] feed on live animal prey such as crickets, grasshoppers, and moths [Nietsch, 1993; Tremble et al., 1993]. *Tarsius dianae*, a species described by Niemitz et al. [1991], is endemic to central Sulawesi. It lives in small family groups of up to seven individuals, which usually consist of an adult male, one to three adult females, and their offspring [Merker, 2003]. The IUCN lists

T. dianae as ''lower risk: conservation dependent'' [Eudey et al., 2000]. Merker et al. [2004] presented evidence that populations of this species are declining.

Study Site

This study was conducted at the northeastern boundary of Lore-Lindu National Park, Central Sulawesi, Indonesia, between July 2000 and November 2001. The ranger station of Kamarora (120°08′15″ E, 01°11′50″ S, altitude 660 m), which represents the type locality for *T. dianae*, was used as the base camp (Fig. 1). The climate is wet, with more than 100 mm rain per month in 10 out of 11 consecutive months in 2001 and ca. 2,700 mm rain per year (in 2001/2002). Irrespective of the time of the year, minimum nightly temperatures average 19.5°C$\pm$1.0°C, and daily highs reach 32.9°C$\pm$1.3°C [Merker, 2003]. At the time of this study, the forest adjacent to the station was characterized by various forms of human land use, including selective logging, rattan extraction, and agroforestry (local farming of coffee and cocoa as cash crops in the shade of the rain forest trees). However, the year 2001 was marked by vast encroachments on the forest, and some of the plots described in the following text were significantly degraded.

Four study plots (10–20 ha and at least 2 km apart) were selected for this study. One patch (H1) was virtually undisturbed old-growth forest. Plot H2 was considered slightly disturbed. It was crisscrossed by small trails and showed signs of bamboo and rattan collection. Plot H3 was disturbed to an intermediate degree. It was interspersed with small forest gardens and was also used for bamboo, rattan, and timber harvesting. The heavily disturbed study plot H4 was a mixed-species plantation outside the natural forest. It was a blend of small cocoa plantations, with *Gliricidia sepium* as shade trees and interspersed patches of dense shrubs, bamboo *Bambusa* spp., alang-alang *Imperata cylindrica*, and corn *Zea mays*. Over the course of this study, the type and intensity of the anthropogenic influences did not change significantly in any of the four plots. According to locals who lived at the forest margin, this was also true for at least the previous 2 years.
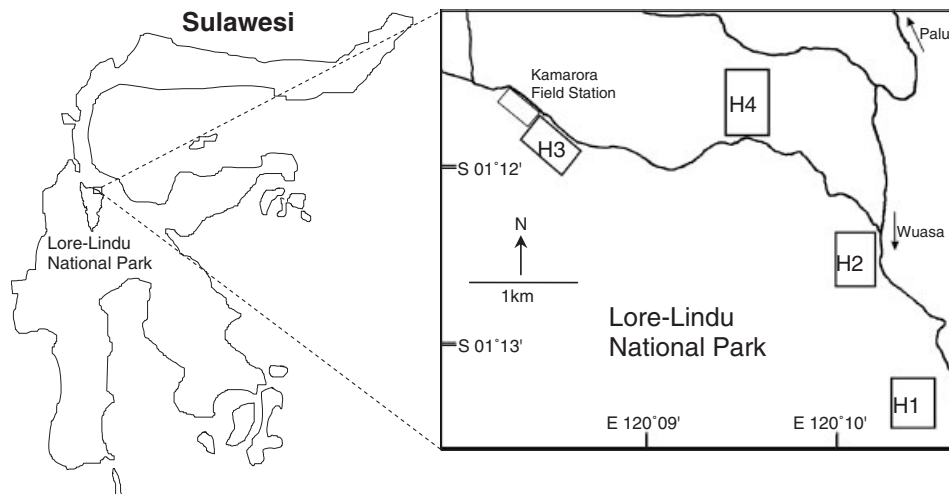

Fig. 1. Map of Sulawesi and location of the study plots along the northeastern boundary of Lore-Lindu National Park.

Table I shows the insect abundance in the four study plots as analyzed by Merker et al. [2005].

Data Collection

In each plot tarsiers were initially located by triangulating the positions of vocalizing individuals during their regularly performed morning duet songs. This was achieved with the help of two to five field assistants at fixed points within a mapped trail system. By closing in on the tarsiers over the course of several days, it was possible to follow the animals to their sleeping sites (which consisted mostly of strangling figs (*Ficus* spp.)). Two to six mist nets (6–12 m long) were positioned around these sites in the undergrowth utilized by the animals. The nets were open between 0500 and 0630 hr and/or between 1700 and 1900 hr. Since tarsiers had previously been observed escaping from mist nets, all nets were continually monitored to ensure a high capture success. When a tarsier was caught in a net it was immediately removed and put into a cotton bag.

Altogether, 71 tarsiers were captured a total of 140 times. All specimens were weighed and measured, and external characteristics were taken. Some animals were marked with colored plastic rings around their tarsus, and whenever possible the tarsal rings were removed after the study. Ear clips were taken from radiotagged tarsiers for genetic analyses (Merker, unpublished data). Females were palpated to avoid radiotracking highly pregnant individuals. In each of the plots, six adult or nearly adult females ($m \geq 80$ g, Table II) were equipped with radiotransmitters (PD-2C; Holohil Systems Ltd., Carp, Canada) weighing a total of 3.9 g each (3.0–4.8% of body weight). In undisturbed forest, six adult males (the mates of the six tracked females; $m > 105$ g, with descended testes) were also fitted with transmitters. The choice of females as the sex to compare between the habitats was based on results regarding male and female range variability in H1 (see Results). All of the animals were released at the place of capture within 2 hr after they were caught.

The average lifespan of a transmitter was set to be 6 months, and the range of transmission in dense forest was 100–200 m. Each radiotag was fine-tuned to a specific frequency at 150–151 MHz to identify individual tarsiers. As the receiver, a Stabo XR100 Special radioscanner with a portable two-element HB9CV antenna (Gesellschaft für Telemetriesysteme, Horst, Germany) was used. Twenty-five of the 30 radiotracked tarsiers were recaptured and their collars were retrieved. Because of illegal clearcut logging that occurred in H1 after the data were collected, five of the study animals could not be relocated even after an intensive search.

TABLE I. Insect Abundance (Mean $\pm$ SD) on the Study Plots[*]

Habitat	n	Light trap	Vocalizing
H1	6	3.6 ± 1.1	7.9 ± 0.6[a]
H2	8	3.1 ± 1.3	9.0 ± 0.6[b]
H3	8	3.7 ± 1.7	9.8 ± 0.9[b]
H4	8	3.8 ± 1.4	6.5 ± 1.0[c]

[*]Given are numbers of insects attracted to a strong light source within 5 min and numbers of insects vocalizing within a 10 m-radius within 5 min. n = number of sample points (three replicates at each point). Different letters denote significant differences between plots (two-way ANOVA, least significant difference test, $P < 0.05$). Redrawn from Merker et al. [2005].

TABLE II. Radio-Tracking Data for 30 Tarsiers in Four Different Habitats of Lore-Lindu National Park, Sulawesi*

Individual no.	Body weight, g	Tracking Period	Total no. of fixes	Home range size (MCP), ha	Home range size (grid cells), ha
H1 M1	119	10/25–11/05/00	79	1.70	1.20
H1 M2	110	10/25–11/05/00	70	1.05	0.84
H1 M3	128	10/25–11/05/00	69	1.33	0.96
H1 M4	129	11/05–11/14/00	66	2.23	1.56
H1 M5	113	11/05–11/14/00	71	1.73	1.12
H1 M6	128	11/05–11/14/00	75	2.57	1.40
H1 F1	107	10/25–11/05/00	78	1.76	1.36
H1 F2	108	10/25–11/05/00	71	1.77	1.08
H1 F3	98	10/25–11/05/00	78	1.54	1.48
H1 F4	89	11/05–11/14/00	65	0.94	0.84
H1 F5	85	11/05–11/14/00	72	1.55	1.24
H1 F6	110	11/05–11/14/00	75	1.90	1.12
H2 F1	90	03/26–04/21/01	78	0.58	0.76
H2 F2	109	03/26–04/21/01	78	1.66	1.48
H2 F3	117	03/26–04/21/01	77	1.40	1.32
H2 F4	104	03/26–04/21/01	78	0.53	0.64
H2 F5	111	03/26–04/21/01	78	1.23	1.16
H2 F6	102	03/26–04/21/01	79	1.08	0.96
H3 F1	112	07/20–07/31/01	80	1.17	1.12
H3 F2	101	07/20–07/31/01	80	1.11	0.96
H3 F3	112	07/20–07/31/01	79	1.07	1.00
H3 F4	80	07/20–07/31/01	80	0.95	0.72
H3 F5	118	07/20–07/31/01	78	1.20	1.16
H3 F6	108	07/20–07/31/01	79	1.07	1.16
H4 F1	109	09/15–09/27/01	76	0.91	1.08
H4 F2	128	09/15–09/27/01	77	1.62	1.36
H4 F3	92	09/15–09/27/01	78	1.48	1.08
H4 F4	106	09/15–09/27/01	78	2.38	1.44
H4 F5	112	09/15–09/27/01	78	2.00	1.64
H4 F6	103	09/15–09/27/01	78	2.47	1.40

*Home range estimates are based on minimum convex polygons (MCP) and traversed 20×20 m grid cells. Individual numbers denote study plot and sex. H1, undisturbed forest; H2, slightly disturbed; H3, intermediate disturbance; H4, heavy disturbance; M, male; F, female.

Each tarsier was radiotracked over the course of about 2 weeks (Table II). Tracking was conducted between 0400–0630 (six sessions per animal), 1800–2200 (three sessions per animal), or overnight from 1800–0600 (once per animal), yielding a total of 65–80 locations per tarsier (Table II). An incremental analysis of ranges showed that this number of fixes is sufficient to adequately sample the tarsiers' home ranges [Merker, 2003].

The position of an animal was estimated by triangulating [Kenward, 2001; White & Garrott, 1990] two consecutive bearings obtained within 2 min from different points that were spaced at least 30 m apart. During regular sessions, each animal was located every 40 min. During overnight tracking, each tarsier was radiotracked every 15 min, for about 48 fixes per night. In undisturbed forest (H1), males and females of mated pairs were tracked simultaneously. Special attention was paid to include individuals of all adjacent groups in each plot in the data set.

Nightly path lengths (or night ranges) were calculated by summing all distances between consecutive locations, which were obtained during overnight tracking. Home range sizes were calculated using minimum convex polygons (MCPs) and grid cell counts [Bearder & Martin, 1980; White & Garrott, 1990]. For the latter, the sum of the areas of 20×20 m cells in which the tarsiers were located gave the total range estimate.

To estimate seasonal effects on ranging patterns of Dian's tarsiers, the following parameters were compared between different months and seasons: 1) monthly rainfall, 2) insect abundance, and 3) home range sizes of selected individuals.

Precipitation was measured using a standard rain gauge placed at the Kamarora field station. Insect abundance was estimated by counting individuals >1 cm that were attracted to a strong kerosene pressure lantern within 5 min, and recording the number of vocalizing insects within a 10 m radius around the sample point within 5 min. This procedure was performed at eight sample points per habitat (with three replicates within 1 week). For a detailed description of the methods used, see Merker [2003] and Merker et al. [2005]. In April 2001, two females in undisturbed forest (H1F4 and H1F5) were tracked during two morning and two evening sessions (within 3 days). The resulting ''3-day ranges'' (MCPs) were compared with the areas used by these tarsiers during the first equivalent sessions when they were regularly tracked in early November 2000.

In intermediately disturbed habitat (H3), the control tracking included six morning and three evening sessions (within 10 days) for three female tarsiers (H3F3, H3F4, and H3F5) in July and September 2001. A more elaborate study design, including a plan to radiotrack tarsiers in undisturbed habitat over much longer periods, was impossible to execute due to vast forest encroachment in 2001 resulting from clearcut logging of the ranges of the respective animals.

STATISTICA for Windows 5.5 (StatSoft Inc., Tulsa, OK) was used for statistical analyses. The data were tested for normality by means of the Kolmogorov-Smirnov test. The paired-sample t-test and one-way and two-way analyses of variance (ANOVAs) with a least significant difference post hoc test were used to detect significant differences between habitats. All tests were two-tailed [Sokal & Rohlf, 1995].

RESULTS

Home Ranges

Table II shows the basic radiotracking data and home range sizes of the 30 focal *T. dianae* individuals. Range estimates are given using MCPs and grid cell counts. Generally, both methods produced very similar means for small ranges. For larger home ranges with the tarsier locations spaced further apart, the values diverged, with higher estimates drawn from the MCP method. For the purpose of simplicity, however, only the more widely used MCPs are illustrated, and values obtained using this method are presented in the following text.

The home ranges of males and females in undisturbed forest overlapped extensively among mated pairs, but only slightly between individuals of different groups (Fig. 2). Range size did not significantly differ between the sexes (paired-sample t-test, $t = 0.67$, $df = 5$, $P = 0.54$; Fig. 3); however, male ranges (1.77 ha) tended to be slightly larger than female ranges (1.58 ha). In Fig. 4, female home ranges in four habitat types are illustrated. In H3 and H4, two females of the same group were tracked. In both cases these animals shared most of their home ranges with the other group member. The overlap between individuals of
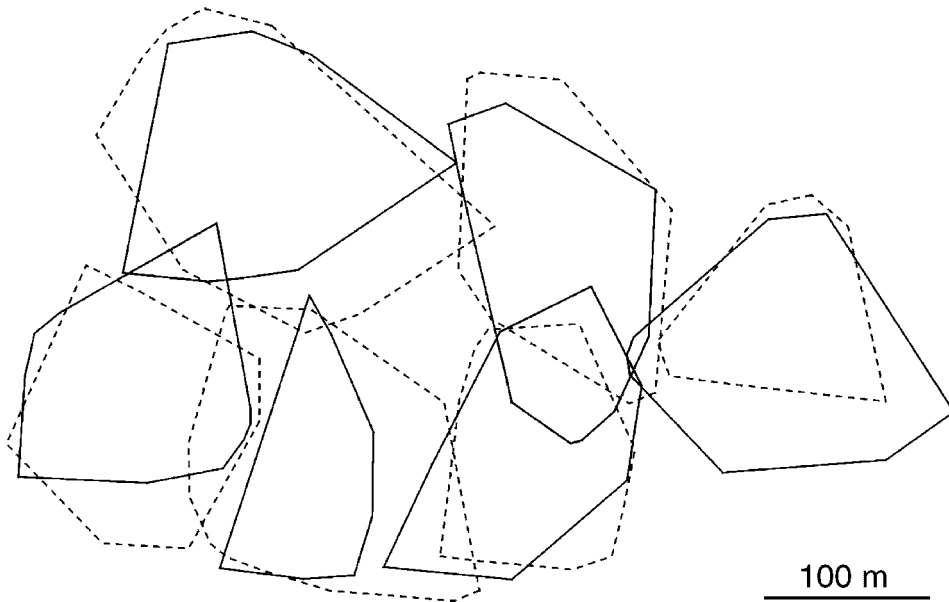
Fig. 2. Home ranges of six adjacent mated pairs of *T. dianae* in undisturbed forest (H1) of Lore-Lindu National Park. Solid line = female; dashed line = male.
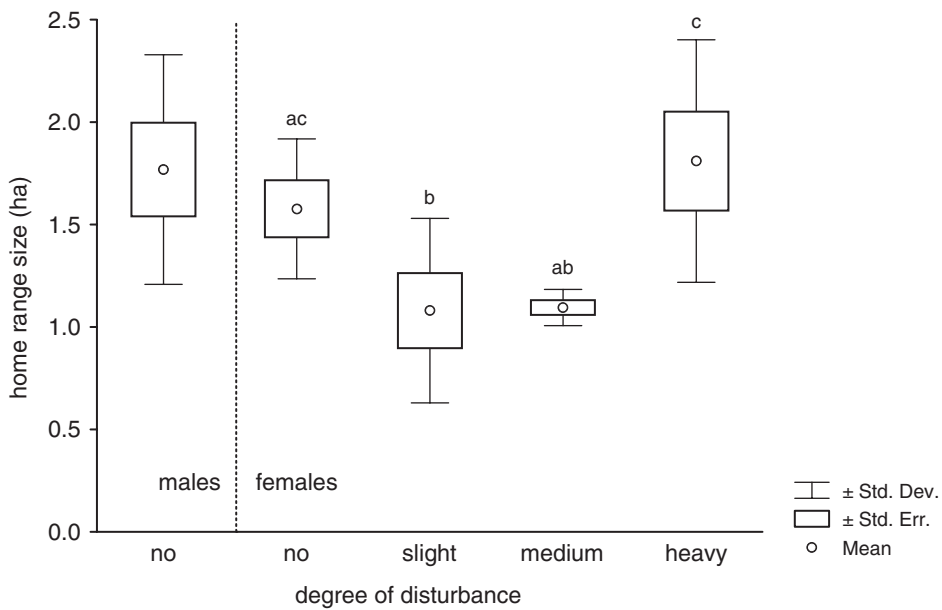

Fig. 3. Home range sizes of *T. dianae* in four study plots (H1–H4) along a gradient of human disturbance (n = 6 for each category). Different letters denote significant differences between plots (ANOVA, least significant difference test, $P < 0.05$).

different social units was small. Although most tarsier groups preferred to use one specific sleeping site (strangling fig, bamboo, or dense shrubs) within their range, some of them regularly used two or more of these sites. The tarsiers most often chose to spend the daylight hours close to the boundary of their home ranges (Fig. 4).

The size of female home ranges varied significantly between habitat types (ANOVA, $F_{3,20} = 4.66$, $P = 0.01$; Fig. 3), with the smallest ranges in slight and intermediate disturbance regimes. The proportion of home ranges traveled per night also differed between the habitats (ANOVA, $F_{3,20} = 3.91$, $P = 0.02$; Table III). In slightly and intermediately disturbed habitats, females covered slightly less than half of their total home range in a single night. In undisturbed and heavily disturbed habitats, female tarsiers used 30% and 35%, respectively, of their ranges during their nightly forays. The males in undisturbed forest traveled an even smaller fraction of their home range during single nights.
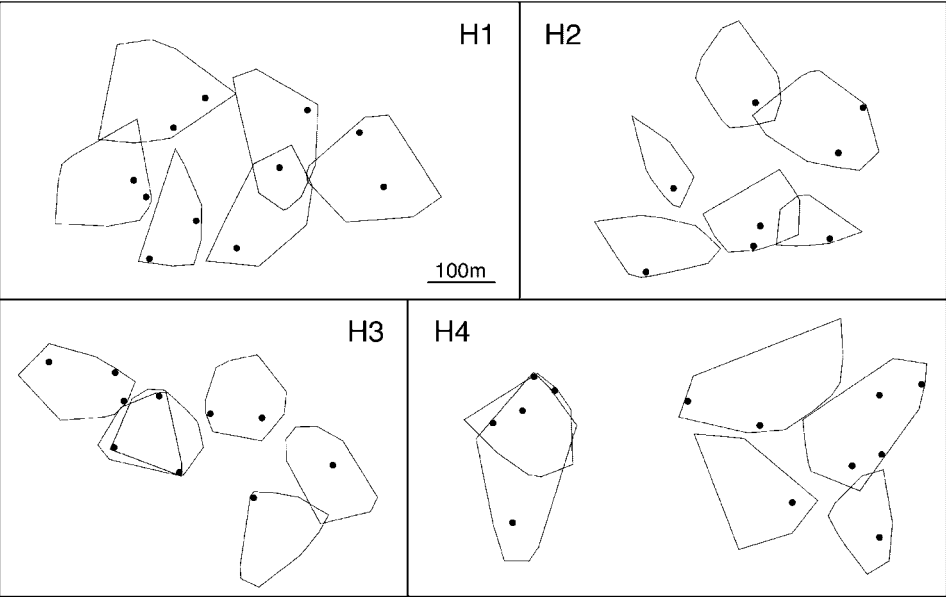

Fig. 4. Home ranges of female *T. dianae* in the four study plots. Individuals of all neighboring groups are represented (H1 and H2: six females of six groups; H3 and H4: six females of five groups). Black dots mark frequently used sleeping sites.

TABLE III. Proportion of Home Range Traversed During Single Nights[*]

Plot no./degree of disturbance	Sex (n)	Proportion of home range used per night
H1–no	M (6)	0.25 ± 0.07
H1–no	F (6)	0.30 ± 0.09[a]
H2–slight	F (6)	0.48 ± 0.09[b]
H3–intermediate	F (6)	0.41 ± 0.11[ab]
H4–heavy	F (6)	0.35 ± 0.09[a]

[*]Different letters denote significant differences between plots (ANOVA, least significant differences test, $P < 0.05$).

Nightly Path Length

Male and female path length in H1 did not significantly differ from each other (paired-sample t-test, $t = 0.26$, $df = 5$, $P = 0.80$; Fig. 5). Although female path lengths were not significantly different between habitats (ANOVA, $F_{3,20} = 1.45$, $P = 0.26$; Fig. 5), there was a trend toward greater travel distances in disturbed areas compared to natural forest.

Activity Rhythm

The average activity rhythm of female *T. dianae* between 1800 and 0600 hr is depicted in Fig. 6. The animals moved farthest shortly after dusk and also just before dawn. The data in Fig. 6 were pooled from 24 females in four habitats. All of the tarsiers exhibited periods of complete (motional) inactivity, but not at a specific time of night.

Seasonality

Rainfall was found to be slightly seasonal, with the least amounts of rain observed during May–September 2001 (Fig. 7). However, during the months of data collection, the monthly precipitation never dropped below 100 mm. Insect abundance in undisturbed forest (H1) did not significantly differ between May and October 2001 (two-way ANOVA, $F_{1,12} = 0.022$, $P = 0.884$ for light trap, $F_{1,12} = 0.788$, $P = 0.392$ for vocalizations; Fig. 7). In intermediately disturbed forest (H3), the number of insects attracted by light (two-way ANOVA, $F_{2,21} = 0.384$, $P = 0.686$), and the number of vocalizing insects (two-way ANOVA, $F_{2,21} = 2.113$, $P = 0.146$) were not significantly different for July, September, and October 2001 (Fig. 7).
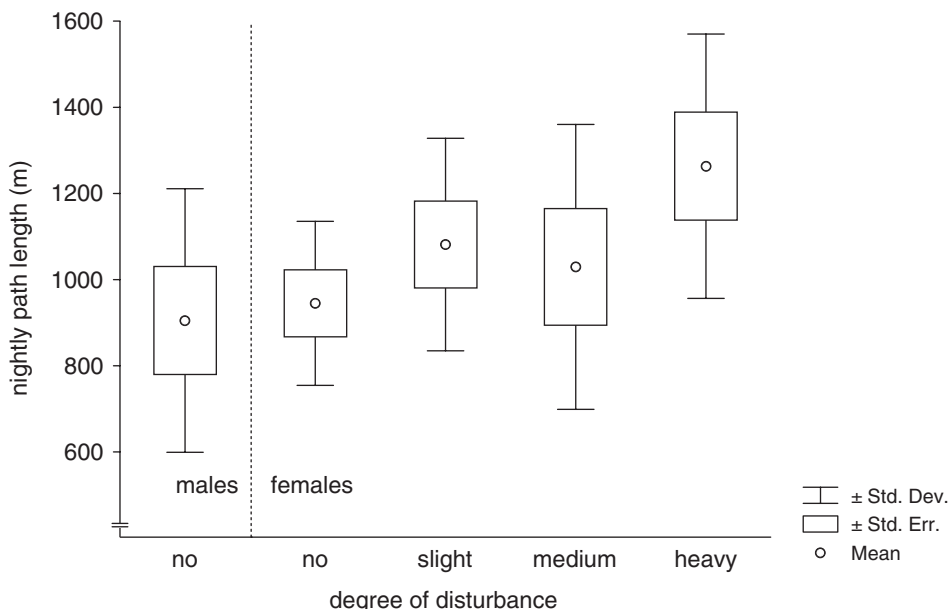

Fig. 5. Nightly path lengths of *T. dianae* in four study plots (H1–H4) along a gradient of human disturbance (n = 6 for each category).
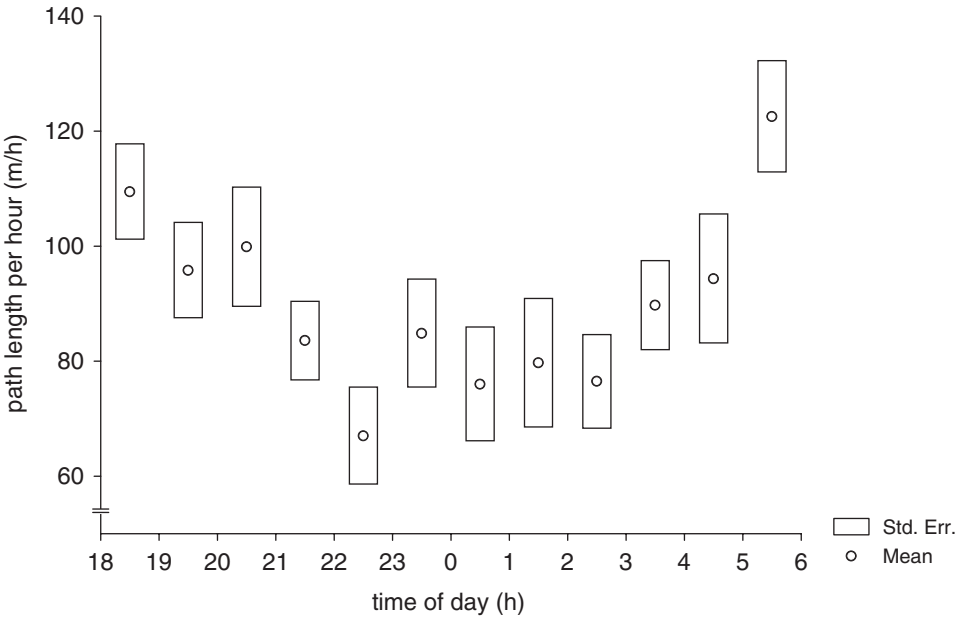
Fig. 6. Activity rhythm of female *T. dianae* between 1800 and 0600 hr, displayed as path length per hour (n = 24, pooled from four study plots (H1–H4)).
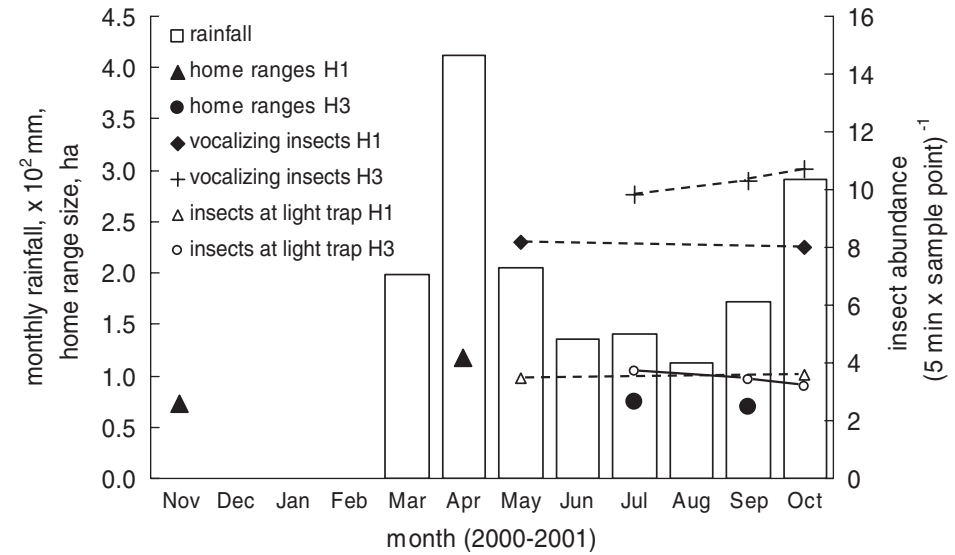

Fig. 7. Seasonal changes in rainfall, insect abundance, and home range sizes of Dian's tarsiers. Range sizes reflect 3-day ranges of two females in undisturbed forest (H1) and 10-day ranges of three females in intermediately disturbed forest (H3).

For two females in undisturbed forest (H1), an average 60% larger 3-day range was observed in April 2001 (0.72 ha) compared to November 2000 (1.18 ha; Fig. 7). For three females in intermediately disturbed habitat (H3), the size of

10-day ranges did not differ between July (0.75 ha) and September 2001 (0.70 ha; Fig. 7). Because of the small sample size, no statistical tests were performed.

DISCUSSION

Home Range

Home range estimates based on MCPs strongly depend on the number of locations utilized to generate the estimates [White & Garrott, 1990]. To overcome this major disadvantage of the MCP method, and to be able to conclusively compare the study habitats in this respect, two steps were taken: 1) an incremental analysis of home range size with increasing numbers of locations was performed (the number of necessary bearings was oriented toward the resulting saturation curve [Merker, 2003]), and 2) all tarsiers were tracked about equally often (with minor exceptions; see Table II).

In undisturbed forest, both males and females of *Tarsius dianae* were radiotracked. Adult males used a slightly (not significantly) larger home range than their mates. A possible explanation for this marginal difference in range use lies in the Sulawesi tarsiers' social behavior. Although the concept that tarsiers are monogamous [MacKinnon & MacKinnon, 1980] was dismissed in the latter part of the last century, strong pair bonds in the frame of facultative polygyny form the basic social unit of the Sulawesi tarsiers' society [Gursky, 1995, 2000a,b, 2002a,b; Nietsch, 1993; Nietsch & Niemitz, 1992]. Group members are essentially synterritorial, and to secure reproductive access to the females in its group, the adult male does not need to cover an area greater than the combined ranges of its one to three mates. Considering the greater body weights and thus the higher energetic demands [Krebs & Davies, 1981] of males, a slightly larger male home range compared to female home range was expected. Since the male tarsiers engage in territorial behavior to a greater extent than do the females [Crompton & Andau, 1986; Nietsch, 1993], female ranges likely reflect the availability of resources better than the male ranges. Male activity patterns are more affected by social status and by the males' endeavors to secure paternity of the females' offspring. In this study, this is reflected in higher variances in home range sizes and nightly path lengths observed for males compared to females. As such, only females were chosen for a comparison of ranging patterns between habitats.

In this study, the home ranges of *T. dianae* (1.6–1.8 ha, n = 30) were found to be larger than the reported 0.5–0.8 ha (n = 4) for the same species radiotracked by Tremble et al. [1993], and smaller than the 2.3–3.1 ha (n = 13) described for *T. spectrum* [Gursky, 1998a, b, 2000c]. The different home range sizes reported in this and the two comparable studies can be attributed to 1) significant differences in sample size and radiotransmitter weight (3.9 g in this study compared to 11.5 g radios used by Tremble et al. [1993]), or 2) habitat differences (perhumid conditions in Kamarora compared to a slightly seasonal climate in north Sulawesi [Gursky, 1998a,b, 2000c]). Three main radiotracking studies have examined tarsiers outside of Sulawesi: Crompton and Andau [1986, 1987] described home ranges of 4.5–11.3 ha for *T. bancanus* on Borneo; Dagosto and Gebo [1997] radiotracked two *T. syrichta* males on the Philippines and reported home range estimates of 0.6 and 1.7 ha; and Neri-Arboleda et al. [2002] tracked the same species and found ranges of 2.5 ha for females and 6.5 ha for males. However, because of major differences in the forest types and social systems involved in those studies, no detailed analysis of differences in ranging patterns between *T. dianae* and those species is given here.

In this study, *T. dianae* females traveled areas of 1.08–1.81 ha, depending on the habitat type. Home ranges were smallest in slightly disturbed forest, and largest in the heavily disturbed mixed plantation. As with other species [Bolen & Robinson, 1995; Heiduck, 2002], tarsiers range and defend smaller areas when resources are plentiful than they do when available food or other essentials, such as locomotor supports or sleeping trees, are scarce. By optimizing their net energy uptake (i.e., the gross energy uptake minus costs of foraging), the animals can attain high fitness values [Begon et al., 1996; Krebs & Davies, 1981]. Thus, the slightly and intermediately disturbed plots can be considered high-quality habitats for *T. dianae*. This is commensurate with increased prey abundance in these areas (Table I) caused by small gaps in the canopy, denser undergrowth, and small forest gardens. On the heavily altered plantation, however, tarsiers have had to adapt their ranging patterns to low insect abundance (Table I), partly because of the application of herbicides, which eradicates breeding substrates for insects, and a decreased density of locomotor supports [Merker, 2003]. The tarsiers' dependence on resource availability has also been demonstrated by Gursky [2000c]: *T. spectrum* in north Sulawesi used larger home ranges in the dry season when prey abundance was low than in the wet season when insects were plentiful. For *T. dianae* in central Sulawesi, however, no significant seasonal effects on ranging patterns were found (see below).

Nightly Path Length

Nightly path lengths of *T. dianae* in Kamarora (905–1,263 m) lie well within the limits shown for other small, arboreal, and nocturnal primates (e.g., tarsiers [Crompton & Andau, 1986, 1987; Gursky, 1998b, 2000c; Neri-Arboleda et al., 2002], and galagos and lemurs [Doyle & Bearder, 1977; Fietz & Ganzhorn, 1999; Harcourt & Nash, 1986]). Males and females in H1 traveled about equal distances per night. Considering the greater body weight and thus higher energy demands of males, the rationale for this remains unclear. One explanation may be a higher prey capture rate for male tarsiers. Possibly, they are more successful hunters and need to cover relatively smaller distances than their mates in search of sufficient food. As mentioned above, the slightly larger home ranges in males may be due to social, rather than energetic, factors.

The night ranges of female *T. dianae* did not differ significantly between habitats. However, a trend of increasing travel distances per night with the degree of disturbance was found. In heavily disturbed habitat, tarsiers covered an approximately 30% greater distance compared to their undisturbed conspecifics. The animals in slightly and intermediately disturbed forest also traveled farther per night than those under pristine conditions did; however, their home ranges were smaller. Consequently, tarsiers in these habitats used a larger fraction of their range during single nights than in undisturbed forest (Table III).

Taking insect abundance into account, a slightly greater travel distance in pristine than in disturbed forest was expected. The reason for the actual finding–that tarsiers in H1 moved the least per night–remains to be determined.

Activity Rhythm

Niemitz [1984] and Crompton and Andau [1987] reported two peaks in leaping activity for *T. bancanus* on Borneo. Neri-Arboleda et al. [2002] observed that *T. syrichta* in the Philippines was most active shortly after dusk, and Nietsch [1993] described a two-peak activity rhythm for *T. spectrum* in northern Sulawesi. A strepsirrhine that exhibits the same pattern is *Galagoides*

zanzibaricus, which was found to move most at the beginning and end of the night [Harcourt & Nash, 1986]. This study on *T. dianae* revealed a very similar activity rhythm, recorded as the distance female tarsiers covered per unit time. An early activity peak shortly after the animals left the sleeping site marks the tarsiers' endeavor to quickly reach their most profitable hunting grounds. Very often, however, the animals traversed their complete home range before they started to forage. Considering the finding that sleeping sites were chosen mostly near the periphery of the ranges, this may also be interpreted as territorial behavior (e.g., renewing scent marks at opposite ends of the home range). This increased activity at the beginning of the night was followed by periods of travel or complete rest. However, apart from a general period of decreased activity after about 4 hr of leaping, individual tarsiers rested and moved without a pattern until the late hours of the night. Shortly before dawn, and most often triggered by their territorial duet songs, *T. dianae* usually covered enormous distances when they returned directly to the group sleeping site. During that time, individual tarsiers were observed to move more than 100 m in 15 min [Merker, 2003]. The activity rhythm of males in undisturbed forest was found to be very similar to that of the females [Merker, 2003].

Seasonality

In the following text, evidence is presented to explain why seasonal effects do not offset the results presented above. Although seasonality in precipitation was observed, rainfall exceeded 100 mm in every month during data collection. Whitmore [1984], citing Mohr [1933], regarded months with this amount of rain as wet (i.e., precipitation exceeds evaporation). Generally, the region of Kamarora is considered perhumid [Whitmore, 1984; Whitten et al., 2001]. This contrasts with the climatic conditions at Tangkoko Nature Reserve in north Sulawesi, where Gursky [2000c] observed that behavioral patterns of *T. spectrum* varied with the seasons. Thus, the amount of rainfall is not a priori considered a major influential factor in the ranging patterns of tarsiers at Kamarora.

Insect abundance did not change significantly over the course of data collection in 2001. Therefore, seasonal variation in prey abundance cannot be deemed a major influential factor in Dian's tarsiers' ranging patterns.

As stated above, a more comprehensive study design had to be abandoned because of intensive logging in the focal area. However, although seasonal variation in the tracked tarsiers' ranges was observed, the following results do not contradict the findings on habitat specificity of ranging patterns: 1) Radiotelemetry in September 2001 revealed significantly larger female ranges in heavily disturbed habitat (H4) than in H2 (April 2001) and H3 (July 2001). However, 10-day control tracking of three females in H3 showed that range sizes did not differ between July and September 2001. 2) In November 2000, radiotelemetry revealed significantly or nearly significantly *larger* female ranges in undisturbed forest (H1) than in H2 (April 2001) and H3 (July 2001). In contrast, 3-day control tracking of two females in H1 indicated *smaller* ranges in November 2000 compared to April 2001. Thus, radiotracking in different months is very unlikely to have accounted for the variation between habitats. It may even have led to an *understatement* of the effect of habitat structure. However, 3 days of data collection are surely not sufficient to make a good estimate of a tarsier's home range. It remains unclear whether the two control animals in H1 changed their range size between November 2000 and April 2001 or just utilized differently sized fractions of their total range during the 3 days of

control tracking. In summary, neither rainfall patterns nor seasonal variation in prey abundance or home range sizes contradict the main findings presented in this study.

CONCLUSIONS

In this study, neither home range size nor path length differed significantly between male and female Dian's tarsiers. However, female ranges and nightly path lengths varied between differentially disturbed habitats. This is mainly attributed to the availability of vital resources, such as food or locomotor supports. The small ranges and nightly travel distances in areas with small-scale agroforestry indicate that even disturbed habitats may still provide good living conditions for tarsiers. Considering the loss of pristine forest on Sulawesi, conservation efforts should also be directed toward encouraging this type of land use over more destructive forms of anthropogenic activity, such as logging.

ACKNOWLEDGMENTS

References

Bearder SK, Martin RD. 1980. The social organization of a nocturnal primate revealed by radio-tracking. In: Amlaner CJ, MacDonald DW, editors. A handbook on biotelemetry and radio-tracking. Oxford: Pergamon Press. p 633–648.

Begon M, Harper JL, Townsend CR. 1996. Ecology: individuals, populations and communities. 3rd ed. Oxford: Blackwell Science. 1068p.

Bolen EG, Robinson WL. 1995. Wildlife ecology and management. 3rd ed. Englewood Cliffs, NJ: Prentice Hall. 620p.

Chapman CA, Lambert JE. 2000. Habitat alteration and the conservation of African primates: case study of Kibale National Park, Uganda. Am J Primatol 50:169–185.

Crompton RH, Andau PM. 1986. Locomotion and habitat utilization in free-ranging *Tarsius bancanus*: a preliminary report. Primates 27:337–355.

Crompton RH, Andau PM. 1987. Ranging, activity rhythms, and sociality in free-ranging *Tarsius bancanus*: a preliminary report. Int J Primatol 8:43–71.

Dagosto M, Gebo DL. 1997. Preliminary study of the Philippine tarsier in Leyte. Asian Primates 6:4–8.

Doyle GA, Bearder SK. 1977. The galagines of South Africa. In: Prince Rainier III of Monaco, Bourne GH, editors. Primate conservation. New York: Academic Press. p 1–35.

Eudey A, Members of the Primate Specialist Group. 2000. *Tarsius dianae*. In: IUCN 2004. 2004 IUCN Red List of Threatened Species. www.redlist.org; downloaded on 24 January 2005.

Fietz J, Ganzhorn JU. 1999. Feeding ecology of the hibernating primate *Cheirogaleus medius*: how does it get so fat? Oecologia 121:157–164.

Ganzhorn JU. 1999. Lemurs as indicators for assessing biodiversity in forest ecosystems of Madagascar: why it does not work. In: Kratochwil A, editor. Biodiversity in ecosystems. Dordrecht: Kluwer Academic. p 163–174.

Gursky S. 1995. Group size and composition in the spectral tarsier, *Tarsius spectrum*: implications for social organization. Trop Biodivers 3:57–62.

Gursky S. 1998a. Conservation status of the spectral tarsier *Tarsius spectrum*: population density and home range size. Folia Primatol 69(suppl 1):191–203.

Gursky S. 1998b. Effects of radio transmitter weight on a small nocturnal primate. Am J Primatol 46:145–155.

Gursky S. 2000a. Sociality in the spectral tarsier, *Tarsius spectrum*. Am J Primatol 51:89–101.

Gursky S. 2000b. Allocare in a nocturnal primate: data on the spectral tarsier, *Tarsius spectrum*. Folia Primatol 71:39–54.

Gursky S. 2000c. Effect of seasonality on the behavior of an insectivorous primate, *Tarsius spectrum*. Int J Primatol 21:477–495.

Gursky S. 2002a. Determinants of gregariousness in the spectral tarsier (prosimian: *Tarsius spectrum*). J Zool 256:401–410.

Gursky S. 2002b. The behavioral ecology of the spectral tarsier, *Tarsius spectrum*. Evol Anthropol 11:226–234.

Harcourt CS, Nash LT. 1986. Social organization of galagos in Kenyan coastal forests: I. Galago zanzibaricus. Am J Primatol 10:339–355.

Heiduck S. 2002. The use of disturbed and undisturbed forest by masked titi monkeys *Callicebus personatus melanochir* is proportional to food availability. Oryx 36:133–139.

Johns AD, Skorupa JP. 1987. Responses of rain-forest primates to habitat disturbance: a review. Int J Primatol 8:157–191.

Kenward RE. 2001. A manual for wildlife radio tagging. 2nd ed. London: Academic Press. 311p.

Krebs JR, Davies NB. 1981. An introduction to behavioural ecology. Oxford: Blackwell Scientific. 292p.

MacKinnon J, MacKinnon K. 1980. The behavior of wild spectral tarsiers. Int J Primatol 1:361–379.

Merker S, Mühlenberg M. 2000. Traditional land-use and tarsiers–human influences on population densities of *Tarsius dianae*. Folia Primatol 71:426–428.

Merker S. 2003. Vom Aussterben bedroht oder anpassungsfähig? Der Koboldmaki *Tarsius dianae* in den Regenwäldern Sulawesis. Ph.D. dissertation, Georg August Universität Göttingen, Göttingen, Germany. 138p. Available online at http://webdoc.sub.gwdg.de/diss/2003/merker.

Merker S, Yustian I, Mühlenberg M. 2004. Losing ground but still doing well–*Tarsius dianae* in human-altered rainforests of central Sulawesi, Indonesia. In: Gerold G, Fremerey M, Guhardja E, editors. Land use, nature conservation and the stability of rainforest margins in southeast Asia. Heidelberg: Springer. p 299–311.

Merker S, Yustian I, Mühlenberg M. 2005. Responding to forest degradation: altered habitat use by Dian's tarsier *Tarsius dianae* in Sulawesi, Indonesia. Oryx 39:189–195.

Mohr ECJ. 1933. De Bodem der Tropen in Het Algemeen en die van Ned.-Indië in Het Bijzonder. Amsterdam: DeBussy. 300p.

Napier JR, Napier PH. 1967. A classification of primate locomotor behavior. In: Napier JR, Napier PH, editors. A handbook of living primates. New York: Academic Press. p 385–391.

Neri-Arboleda I, Stott P, Arboleda NP. 2002. Home ranges, spatial movements and habitat associations of the Philippine tarsier (*Tarsius syrichta*) in Corella, Bohol. J Zool 257:387–402.

Niemitz C. 1984. Activity rhythms and use of space in semi-wild Bornean tarsiers, with remarks on wild spectral tarsiers. In: Niemitz C, editor. Biology of tarsiers. Stuttgart/New York: Gustav Fischer. p 85–115.

Niemitz C, Nietsch A, Warter S, Rumpler Y. 1991. *Tarsius dianae*: a new primate species from central Sulawesi (Indonesia). Folia Primatol 56:105–116.

Nietsch A, Niemitz C. 1992. Indication for facultative polygamy in free-ranging *Tarsius spectrum* supported by morphometric data. In: XIVth Congress of the International Primatology Society, Strasbourg, France. p 318.

Nietsch A. 1993. Beiträge zur Biologie von *Tarsius spectrum* in Sulawesi. Ph.D. dissertation, Freie Universität Berlin, Berlin, Germany. 140p.

Nijssen EC, Sterck EHM. 2000. The effects of human disturbance on Callitrichid social organization. Folia Primatol 71:235.

Sokal RR, Rohlf FJ. 1995. Biometry. 3rd ed. New York: Freeman and Co. 887p.

Tremble M, Muskita Y, Supriatna J. 1993. Field observations of *Tarsius dianae* at Lore Lindu National Park, central Sulawesi, Indonesia. Trop Biodivers 1:67–76.

White GC, Garrott RA. 1990. Analysis of wildlife radio-tracking data. San Diego: Academic Press. 383p.

Whitmore TC. 1984. Tropical rain forests of the Far East. 2nd ed. Oxford: Oxford University Press. 352 p.

Whitten AJ, Mustafa M, Henderson GS. 2001. The ecology of Sulawesi. Singapore: Periplus Editions. 754p.