NATURAL HISTORY OBSERVATIONS OF THE FLYING LIZARD, *DRACO VOLANS SUMATRANUS* (AGAMIDAE, SQUAMATA) FROM SARAWAK, MALAYSIA

Akira Mori and **Tsutomu Hikida**

ABSTRACT.- A field study of *Draco volans sumatranus* was conducted in Sarawak, Malaysia. Adult females were significantly larger than adult males in snout-vent length (SVL). Clutch size varied, independent of maternal SVL, from one to five. The lizards were strictly arboreal and diurnally active with two peaks of activity before and after noon. There were no differences in perch height between the sexes. The number of males observed was correlated with air temperature. Lack of thermoregulatory behavior and the relationship between body temperature and air temperature suggest that the flying lizard is thermally passive. Home ranges of resident males consisted of one to three adjacent trees, which wholly overlapped with those of one to three females. In most cases, resident males were larger than intruder males both in SVL and dewlap length.

INTRODUCTION

The family Agamidae is the Old World counterpart of New World Iguanidae. Lizards in these two families exhibit remarkable similarities in morphological structure, behavior patterns, and ecological exploitation (Stamps, 1977; Avery, 1982), providing excellent material for the comparative study of evolutionary processes. However, compared to iguanids, there have been few ecological and behavioral studies on agamids.

Flying lizards of genus *Draco* Linnaeus, 1758 are arboreal agamid lizards, consisting of about sixteen species distributed in South India and South-East Asia (Musters, 1983). The most unusual behavioral character of these lizards is their gliding ability. In fact, *Draco* is the only extant reptile that is a "true" glider (Oliver, 1951; Klingel, 1965). *Draco* species have a wing-like structure formed from a membrane of skin stretched over greatly elongated ribs (Colbert, 1967; John, 1970a). The wings are usually folded along the body unless the lizards are gliding or performing social displays (Hairston, 1957; Alcala, 1967). Males have a large gular appendage, a dewlap, which is used for social displays (Alcala, 1967; John, 1967a). There are several reports concerning the gliding habit of *Draco* (e.g., Lederer, 1932; Hairston, 1957; Herre, 1958; Klingel, 1965), but little has been reported about their natural history and ecology since

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a series of publications of John (e.g., John, 1962, 1967a, b, 1970b) and a study of Alcala (1967).

Over two visits to Sarawak, Malaysia, we conducted a field study of the flying lizard, *D. volans sumatranus* Schlegel, 1844. This subspecies is common in the southern part of Sarawak and inhabits relatively open areas. This paper provides basic ecological and behavioral information on activity, thermal biology and spacing pattern of this subspecies.

MATERIALS AND METHODS

Field work was carried out in a small park (ca. 80 x 130 m) at Red Bridge, Matang (1° 35'N, 110° 13'E), 15 km north-west of Kuching, Sarawak, Malaysia. The park was located near a lowland tropical rain forest. Northern and eastern sides of the park were bordered by a small river from the adjacent forest (Fig. 1). About 40 trees (10-25 m high) and several clumps of bamboo (less than 5 m high) were scattered in the park. There were no dominant trees, except the bamboo, in the park: most of them are different species. The floor of the park was covered with cultivated grass, which was mowed periodically. There were few burrows or stones on the ground. Direct sunlight penetrated to almost the entire floor. Observations were made mainly in the southern half of the park during the first survey from 4 to 29 January 1990. The entire area was surveyed during the second period from 15 December 1990 to 8 January 1991. December and January are months of the wet season in Sarawak.

The field study utilized three methods: capture-mark-release, census, and direct behavioral observation. During the first two to three days of each survey, as many lizards as possible were captured, measured, marked for individual recognition by toe clipping and color painting, and released at the base of the trees where they were first seen as soon as possible. Lizards were induced to glide and to land at the bases of trees or on the ground, by knocking them down from above with a pliable tip of a long fishing rod. The following data were recorded for each individual: (1) cloacal body temperature (BT) and ambient air temperature in shade 1 m above the ground at the base of the trees (AT) measured by a thermistor (Takara, Digimulti D611); (2) time; (3) weather condition; (4) snout-vent length (SVL); (5) dewlap length (DL) of males measured from the tip of the snout to the posterior tip of dewlap in folded state; (6) sex determined by the presence or absence of a large yellow dewlap characteristic of males; (7) perch tree; (8) perch height (crude estimation to nearest 0.5 m); (9) light condition of the perch site (i.e., full sun, filtered sun, or shade) and (10) posture and behavior performed when the lizards were first sighted.

Censuses were carried out in bouts while systematically walking through the study site. Each bout lasted 30 to 50 min, and individuals were located by carefully searching each tree by means of binoculars (x 8). A total of 27 censuses (1000 - 1200 h 10 times, 1200 - 1400 h eight times, 1400 - 1700 h nine times) were made in the southern half of the study site during 11 days of the first survey. In the second survey, the entire area was censused on 11 mornings (0900 - 1200 h), and on one afternoon (1500 - 1600 h). At the beginning of each census, air temperature was measured and cloud amount was estimated (expressed as integers 0 to 10; 0 = less than 5 % of the sky was clouded over, 10 = entirely clouded over). For each lizard, above variables (2), (3), (6), (7), (8), (9), and (10) were recorded as well as (11) identification number (Id.no.) marked by color painting. All lizards observed during censuses were regarded as "ac-
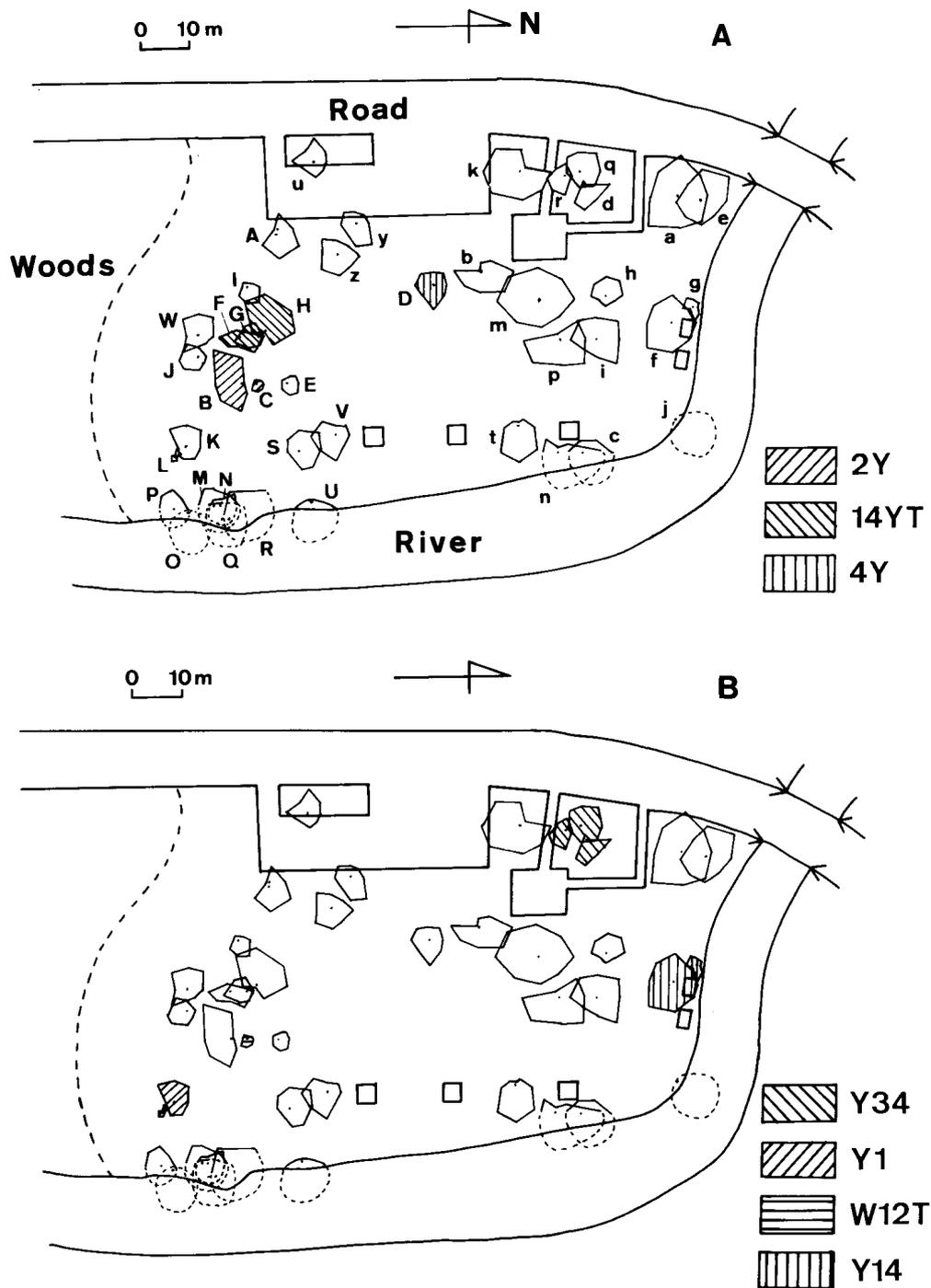
Fig.1. Schematic map of the study area showing arrangements of trees (except bamboo and small trees less than 3 m high). Location of trunk and overhead canopy are indicated by a small dot and an octagonal figure, respectively. A, Trees occupied by three resident male *Draco volans sumatranus*, 2Y, 14YT, and 4Y observed during the first survey. Alphabetical letters indicate identification numbers (Id.no.) of trees; B, Trees occupied by four resident male *D. v. sumatranus*, Y34, Y1, W12T, and Y14 observed during the second survey.

tive". Even if unmarked lizards were found, they were not captured during censuses.

Observations of lizard behavior were made with the aid of binoculars. Some lizards were continuously observed as long as possible. Detailed descriptions of behavior are presented elsewhere (Mori & Hikida, 1994). All field observations were done between 0900 h and 1800 h.

During the last two or three days of each survey, as many lizards as possible were captured, and variables (1) - (10) were recorded again. Lizards were then sacrificed to be preserved specimens and brought back to our laboratory, where the reproductive state of each animal was examined. Criteria for sexual maturity were: enlarged testis or epididymis in males; developed, yolked ovarian follicles, thickened muscular oviducts, or oviductal eggs in females.

RESULTS

Morphometrics.- Twenty-five males and 15 females were dissected to determine the reproductive condition. The smallest male with enlarged testis or epididymis was 59.6 mm in SVL, and the largest one without such features was 57.5 mm. The smallest female determined as sexually mature was 73.4 mm in SVL, and the largest immature female was 52.1 mm. We have therefore used the SVL of 59 mm and 70 mm as the criterion of sexual maturity for other males and females, respectively, that were marked but not recaptured. Adult females were significantly larger in SVL than adult males (males, n = 23, $\bar{x}$ = 71.7, SE = 0.80; females, n = 28, $\bar{x}$ = 76.0, SE = 0.43; U-tests, z = 3.90, P < 0.001). The DL was significantly correlated with SVL in both juvenile and adult males (juvenile, Y = 1.48X—1.34, r = 0.95, P < 0.01; adult, Y = 0.81X—0.11, r = 0.86, P < 0.001, log transformed data). The slope of SVL vs. DL was significantly different between juvenile and adult males (ANCOVA, df = 1, 23, F = 9.75, P < 0.01). Eleven out of 12 adult females had one to five yolked ovarian follicles or oviductal eggs ($\bar{x}$ = 3.5). There was no significant relationship between clutch size and SVL of females (Kendall rank-order correlation test, τ = — 0.2, P > 0.05).

Diurnal activity.- A total of 186 lizards consisting of 60 males, 78 females, and 48 unknown sexes were observed during censuses. The average number of lizards per census fluctuated throughout a day, with two peaks, one around noon and the other in the afternoon (Fig. 2). There were no apparent differences in the fluctuation patterns between males and females.

All lizards perched on the trunks, branches or twigs of trees: no lizards were observed on the ground or on bamboo. There were no significant differences in perch height between males and females (male, n = 53, $\bar{x}$ = 6.8 m, SE = 0.38; female, n = 55, $\bar{x}$ = 6.5 m, SE = 0.32; U-tests, z = 0.31, P > 0.05: Fig. 3).

The relationships between air temperature, cloud amount, and the number of lizards observed during each census were examined, using partial correlation coefficients (Sokal & Rohlf, 1981). This analysis allowed us to test the influence of a variable (air temperature or cloud amount) on the number of lizards observed while holding another variable (cloud amount or air temperature) constant. The number of males was positively correlated with air temperature

Fig. 2

Fig. 3

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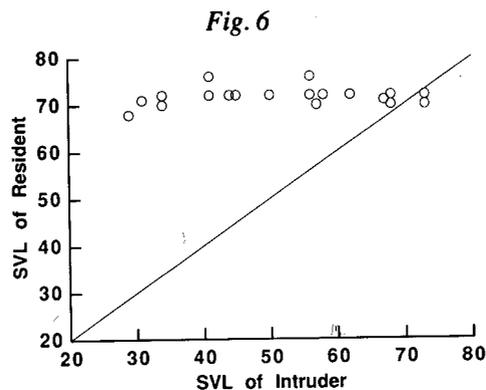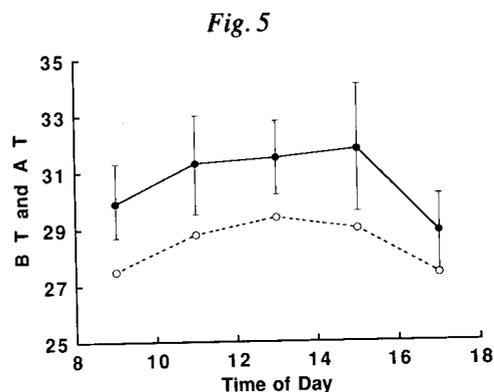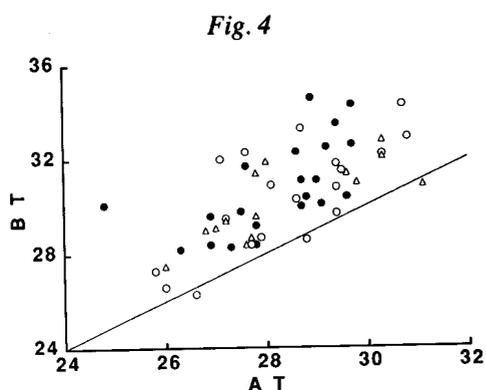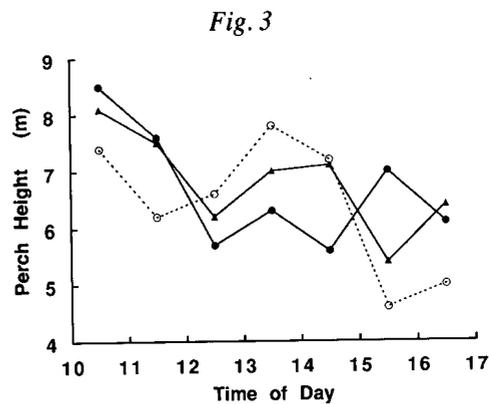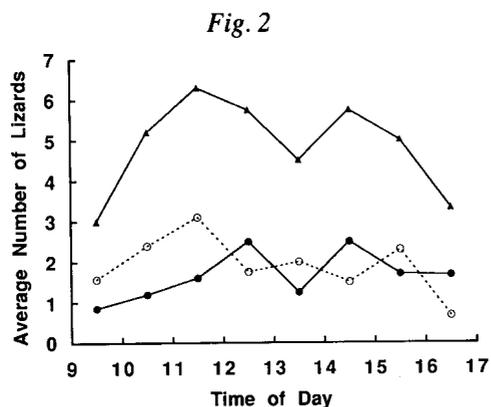
Figs. 2-6. 2, Daily changes in number of *Draco volans sumatranus* observed in censuses. Solid circle: male, open circle: female, triangle: total (including males, females, and animals with unidentified sexes); 3, Daily changes in perch height of *Draco volans suma tranus* observed in censuses. Only the data obtained during the first survey was shown. Solid circle: male, open circle: female, triangle: total (including males, females, and animals with unidentified sexes); 4, Relationship between air temperature (AT) and body temperature (BT) in *Draco volans sumatranus*. The line where body temperature is equal to air temperature is also shown. Solid circle: male, open circle: female, tirangle: juvenile; 5, Daily fluctuation of mean body temperature of *Draco volans sumatranus* (BT: solid line) and mean air temperature (AT: dashed line). Mean values were calculated for every two hours from 800h. Vertical lines represent 2SE; 6, Relationship of SVL between resident males and intruder males in *Draco volans sumatranus*. The line where SVL of residents is equal to that of intruders is also shown.

measured just before the census ($r = 0.46$, $t = 3.06$, $df = 35$, $P < 0.005$), but not with cloud amount ($r = 0.15$, $t = 0.89$, $df = 35$, $P > 0.05$). The number of females was not significantly correlated with either air temperature ($r = 0.18$, $t = 1.06$, $df = 35$, $P > 0.05$) or cloud amount ($r = 0.04$, $t = 0.23$, $df = 35$, $P > 0.05$).

Thermal activity.- For analyses of BT, data of recaptured individuals were not used, i.e., each data point indicates a different individual. There were no significant differences in BT among males, females, and juveniles (ANOVA, $df = 2$, $F = 0.38$, $P > 0.05$; male, $\bar{x} = 30.8$, female, $\bar{x} = 30.4$, juvenile, $\bar{x} = 30.2$). There were no significant differences in the regression of BT on AT among males, females, and juveniles (ANCOVA; slope, $df = 2$, 49, $F = 0.43$, $P > 0.05$; elevation, $df = 2$, 51, $F = 1.36$, $P > 0.05$). Thus all data were pooled for following analyses. The BT was significantly correlated with AT ($r = 0.68$, $P < 0.001$; Fig. 4). The slope was not significantly different from 1 ($df = 1$, 53, $F = 0.10$, $P > 0.05$), but BT was significantly higher than corresponding AT (paired t-tests; $t = 11.25$, $P < 0.001$). Daily changes in mean BT and AT were shown in Fig. 5. Fluctuation pattern of mean BT approximately corresponded to that of mean AT.

To examine the selection of the light condition of perch sites, census data recorded only in sunny weather were analyzed. Although some data were obtained from the same individuals, we used all data as independent variables because not all individuals could be identified. Forty-seven lizards out of 80 were perching in shade, whereas ten were in direct sunlight (Table 1). Males tended to perch more in direct or filtered sunlight than females (Fisher's exact probability test, $P < 0.05$). Few lizards were observed in sun or filtered sun between 1200 h and 1400 h (Table 2).

Table 1. The number of *Draco volans sumatranus* and light condition of perch sites observed in censuses.

Sex	Light condition		
	Sun	Filtered sun	Shade
Male	2	9	12
Female	1	5	24
Unknown	7	9	11
Total	10	23	47

Table 2. Daily pattern of the number of *Draco volans sumatranus* observed in censuses, and light conditions of their perch sites.

Light condition	Time of day								
	9	10	11	12	13	14	15	16	17
Sun	1	2	3	1	1	2	0	0	
Filtered sun	1	7	7	0	0	7	0	1	
Shade	4	8	8	11	8	5	1	2	
Total	6	17	18	12	9	14	1	3	

Home range.- Eight adult males, 13 adult females and nine juveniles (four males and five females) were marked in the first survey. Ten adult males, 11 adult females and 10 juveniles (six males and four females) were marked in the second survey. The daily appearance of each marked individual and its perch trees show that both males and females can be classified into two groups: one consists of those observed frequently on the same one to three clumped trees (hereafter called resident; Fig. 1A, B), and the other consists of those observed less frequently, and on scattered trees. Because flying lizards move all over a given tree, from the lower trunk to the tip of extended twigs (Mori & Hikida, 1994), it is reasonable to regard each tree as a unit of activity range for the lizards in this study. Perch trees of each resident male except one co-incided with those of one to three resident females: i.e., the activity range of the resident male wholly overlapped with those of one to three resident females.

Although some other trees not indicated in Fig. 1 might be used as unidentified males' home ranges, it was apparent that some trees were not included in any males' home ranges. It is likely that there were some "preferred" perch trees. In the first survey, height and diameter at breast height (DBH) were measured for each tree planted in southern half of the study area to investigate the relationship between these variables and choice of perch trees by the lizard. In this analysis additional three trees which were not indicated as residents' trees in Fig. 1 were regarded as perch trees of resident males since residency of a male was suggested by the continuous presence of an unmarked individual. There were no significant differences either in height or in DBH between the trees with residents and without residents (height, trees with residents, $\bar{x} = 16.1$ m, SE $= 0.7$, n $= 9$; trees without residents, $\bar{x} = 13.7$ m, SE $= 1.1$, n $= 13$; U-tests, z $= 1.71$, P > 0.05: DBH, with residents, $\bar{x} = 47.0$ cm, SE $= 6.7$, n $= 9$; without residents, $\bar{x} = 39.5$ cm, SE $= 3.8$, n $= 12$; z $= 0.85$, P > 0.05). In the second survey no flying lizards were observed on Trees B and D where many lizards had been observed in the first survey, although we could not find any noticeable differences in appearance of those trees between the first and second surveys.

A resident male defended his perch trees from other males (intruders) by displaying and directly chasing them (Mori & Hikida, 1994). In most cases, resident males were larger than intruders both in SVL and DL (Fig. 6). All intruders were male non-residents. Recapture of a resident male at the end of the first survey resulted in an unexpected removal experiment of a resident. About two hours after the resident had been removed, one adult and one unmarked juvenile males were found on the trees within the home range of the resident. These two males were captured and removed by us. The next day, one adult male and four juvenile males (three unmarked) were found on the vacant trees during a 45 min observation period.

DISCUSSION

Draco v. sumatranus in Matang is strictly arboreal and diurnal with two activity peaks, one in the morning and the other in the afternoon. This observation is similar to those of *D. v. reticulatus* (Hairston, 1957; Alcala, 1967) and *D. dussumieri* (John, 1967b). Hairston (1957) mentioned that midday inactivity was related to light intensity rather than temperature, whereas Alcala (1967) and John (1967b) suggested the negative effects of high temperature on activity. Results of the present study were ambiguous. Midday inactivity of *D. v. sumatranus* might

correspond to the slightly higher air temperature of that period of the day. Nonetheless, the number of lizards observed was positively correlated with air temperature in males. On the other hand, there were no relationships between the number of active lizards and cloud amount. These results suggest temperature may be a more important factor than light intensity on activity of the lizard, but further investigations are necessary to verify the prediction.

Several lizards from forests and other densely vegetated habitats in tropical climates have a wide range of activity temperature (Avery, 1982). They passively depend upon the ambient temperature, and thermoregulation by basking is uncommon except for skinks. Most anoline lizards and a few agamids including *D. v. reticulatus* are reported to be thermally passive (Alcala, 1967; Avery, 1982; Tanaka, 1986). The positive correlation between body temperature and ambient air temperature, the wide range of activity temperature, and the scarcity of basking in the direct sunlight suggest the thermal passivity of *D. v. sumatranus*. There were, however, some differences between males and females with regard to thermal activity. Males were more frequently observed in direct or filtered sun than females, and the number of males observed were positively correlated with ambient air temperature. These facts suggest that males prefer higher activity temperature than females, but we could not detect differences of average body temperature between the sexes. Thus, the observed sexual difference of thermal activity may simply reflect the higher activity ratio, especially social activity, of males than females (Mori & Hikida, 1994) rather than the different thermal preference between the sexes.

Resource partitioning among sympatric congeners and between sexes have been reported in some anoline lizards (e.g., Schoener, 1968; Andrews, 1971) and agamids (Lin & Lu, 1982). Inger (1983) reported differences in perch height among six species of *Draco*. He showed that *D. melanopogon* and *D. quinquefasciatus* were generally found below 6 m, and the other four species were higher on the tree. There was no restriction in perch height in *D. v. sumatranus* in the present study site where there are no syntopic congeners. In fact the lizards used virtually the entire tree from 1 m to more than 15 m off the ground. There were no differences in perch height between males and females.

The present study, coupled with the observations of aggressive behavior of males (Mori & Hikida, 1994), reveals that males of *D. v. sumatranus* are definitely territorial (Rand, 1967a). A resident male defended his home range from intruder males, and drove them away by displaying or directly chasing them (Mori & Hikida, 1994). In one instance, removal of a resident male resulted in successive intrusions into the vacant area by seven males.

Territorial defense by males has been reported for several species of *Draco* (Schmidt, 1935; Hairston, 1957; Pfeffer, 1962; Alcala, 1967; John, 1970b), but the mating system has not yet been clear for any species. John (1962) and Smith (1935) stated that the lizards (*D. dussumieri*, and *D. maculatus* and *D. beccarii*, respectively) were often seen in pairs, one male and one female. Alcala (1967) reported large overlapping home ranges between males and females. The present study shows that the area of a resident male territory wholly overlapped with the home ranges of one to three females. All observed courtship behavior was performed by resident males within their territory (Mori & Hikida, 1994). These facts suggest that each resident male possesses a harem.

The adaptive significance of territoriality in lizards has been discussed by various authors (e.g., Rand, 1967a; Manzur & Fuentes, 1979; Stamps, 1983). Food, mates, and other resources such as basking sites, retreats, and nest sites are defended. It appears that access to female is one of the most important role of territoriality in male *D. v. sumatranus*, because: 1) only males were driven away from resident males' territories, 2) males' territories overlapped with home ranges of females, 3) courtship by the resident males was observed in their territories, and 4) females did not defend their home ranges (see Mori & Hikida, 1994).

Food does not appear to be a defended resource in *D. v. sumatranus*. Ants are the predominant food items in all flying lizards (Villadolid, 1934; McCann, 1940; Alcala, 1967; Reyes, 1968; Inger, 1983; Mori & Hikida, 1994). Although quantitative analyses were not done, ants were very abundant on most trees in the study site, and no apparent relationship was observed between the presence of ants and resident flying lizards. There were no apparent differences in feeding frequency between resident and non-resident males (Mori & Hikida, 1994). In addition, territorial behavior was never observed in females (Mori & Hikida, 1994). Therefore, it is unlikely that defense of food resources is an important role of territoriality in *D. v. sumatranus*.

Stamps (1977) inferred that specialization on the eating of ants resulted in loss of territoriality in the iguanid *Phrynosoma* and agamid *Moloch*. He suggested that the clumped distributions of ants and the considerable distance between ant trails in the desert habitats have reduced the advantage of territorial defense. In contrast, *Draco*, a specialized ant-eater, showed marked territoriality. This difference may be due to the distribution pattern of ants: in tropical rain forests ants are not dispersed, clumped food resources but, as mentioned above, rather abundant and uniformly distributed.

Territoriality is common both in iguanids and agamids (Stamps, 1977). In many species, territorial males are larger than intruder males, and winners of aggressive fights are larger than losers (Rand, 1967b; Ruby, 1984; Anderson & Vitt, 1990). Consequently, large resident males may gain greater opportunity of access to females and thus higher reproductive success. Therefore, sexual selection for large body size may be operative in males. In fact, most iguanid and agamid males that have this type of social system are larger than females (Fitch, 1981).

Draco v. sumatranus also shows a similar social system that may promote larger body size in males. Despite this, females are significantly larger than males. This reversed sexual size dimorphism is a common trend in flying lizards (Inger, 1983; Musters, 1983). Reversed sexual size dimorphism is well known in birds of prey and bats, and several hypotheses concerning the relationship between active flight performance and the reversed sexual dimorphism have been proposed (e.g., Myers, 1978; Andersson & Norberg, 1981; Schantz & Nilsson, 1981; Wheeler & Greenwood, 1983). In the flying lizards, increased gliding maneuverability, which favors smaller size (Norberg, 1990), may be more important in males than females to patrol and chase away intruders from their territories (Colbert, 1967; Mori & Hikida, 1994). There are, of course, several other explanations for the reversed sexual size dimorphism such as difference of age distribution between the sexes. Comparisons of wing morphology between males and females and an aerodynamic study of gliding performance, as well as a more basic ecological and behavioral study, are necessary to evaluate the evolution of the reversed sexual size dimorphism in flying lizards (see Mori & Hikida, 1992).

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