Colour dimorphism in *Elaphe quadrivirgata* (Serpentes: Colubridae) on Yakushima Island, with special reference to its thermal biology

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DOCTORAL THESIS

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CONTENTS

GENERAL INTRODUCTION

Animal colouration has been received much scientific attention from biologists in various fields. Although there are many different approaches (e.g. physiological, ecological, behavioural) to interpret the biological significance of animal colouration, a common underlying view is that animal colouration has (had) some adaptive functions because it has been evolved through selection that eliminates functionally deleterious colouration (Darwin, 1874; Cott, 1940; Endler, 1978; Caro, 2005). To elucidate these functions and selection forces that act to animal colouration, numerous studies have been conducted on a wide variety of animals (e.g. Darwin, 1874; Cott, 1940; Cooper & Greenberg, 1992 and references therein). If animal colouration is a product of selection forces, colour polymorphism is likely to occur and be maintained under specific conditions.

Reptiles are a suitable group for studying the biological significance of animal colouration because they often exhibit conspicuous colour polymorphism (Bechtel, 1995). Reptile colouration has been viewed as an adaptive compromise among conflicting demands such as social, foraging, antipredatory, and thermoregulatory demands (Cooper & Greenberg, 1992). Depending on the nature of the organism, several compromise solutions may be

possible to balance these conflicting demands. Colour morphs of a polymorphic species can be viewed as an expression of this compromise within a species.

Colour dimorphism is a specific case of polymorphism in which two discontinuous colour morphs occur in a species. In particular, due to the striking visual impact of black colouration, occurrence of melanistic/normal colour dimorphism (polymorphism) in wild populations has attracted many researchers (e.g. Kettlewell, 1973; Majerus, 1998 and references therein). However, ultimate mechanisms of the maintenance of melanism in a population are not yet fully understood in many animals (e.g. Forsman, 1995a, b; Bittner, King & Kerfin, 2002; Visser, Fertl & Pusser, 2004).

In snakes, the following explanation has been cited as the most common hypothesis for the mechanism of the maintenance of melanistic/normal colour dimorphism: melanistic individuals enjoy thermal superiority compared to normal coloured individuals (Gibson & Falls, 1979), whereas normal colouration (e.g. striped, ringed, blotched patterns) acts as protection against visually oriented predators (Jackson, Ingram & Campbell, 1976; Pough, 1976; Wüster et al., 2004; Niskanen & Mappes, 2005) more efficiently than melanistic colouration (Andrén & Nilson, 1981; Gibson & Falls, 1988; Forsman 1995a; but see Bittner, 2003).

As a demonstration of the thermoregulatory advantages of melanism, Gibson & Falls (1979) found that, when experimentally exposed under the natural insolation, that melanistic individuals of the garter snake (*Thamnophis sirtalis*) maintained higher body temperature (T_b) than striped individuals, that mean T_b of free-ranging melanistic individuals were higher than that of striped individuals during the colder period of the active season, and that mean heat-flow value of excised skin was greater in melanistic individuals than in striped individuals. The visual advantages of normal coloured morphs were demonstrated in a study that showed that normal coloured adders (*Vipera berus*) were less subject to attacks by visually oriented predators than melanistic individuals (Andrén & Nilson, 1981).

Since these pioneering works, numerous biological consequences that are derived from 'thermal superiority in melanism' have been reported. Despite considerable scientific attention to the biological mechanisms that maintain melanistic/normal colour dimorphism in snakes, studies verifying 'thermal superiority in melanism', the central premise for the adaptive persistence of melanistic morphs, under natural condition are scarce. The Japanese four-lined snake (*Elaphe quadrivirgata*) is a suitable candidate for studying this respect because the snake

exhibits colour polymorphism including melanism (Stejneger, 1907; Goris & Maeda, 2004; Mori et al., 2005).

Yakushima is a large island (503 km² in area and 1935 m at highest elevation), located 100 km SW of the main-islands of Japan. *Elaphe quadrivirgata* on this Island exhibits distinct melanistic/normal colour dimorphism and ratio of melanistic individuals is relatively high (H. Ota, pers. comm.). Thus, Yakushima Island is suitable site for studying the biological significance of melanism in snakes.

In the present study, to test the thermal superiority of melanism and general adaptive significance of colour dimorphism in snakes, I investigated the thermal biology of *E. quadrivirgata* both under experimental and natural conditions. In chapter one, I presented basic information on natural history of *E. quadrivirgata* on Yakushima Island. Considerably high ratio of melanistic individuals, small body sizes, low frequency of occurrence in striped individuals in winter, and different food habits from main-island populations were shown. In chapter two, to test effect of body size and colouration on thermal aspects of *E. quadrivirgata*, I conducted a heating experiment in a laboratory. In chapter three, to test common hypotheses and generalize results of previous studies, I investigated thermoregulation of free-ranging melanistic and striped individuals

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of *E. quadrivirgata* on Yakushima Island using temperature-sensitive

radio transmitters and physical models of the snake.

CHAPTER 1. Natural History of *Elaphe quadrivirgata* on Yakushima Island

1-1. INTRODUCTION

Several previous studies demonstrated that in snakes traits relevant to their natural history sometimes vary considerably among conspecific local populations. In some species, for example, diet shows an extensive geographic variation (e.g. Kephart, 1982; Schwaner, 1985; Shine, 1987; Hasegawa & Moriguchi, 1989; Gregory & Nelson, 1991; Henderson, 1993; King, 1993; Daltry, Wüster & Thorpe, 1998), whereas body size varies geographically in other species (e.g. Schwaner, 1985; Hasegawa & Moriguchi, 1989; Forsman, 1991; Kohno & Ota, 1991; Mori, 1994). Although a large proportion of such variation is assumed to reflect snakes' evolutionary or phenetic responses to differential biotic and abiotic environmental factors, actual environmental correlates have not yet been well documented for most of the geographically varying traits due to an insufficiency in relevant data and information.

A moderate sized diurnal colubrid, *Elaphe quadrivirgata*, occurs in broad areas of the main-islands of Japan and adjacent islets (Stejneger, 1907; Maki, 1931). Based on field studies, Fukada (1992) described various natural history aspects of the snake in Kyoto, central Japan. Kadowaki (1992) also studied natural history of the

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snake in Yamagata Prefecture, northern Japan. In both studies, study sites were located in flat open fields exposed to distinctly seasonal climates and to strong and strictly seasonal human activities, such as rice-planting, rice-harvesting, and cultivation.

Elaphe quadrivirgata on Yakushima Island are said to exhibits distinct melanistic/striped colour dimorphism (H. Ota, pers. comm.). However, no quantitative data are available on natural history traits of *E. quadrivirgata* on this island. Thus, I conducted field survey to obtain basic information for melanistic and striped morphs of *E. quadrivirgata* on Yakushima Island, and compared the ecological traits with those of the previous studies conducted in the main-island of Japan.

1-2. MATERIALS AND METHODS

Yakushima Island (30°22'N, 130°22'E) is located 100 km SW of Kagoshima Prefecture, Japan. Climate of the island is characterized by warm temperate (annual mean air temperature is approximately 21°C) with extensive precipitation (> 2500 mm/year) (Tagawa, 1983, Eguchi, 1985). The road runs around the island along the coast and is surrounded by secondary forests. I conducted field survey at a western part of the island.

Field survey was carried out for a total of 70 days between 21

June 1998 and 21 October 2000. On each day, a route census was conducted from 0800 to 1700 h by slowly walking forth and back along a path (Western Woodland Path) between Nagata and Kawahara (approximately 10 km).

Snakes encountered during the census were caught by hand, and the following data were recorded for each snake: body temperature (T_b: measured to the nearest 0.1°C by inserting a thermistor bulb into cloaca in the shade), air temperature (T_a: measured to the nearest 0.1°C in the shade, ca. 1.0 m above the ground), substrate temperature (T_s: measured to the nearest 0.1°C without shading), sex (judged by forced protruding of hemipenis, or occasionally by probing), snout-vent length (SVL: measured to the nearest 1 mm by tape scale), and body mass (BM: weighed by an electric toploading balance). Presence or absence of stomach contents was also examined by palpation, and when present, prey items were obtained by forced regurgitation. Each item from the stomach was identified to as low taxonomic level as possible, and then re-fed to the snake. I examined stomach contents of fresh road-killed individuals on the path. Examinations were not made for fecal samples because identifiable remains had never been contained. Colouration (striped or melanistic) of each individual was recorded. Each snake was then marked by ventral scale clipping and

released at the capture site. I regarded mean value in all T_a data

obtained in a given month as the standard T_a (SAT) in the month.

To examine temporary changes in frequencies of the two colour

morphs of *E. quadrivirgata*, colouration data were compared with

data obtained by Ota in August 1981 (H. Ota, pers. comm.). In an

analysis of seasonal fluctuation in the frequency of occurrence of

melanistic individuals, I excluded additional records for individuals

captured more than once within the same season (spring, May;

summer, June to August; autumn, September and October; winter,

November and December) in the same year.

Fukada (1992) reported that fast growing individuals of the

Kyoto population of *E. quadrivirgata* reached sexual maturity at

approximately one year and nine months of age in both sexes, and

that the minimum SVLs in males and females at this age (as

determined by field recaptures of released captive-born snakes)

were 487 mm and 566 mm, respectively. Thus, for comparisons of

adult mean SVL and BM between the Yakushima and Kyoto

populations, I tentatively used size data for individuals with SVL $\geq$

500 mm for both sexes. Because Fukada (1992) presented only mean

values, results of the comparisons could not be assessed statistically.

1-3. RESULTS

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A total of 102 individuals of *E. quadrivirgata* (52 males, 49 females, and 1 undetermined sex) were captured. Six melanistic individuals (three females and three of undetermined sexes) of *E. quadrivirgata* were also found road-killed. Of males and females, 90.4% (47/52) and 86.5% (45/52) were melanistic, respectively. No significant differences in frequency of melanistic individuals were evident between sexes (Fisher's exact test, $P = 0.380$), or between animals observed in 1998 (83.3%) and 1999 (91.4%) ($P = 0.253$: Table 1-1). Ota found that 56.4% (22/39) of animals observed in 1981 (not sexed) were melanistic (H. Ota, pers. comm.), and the difference in frequency of melanistic individuals between 1981 and 1998 was statistically significant ($P = 0.0107$: Table 1-1). In the 1998-2000 survey, the frequency of occurrence of melanistic individuals was lowest in spring, followed by those in summer, autumn, and winter in order (Fig. 1-1). However, the seasonal fluctuation was statistically not significant (G-test, $G_{adj} = 4.67$, $P > 0.05$).

Thirty-four of 120 examined *E. quadrivirgata* (28.3%) had prey items in the stomach. The snakes consumed only reptilian prey (Table 1-2). Most snakes contained single prey item, and multiple prey (two or three items) was observed in only seven snakes. Of these, four snakes consumed two individuals of the same lizard species (either *Eumeces japonicus* or *Takydromus tachydromoides*),

and two had one *E. japonicus* and one or two *T. tachydromoides*. The remaining one had one *E. japonicus*, one *T. tachydromoides*, and one viperid snake *Gloydius blomhoffii*.

To examine intermorph difference of food intake, I included additional data obtained after the 2000 survey. I found that proportion of stomach that contained a food was higher in melanistic individuals (54/198 = 27.3%) than in striped individuals (4/34 = 11.8%; recaptures were excluded, $P < 0.037$). Dietary data were presented in Appendix.

Mean adult SVL and BM of *Elaphe quadrivirgata* from Kyoto, estimated from Fukada's (1992) data, are compared with corresponding values for the Yakushima populations of the snake in Table 1-3. Mean values of both SVL and BM in the Yakushima population were smaller than those in the Kyoto population in both sexes. The difference was especially remarkable in mean BM, where the value for the Yakushima population was smaller than one third of that in the Kyoto population in both sexes.

Size frequency distribution in SVL showed remarkable intermorph difference (I included additional data obtained after the 2000 survey: Fig. 1-2). In males, melanistic morph exhibits bimodal distribution with one peak at 300 mm and another at 900 mm, whereas striped morph exhibits unimodal distribution with a peak at

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700 mm (Fig. 1-2A). In females, melanistic morph also exhibits two peaks at 300 mm and 700 mm, whereas striped morph exhibits a peak at 700 mm (Fig. 1-2B).

Growth in SVL of recaptured individuals was shown in Figure 1-3. Growth seems surprisingly slow, and nearly zero at approximately 950 mm SVL (Fig. 1-3). Growth rate was calculated as follows: (SVL at the last capture - SVL at first capture)/the day elapsed between the two capture events. If the two capture events occurred different year, I excluded a 90-day per year, as growth of hibernating snakes was zero. Residuals calculated from linear regression equation of the growth rate on the initial SVL showed negative values in both of the two striped individuals (Fig. 1-4).

Reproductive data obtained from wild-caught females showed remarkable feature with respect to ratio of melanistic individuals (Tab. 1-4). Ratio of melanistic individuals at hatching was low compared to that obtained by wild-caught animals. No significant differences in frequency of melanistic individuals at hatching were evident between sexes ($P = 0.57$).

There were no significant differences in T_b between the two colour morphs (Mann-Whitney U-test, $Z = -0.531$, $P = 0.596$) or between sexes ($Z = -0.540$, $P = 0.589$). Thus, all T_b data were combined. Mean T_b, T_a, and T_s were shown in Table 1-5. The T_b was

highly correlated with both T_a and T_s (Spearman's correlation coefficient, $r_s = 0.705$ with T_a, and 0.797 with T_s, all $P < 0.01$). In contrast, the correlation between T_b and SVL was very low ($r_s = 0.175$, $P > 0.05$). Figure 1-5 shows the monthly dynamics of T_b and of SAT. Mean T_b was consistently higher than SAT in all months.

1-4. DISCUSSION

The ecological and evolutionary significances in the occurrence of melanism in snake populations are not yet fully understood. Several authors have reported that in the adder, *Vipera berus*, the frequency of melanistic individuals was significantly higher in females than in males (Luiselli, 1992, 1993; Forsman, 1995a). This phenomenon was interpreted as indicative of greater advantage of melanism in females than in males due to its superiority in thermal efficiency (Gibson & Falls, 1979): black mothers may shorten the gestation period and have more time to replenish their energy reserves prior to hibernation (Luiselli, 1992; Forsman, 1995a), resulting in a higher reproductive frequency than the non-melanistic females (Capula & Luiselli, 1994). In *E. quadrivirgata* of Yakushima, however, there was no significant intersexual difference in the frequency of melanistic individuals. This may reflect differential advantages of being melanistic between viviparous (*V. berus*) and oviparous species (*E.*

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quadrivirgata).

The apparent increase in the proportion of melanistic individuals in the Yakushima *E. quadrivirgata* since 1981 is puzzling because no obvious environmental changes occurred around the study site between 1981 and 2000. Considering that the frequency of occurrence of melanistic individuals was relatively low in summer during the present observations (Fig. 1-1), limitation of the 1981 fieldwork to August and relatively few observations of snakes in midsummer during the1998-2000 fieldwork may be responsible for such a difference. Further monitoring for temporal dynamics in the frequency of melanistic individuals and environmental variables is desired to give a plausible explanation for the present results.

Fukada (1959, 1992) and Kadowaki (1992, 1996) demonstrated that frogs are the main prey items of *E. quadrivirgata* in their study sites. The predominance of lizards, as well as the complete absence of anuran prey, in diets of *E. quadrivirgata* on Yakushima offers a sharp contrast to the results of these previous studies. *Elaphe quadrivirgata* is considered to dietary generalist (Mori & Moriguchi, 1988), and thus interpopulation differences of the food habits may be attributable to differences of relative abundance of prey animals.

Proportion of stomach that contained food was significantly higher in melanistic individuals than in striped individuals. This

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difference may be attributable to difference of thermoregulation ability. If melanistic individuals are effective thermoregulators than striped individuals, the former can devote more time for foraging, resulting higher food intake.

In both mean SVL and BM, *E. quadrivirgata* in this study site was smaller than that in Kyoto. On islands, body size of snakes sometimes shows substantial variations, chiefly under the influences of varying size and abundance of prey (Case, 1978; Schwaner, 1985; Schwaner & Sarre, 1988; Hasegawa & Moriguchi, 1989; Kohno & Ota, 1991; Mori, 1994). Thus, size variation between the two populations may reflect differential prey conditions for the snake on Yakushima as compared to those in Kyoto.

Unimodal size frequency distribution of striped morph may indicate higher mortality of striped individuals at early life stages. Alternatively, the result was artifact. I may fail to detect striped individuals more often because of cryptic colouration of juvenile. Furthermore, behavioural patterns (e.g. activity time, habitat selection) of striped juveniles may differ from melanistic juveniles, and difficult to detect by route census method.

Growth rate in the wild was considerably low. It is difficult to make a conclusion for intermorph difference of growth rate because of small sample size. At least, growth rate of striped individuals were

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not so high compared melanistic individuals at all.

At hatching, ratio of striped individuals was high compared to that obtained by wild-caught animals. It may indicate low survivorship of striped individuals before they reach adult size class.

No intermorph difference of T_b was detected. However, interpretation of the result should be done carefully because of opportunistic measurements of T_b and environmental temperature. Thus, studies using physical models (see Peterson, Gibson & Dorcas, 1993 for review) and temperature-sensitive radio transmitters are desired to accurately compare thermal aspects between the two colour morphs. Results of these studies are described in chapter three.

CHAPTER 2. Thermal Aspects of Melanistic and Striped

Morphs of *Elaphe quadrivirgata* under an Experimental

Condition

2-1. INTRODUCTION

Ectotherms rely on external resources for heat gain, and thus

temperature is a critical factor limiting their distribution, diversity,

and activity (e.g. Cowles & Bogert, 1944; Huey, 1982; Coxwell & Bock,

1995). Although the range of body temperature (T_b) available to

them is constrained by environmental factors, they can adjust T_b by

physical, physiological, and behavioural means (see Lillywhite, 2001

for review). For many ectotherms, thermoregulation is of central

importance in their daily life because T_b directly affects their

physiological processes, performance, and behaviour (e.g. Dawson,

1975; Christian & Tracy, 1981; Hertz, Huey & Nevo, 1983; Stevenson,

Peterson & Tsuji, 1985; Bennett, 1987; van Berkum, 1988; Huey &

Kingsolver, 1989; Willmer, 1991; Bauwens *et al.*, 1995; Dorcas,

Peterson & Flint, 1997; Forsman, 1999). Thus, selection should act to

favor characteristics that enhance the thermoregulatory ability of

ectotherms, because the latter is biologically important to them.

Colouration and body size are two physical properties that

influence the T_b of ectotherms (e.g. Watt, 1968; Gibson & Falls, 1979;

Brakefield & Willmer, 1985; Stevenson, 1985; Stewart & Dixon, 1989;

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Forsman, 1995b, 1997; De Jong, Gussekloo & Brakefield, 1996;

Bittner, King & Kerfin, 2002; Forsman *et al.*, 2002; Gross, Schmolz &

Hilker, 2004). These two properties are consequences of adaptive

compromise among various conflicting demands, such as social,

predatory, antipredatory, and thermoregulatory demands (Cooper

& Greenberg, 1992). Thus, if a particular combination of colouration

and size is advantageous to the thermoregulation of a certain species,

and innocuous for other demands, it is possible that these two

properties will be highly correlated with each other.

Snakes are a suitable experimental ectothermic animal for

examining the influence of colouration and body size on T_b because

they exhibit a wide range of variation in these two physical

properties, yet have a simple body form (Greene, 1997).

Furthermore, the occurrence of intraspecific variation in both

properties (e.g. Mitchell, 1977; Rossman, Ford & Seigel, 1996;

chapter one) enables us to examine the relationship between

colouration and body size and their effects on thermal properties

without confounding factors of phylogenetic constraints.

Among many colour variants of snakes, the melanistic morph

has been attractive for numerous studies that attempted to elucidate

the biological significance of colour morphs. Because the melanistic

morph has been thought to have thermoregulatory advantages over

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normal coloured morphs (Gibson & Falls, 1979), studies of melanism in snakes have heavily focused on the thermal aspects. For example, Bittner et al. (2002) investigated the effects of colour and body size on T_b of the garter snake, Thamnophis sirtalis, and found that the melanistic morph has a higher equilibrium temperature than the striped morph only in large size classes, whereas heating rate does not differ between the two colour morphs in any size class. Based on their results and those of Shine & Kearney (2001), who investigated the effects of several attributes of a physical model (e.g. colour, size) on its temperature, Bittner et al. (2002) suggested that the thermal advantages of melanism would be restricted to larger individuals. Forsman (1995b) found that when exposed to natural insolation, the melanistic morph of the adder (Vipera berus) heated faster and reached slightly higher T_b than the normal coloured morph, whereas no consistent difference occurred in daily T_b variation between free-ranging melanistic and normal coloured individuals, monitored by radiotelemetry.

The Japanese four-lined snake (Elaphe quadrivirgata) differs from the garter snake and the adder in several life-history traits. For example, T. sirtalis and V. berus are viviparous, whereas E. quadrivirgata is oviparous. In addition, the female is the larger sex in T. sirtalis and V. berus, whereas the male is the larger sex in E.

quadrivirgata. These biological differences may affect the relative importance of body size and colouration to thermal aspects of each species in different ways. Thus, to test the thermal superiority of melanism, specific data on thermal aspects (e.g. heating rate) of *E. quadrivirgata* are necessary to identify.

In this chapter, I investigated the effects of colour and body size on thermal aspects of *E. quadrivirgata* under experimental conditions. Specifically, I compared the relationship of body size to heating rate between melanistic and normal coloured (striped) individuals.

2-2. MATERIALS AND METHODS

2-2-1. SUBJECT ANIMALS

Elaphe quadrivirgata is a diurnal snake widely distributed in Japan (Stejneger, 1907; Goris & Maeda, 2004). The normal colouration of adult snakes is a brown ground colour with four black longitudinal stripes. Colour patterning is, however, variable both among and within populations (e.g. variants include yellowish ground colour with vivid stripes, or dark-brown ground colour with pale stripes: Mori *et al.*, 2005). Melanistic snakes are black from hatching, and thus melanism is not an ontogenetic darkening of the ground colour, as is seen in the adders (Naulleau, 1973; Forsman, 1995a, b).

From 1998 to 2004, I have been conducting an ecological study of the snakes on Yakushima Island. *Elaphe quadrivirgata* on this island exhibits features of both colouration and body size that differ from those of main-island populations. There is a distinct striped/melanistic colour dimorphism, with a high proportion of melanistic individuals (approximately 85%; chapter one). Body size is smaller than that of the main-island populations (chapter one). For example, mean snout-vent length (SVL) and body mass (BM) of adults on Yakushima Island are approximately 80% and 30%, respectively, of those in the Kyoto population studied by Fukada (1992) (mean male SVL 1078 mm and 828 mm for Kyoto and Yakushima, respectively, and mean BM 300 g and 114 g, respectively; chapter one).

Experimental subjects were wild-caught adults comprising 13 melanistic (8 males and 5 females) and 14 striped snakes (8 males and 6 females). All melanistic snakes and two striped females were collected from Yakushima Island. Due to the difficulty of obtaining striped individuals from Yakushima (I captured only 33 striped individuals during a 7-year survey), the remaining striped snakes were collected from Shiga Prefecture (34°55'N, 136°05'E), the main-island of Japan. All striped snakes used in the experiment had a brown ground colour with vivid stripes, and all melanistic snakes

were jet-black. Although striped snakes came from two populations, the small sample size precluded the analysis of population effects on thermal properties. However, at least the appearance of the snakes did not differ between the two populations, and thus I assumed that population effects, if any, were negligible.

Prior to experimental trials, each snake was housed individually in a plastic cage (35 x 20 x 15 cm) with a water dish, in a building in which air temperature fluctuated with changes in ambient temperature throughout the experimental period (range 22-34°C).

2-2-2. HEATING EXPERIMENT

As has been done in other studies (e.g. Forsman, 1997; Bittner *et al.*, 2002), I used an artificial heat source, in this case a 100-watt light bulb (Vivarium Basking Spot, Pogona Club Inc., Japan) hung 40 cm above the snake. This was done because experiments under natural conditions introduce many uncontrollable factors. To simulate the emergence of a snake from an overnight refugium, the heating experiment was performed in a walk-in environmental chamber at a temperature of 25°C, which is the approximate air temperature measured when *E. quadrivirgata* was captured between 0700 and 1000 h on Yakushima Island (N = 82, mean = 25.7°C, SE = 0.30°C; K. Tanaka, unpubl. data). Snakes were not fed for at least 3 days prior

to trials so that they could expel their gut contents.

On the day before an experimental trial, a snake was removed from its cage, put into a 5 mm mesh nylon bag, and kept in an incubator at 18°C until the trial began. Immediately before the trial, the snake was removed from the incubator. The small sensor bulb of a thermistor was inserted into the cloaca of the snake, and the wire of the thermistor probe was taped to its tail to prevent the sensor bulb from pulling out (Lutterschmidt & Lutterschmidt, 2002). The snake was then put into another 5 mm mesh nylon bag, which was sewn onto a 25 x 20 x 2.2 cm board of styrofoam to restrict the snake's movements and to minimize inter-trial differences in position of the snake relative to the heat source. Because these handling procedures affected T_b, I allowed the snake to re-equilibrate in the incubator to a T_b of approximately 20°C. The board with the snake was then transferred to the walk-in environmental chamber and placed under the heat source within 30 sec after removal from the incubator.

I turned on the heating bulb when the T_b of the snake reached approximately 21.0°C (time zero of a trial), and began to record T_b at 1 min intervals. The mesh of the bag was large enough that most of the radiation reached to the snake. I simultaneously recorded the behaviour of the snake. I terminated each trial either after 40 min

had elapsed or when T_b reached 40°C, whichever came first. After the trial, I verified that the bulb sensor of the thermistor had remained in the cloaca, and I measured SVL and BM of the snake. Mean SVLs of the melanistic and striped morphs were 889 mm (range 780-1068 mm) and 869 mm (range 740-1010 mm), respectively, and mean BMs were 150 g (range 102-208 g) and 147 g (range 91-208 g), respectively. ANCOVA (with morph as factor, BM as dependent variable, and SVL as covariate) revealed that neither SVL-adjusted BM (t-test, d.f. = 1,24, F = 1.03, P = 0.21) nor SVL (d.f. = 25, t = 0.53, P > 0.6) differed between the two morphs. One to four snakes were tested in a day. After the experiment, all snakes were released at the site of capture.

2-2-3. DATA ANALYSES

Immediately after each day's experiments, T_b data for each snake were fitted to the following von Bertalanffy equation:

$$T_b = A \{1 - B \exp [-C (\text{time})]\},$$

where A is equilibrium temperature, B is proportion of A realized at time = 0, and C is a heating coefficient, which has units of time^{-1}. If data from a snake failed to converge on this equation due to a constant rise in T_b throughout a trial, the snake was re-tested another day.

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Homogeneity of variance was checked with Bartlett's test before parametric tests were adopted. All statistical analyses were conducted with JMP (version 3) statistical software (SAS Institute, Inc., 1995) with $\alpha = 0.05$. Data were presented as mean $\pm$ 1 SE.

2-3. RESULTS

Equilibrium temperatures obtained by the von Bertalanffy equation exceeded 50°C (Table 2-1). On Yakushima, operative environmental temperatures (Bakken & Gates, 1975; Bakken, 1992) under full sun during the active seasons of the snake frequently exceed 50°C (chapter three), and thus the heating curve may well represent changes in T_b of a basking snake in full sun. However, T_b of free-ranging snakes on Yakushima never exceeds 35°C (chapters one and three), and the equilibrium temperatures obtained were obviously much higher than a lethal temperature. Thus, detailed analyses of equilibrium temperatures exceeding 50°C are biologically meaningless. Nonetheless, this does not necessary mean that the heating curve obtained is irrelevant. Topology of the heating curve may differ between free-ranging and experimental conditions only above a particular T_b at which a basking snake in the wild would begin to move to another place. I assumed this point to be 35°C, for the following reasons. First, in the experiment, most snakes of both

morphs began to move vigorously, with tongue flicking, when their T_b reached approximately 35°C. Second, the maximum T_b of *E. quadrivirgata* measured in the field on Yakushima Island was 34.6°C (chapter one). Third, the maximum voluntary T_b of *E. quadrivirgata* recorded under a laboratory thermal gradient was 34.9°C (chapter three). Thus, in the following analyses, I limited T_b data to no higher than 35°C in order to examine heating during basking (i.e. from the beginning of basking until moving to another place). Use of linear regression equation was justified because the exponential curves represented by the von Bertalanffy equation approximate a straight line (all, $r > 0.96$, $P < 0.001$; Fig. 2-1) during the presumed basking stage (i.e. $T_b \leq 35°C$).

Heating rate (slope of T_b against time) during the presumed basking stage did not significantly differ between males and females in both morphs (melanistic, d.f. = 11, $t = 1.00$, $P = 0.34$; striped, d.f. = 12, $t = 1.38$, $P = 0.19$). Thus, I pooled the data from both sexes in the following analyses. Heating rate was negatively correlated with SVL (melanistic, $r = -0.592$, $P = 0.03$; striped, $r = -0.58$, $P = 0.03$) and BM (melanistic, $r = -0.65$, $P = 0.02$; striped, $r = -0.55$, $P = 0.04$; Fig. 2-2) in both morphs. ANCOVA (with morph as factor, BM as covariate, and heating rate as dependent variable) showed a significant difference in intercept between the two morphs, but no significant

difference in slope (intercept, d.f. = 1,24, F = 7.43, P = 0.01; slope, d.f. = 1,23, F = 2.24, P = 0.15), although the slope was steeper in the melanistic morph (-0.00272) than in the striped morph (-0.00113) (use of SVL as covariate yielded the same conclusion). This means that the melanistic morph heats faster than the striped morph, but that the effect of BM (or SVL) on heating rate does not differ between the two morphs. These results did not change even when I used another T_b value, such as the upper set-point (75% quartile; Hertz, Huey & Stevenson, 1993) or median selected T_b under the thermal gradient, as the end point (31.6°C and 30.2°C, respectively; chapter three). The melanistic morph attained a T_b of 35°C significantly faster than the striped morph (melanistic, 27.0 ± 2.1 min, range 16-40 min; striped, 32.4 ± 1.4 min, range 24-40 min; d.f. = 25, t = -2.18, P =0.04).

2-4. DISCUSSION

The heating rate during the presumed basking stage was negatively correlated with body size in both morphs. This result corresponds with those of previous empirical and theoretical studies (e.g. McNab & Auffenberg, 1976; Stevenson, 1985; Turner & Tracy, 1985; Seebacher, Grigg & Beard, 1999). An interesting trend in relation to heating rate and body size shown by the present study is that the

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slope of the regression equation for heating rate against BM is steeper in the melanistic morph than in the striped morph, although the difference is not statistically significant. This statistical non-significance may be due to the narrow range of body size used in the experiment or to small sample sizes. A larger intermorph difference in heating rate in small snakes than in large snakes may be a key to explaining the small body size and high frequency of melanism on Yakushima Island. Considering the superior heat absorption by black colour, it may be possible that small body size helps maintain this prevalence of melanism.

Under natural insolation, the melanistic morph of the garter snake maintains higher T_b than the striped morph (Gibson & Falls, 1979), and the melanistic morph of the adder heats faster and reaches slightly higher T_b than the normal coloured morph (Forsman, 1995b). The melanistic morph of *E. quadrivirgata* also heats faster than the striped morph. Rapid attainment of the preferred range of T_b is advantageous for ectotherms. This ability releases snakes from various time and environmental constraints associated with thermoregulation. For example, rapid heating enables a snake to utilize intermittently available, short-duration sun as a heat resource. Additionally, if thermally suitable sunlit sites are rare and appear patchily, and thus active movement is required for every

basking effort, slow heaters must waste more time in thermoregulation than rapid heaters. This is because slow heaters may be unable to reach a T_b within their preferred range during a patch of clear sky. Furthermore, slow heaters may be restricted in their activities to the vicinity of thermally suitable microhabitats. The snake population on which I focused inhabits secondary forests, and the snakes may not be able to attain their preferred T_b using of average thermal microhabitats, except during summer (chapter three). In addition, unsettled weather conditions and high rainfall are well known climatic features of Yakushima Island (Eguchi, 1985). Thus, the hypothetical situations presented above are feasible ones.

In the wild, there are four possible ways in which slow heaters could manage their thermal inferiority. First, they could maintain a level of thermoregulation similar to that of melanistic morphs and accept a suboptimal T_b for activities. Second, they could turn into thermoconformers. Third, they could devote the time required and restrict other activities to the vicinity of a specific habitat to attain a T_b comparable to fast heaters. Fourth, they could lower their preferred T_b. To verify the ecological relevance of a rapid increase in T_b and its consequences, field studies of the thermal biology of *E. quadrivirgata* on Yakushima Island using temperature-sensitive radio transmitters will be necessary.

While some studies were consistent with the present study (see above), Bittner *et al.* (2002) reported inconsistent results. They revealed that when exposed to a light-bulb heat source, large melanistic garter snakes exhibited a higher equilibrium temperature than large striped ones, but heating rate did not differ between the two morphs. Interspecific differences in some characteristics (e.g. physiological differences, differences in skin properties; also see Introduction) are possible causes of the inconsistency, but, a detailed discussion is impossible due to the lack of direct comparative data.

Lastly, I should mention the remarkable variance of T_b among individuals at a given time (see Fig. 2-1). It is obviously due, in part, to variation in body size (BM explained 42.5% and 30.0% of the total variation in heating rate for melanistic and striped morphs, respectively). In addition, either undetermined factor(s) or subtle differences in behavioural and physiological responses (see Bartholomew, 1982; Lillywhite, 2001 for reviews) among individual snakes might have influenced their T_b change in complicated ways.

The present study revealed that physical properties play an important role in the heating of *E. quadrivirgata*. To validate the thermal superiority of the melanistic morph in an ecological context, it is necessary to study the differences of thermoregulation strategy

in response to thermal environments between the two morphs in the wild. I present results of these studies in chapter three.

CHAPTER 3. Thermal Biology of Free-ranging Melanistic and Striped Morphs of *Elaphe quadrivirgata* on Yakushima Island

3-1. INTRODUCTION

From the adaptational view, animal colouration has (had) some adaptive functions that have been acquired through selection that eliminate functionally deleterious colouration (Darwin, 1874; Cott, 1940; Endler, 1978; Caro, 2005). If so, polymorphism is likely to occur and be maintained under specific conditions. Many researchers have attempted to identify the mechanisms promoting the maintenance of colour polymorphisms. For example, colour patterns of guppies in a particular place represent balance between sexual selection and crypsis (Endler, 1978). Differences in mating behaviour between silver and melanistic males and selective predation contribute to the persistence of melanistic individuals in mosquitofish (Horth, 2003, 2004). Variability in responses of predator hawks to different colour patterns of fox squirrels are suggested as a possible factor favouring retention of genes for black dorsal colouration (Kiltie, 1992). Opposing fitness consequences of colour pattern in males and females, sex-specific habitat selection, and gene flow in combination with spatial variation in relative fitness of morphs are suggested to be the mechanisms of

maintenance of colour polymorphism in the scincid lizard *Lampropholis delicata* (Forsman & Shine, 1995).

As I described in General Introduction, the following explanation has been cited as the most common hypothesis for the mechanism of the maintenance of melanistic/normal colour dimorphism in snakes: melanistic individuals enjoy thermal superiority compared to normal coloured individuals (Gibson & Falls, 1979), whereas normal colouration (e.g. striped, ringed, blotched patterns) acts as protection against visually oriented predators more efficiently than melanistic colouration (Jackson, Ingram & Campbell, 1976; Pough, 1976; Andrén & Nilson, 1981; Gibson & Falls, 1988; Forsman 1995a; but see Bittner, 2003).

Since the pioneering works that originate the common hypothesis, numerous biological consequences derived from 'thermal superiority of melanism' have been reported. For example, thermoregulatory superiority allows melanistic individuals to remain active for longer periods, and consequently enables them to collect more food, resulting in a higher growth rate and larger body sizes (Andrén & Nilson, 1981; Madsen & Stille, 1988; Luiselli, 1993; Monney, Luiselli & Capula, 1995; but see Forsman & Ås, 1987; King, 1988; Forsman, 1993). Further consequences of this advantage are a higher mating success of melanistic individuals (Andrén & Nilson,

1981; Madsen, 1988) because longer and heavier males usually win male-male combat (e.g. Andrén & Nilson, 1981; Shuett & Gillingham, 1989), and higher fecundity as larger females have a larger clutch size (see Fitch, 1970; Seigel & Ford, 1987 for reviews). Reproductive frequency of melanistic females is also high (Capula & Luiselli, 1994), and post-partum mortality was found to be low in one species of snake (Luiselli, 1992).

Evidence of the disadvantages of melanism has also been accumulated. Madsen & Still (1988) found that larger male adders, usually melanistic individuals, suffered higher mortality during periods of low prey densities. Based on survival rate of individually marked adders, Forsman (1995a) suggested that predation might be higher in melanistic males.

Despite considerable scientific attention to the biological mechanisms that maintain melanistic/normal colour dimorphism in snakes, studies verifying 'thermal superiority in melanism', the central premise for the adaptive persistence of melanistic morphs, under natural condition are scarce. To the best of my knowledge, Forsman's (1995b) study is the only one that tested this premise. He found no consistent differences either in daily body temperature variation or in proportion of exposure to observers between telemetered melanistic and zigzag-patterned adders. He concluded

that colour may only exert a trivial effect on T_bs of the adders or melanistic individuals may use their thermoregulatory advantage differently depending on sex and reproductive condition.

Snakes are a highly diversified taxon (Greene, 1997), thus comparative studies of biologically dissimilar species are desirable to confirm common hypotheses and generalize results of previous studies. The Japanese four-lined snake (*Elaphe quadrivirgata*) is a suitable candidate in this respect because not only does the snake exhibits colour polymorphism including melanism but it also differs in various biological aspects from those of the adder: phylogeny, reproductive mode, foraging mode, sex of larger body size, and body form (Colubridae vs. Viperidae, oviparous vs. viviparous, active vs. sit-and-wait, male vs. female, and slender vs. stout). Furthermore, *E. quadrivirgata* exhibits the melanistic morph from hatching (Fukada, 1954; K. Tanaka, pers. observ.), whereas most individuals of melanistic adders attain their black colour gradually through ontogeny (Naulleau, 1973; Forsman, 1995a, b). Considering these differences, it is likely that the adaptive significance of melanism in *E. quadrivirgata* may be different from that of *V. berus*.

Temperatures during embryonic development could affect post-hatching behaviour and morphometrics of hatchlings (e.g. Vinegar, 1974; Osgood, 1978; Gutzke & Packard, 1987; Burger, 1989,

1990; Blouin-Demers, Kissner & Weatherhead, 2000; Deeming, 2004; Lourdais *et al.*, 2004). Precise thermoregulation is critical for viviparous snakes that retain embryos in their oviducts for relatively long periods, whereas appropriate nest-site selection would be more critical for oviparous snakes to produce healthy hatchlings (Plummer & Snell, 1988; Shine *et al.*, 1997; Shine, 2004). If this is true for *V. berus* and *E. quadrivirgata*, we can expect that thermal benefits of melanism are strongly related to sex in *V. berus* but not in *E. quadrivirgata*.

The ontogenetic timing of melanization is also important when we consider adaptive significance of this morph. For example, supposing that melanistic individuals are visually inferior and thermally superior, gradual ontogenetic melanization suggests that avoidance of predation risk rather than thermoregulation is a more critical demand for juveniles (Webb & Whiting, 2005). That is, 'being melanistic' is deleterious for young adders. On the other hand, inborn melanism of *E. quadrivirgata* may suggest that thermal superiority is one of the critical characteristics for young snakes (i.e. balancing of selection between thermal superiority and visual inferiority). Young snakes would be more vulnerable to predators than adults. Crypsis may be a critical demand for young sit-and-wait forager because they are exposed to predators for relatively long

time. On the other hand, thermal superiority may be an important for active forager because it enables them to act at optimal T_b for performance. Alternatively, thermal superiority is insignificant characteristics for young snakes and 'being melanistic' is not deleterious for them (i.e. neutral to selection forces).

To test the thermal superiority of melanism and general adaptive significance of colour dimorphism in snakes, I investigated the thermal biology of free-ranging *E. quadrivirgata* using temperature-sensitive radio transmitters. I evaluated the thermal quality of habitats using physical models of the snake. In addition, by laboratory experiment, I estimated the set-point range of the snake (T_{set}: Hertz, Huey & Stevenson, 1993), which is the target body temperature range of an animal when costs of thermoregulation are negligible.

3-2. MATERIALS AND METHODS

3-2-1. STUDY SPECIES AND STUDY SITE

Melanistic individuals of *E. quadrivirgata* occur throughout Japan, but the ratio the population displaying this morph varies with locality (Stejneger, 1907; Goris & Maeda, 2004; Mori *et al.*, 2005). On Yakushima Island, where the present study was conducted, approximately 85% of individuals are melanistic (chapter one).

The study site is covered by primary and secondary evergreen broad-leaved forest, which consists mainly of Fagaceae, Myrsinaceae, and Lauraceae (Tagawa, 1980; Agetsuma, 1995). A road runs around the island along the coast and is surrounded by forest.

3-2-2. SELECTED TEMPERATURE RANGE IN THE LABORATORY

Selected temperature range of *E. quadrivirgata* was measured in a thermal gradient apparatus (180 x 60 x 40 cm), which consisted of a steel floor and roof, and polypropylene walls. This apparatus was placed in a room, in which temperature was roughly controlled because ambient temperature affected temperature of the apparatus floor. One end of the apparatus was heated by six 60-w light bulbs located under the floor. The other end was cooled by cooling gel sheets, which were attached directly beneath the floor. As a result, surface temperature of the apparatus floor provided a thermal gradient ranging from 9 to 63°C.

Snakes were caught on Yakushima Island and brought to the laboratory, where they were individually housed in plastic cages (35 x 20 x 15 cm) with a water dish and paper substrate. The cages were placed outdoors in the botanical garden of Kyoto University to minimize the effect of thermal acclimation (Spellerberg, 1973; Scott & Pettus, 1979). Thus, snakes were exposed to the natural sunlight

(filtering down through the leaves of trees) and the natural

temperature regimes. The trials were conducted in 2003 (July,

August, and October) and 2004 (May through August). A maximum

of 33 days elapsed from capture to commencement of the trial.

In the morning, I transferred a subject snake, which had been

fasted for at least three days prior to the trial to expel gut contents,

to the experimental room. I turned on the heating light and attached

the cooling gel sheets. One hour later, I introduced the subject into

the apparatus. T_b of the subject was measured twice during a trial

using a standard thermometer (testo 925, testo K.K., Japan) to

determine the influence of daily rhythms of selected T_b in a

laboratory (e.g. Tosini & Avery, 1994; Firth & Belan, 1998). I picked

up the subject from the apparatus 1.5 h after the introduction, and

immediately the tip of the temperature probe of the thermometer

was inserted into a cloaca to measure T_b. After the measurement, the

subject was re-introduced into the apparatus and left undisturbed

until the second measurement. The measurements were always

taken at 1300 h and 1530 h.

I discarded T_b reading of subjects coiled at a corner of the

apparatus to avoid the corner effect. I treated two T_b readings of each

subject as independent data points. However, I discarded both of the

two T_b readings of a subject if it coiled at a corner in either

measurement to avoid individual bias. Thus, all subjects contributed to two data points.

The bounds of the central 50% of T_bs selected in the experiment were used to estimate T_{set} of the population (Hertz et al., 1993). After the experiment, all snakes were released at the site of capture.

3-2-3. RADIOTELEMETRY

I radio-tracked E. quadrivirgata at a western part of the Yakushima Island (approximately 200 m a.s.l.) using temperature-sensitive radio transmitters (BD-2T, Holohil Systems Ltd., Canada) for monitoring the snake's T_b. Weight of the transmitter was less than 2% of the snake body mass (range 0.82-1.95%). Before implantation, the transmitters were calibrated against a standard thermometer in a water bath with a temperature range of approximately 0 to 45°C. Equations obtained from this calibration were used to convert pulse intervals of the transmitters to the snake's T_b. Surgical implantation of the transmitters followed the procedures of Reinert & Cundall (1982) and Nishimura et al. (1995) with slight modifications. One to three days after the surgery, each snake was released at the place of capture. A total of five melanistic (all males) and three striped individuals (one male and two non-gravid females) were radio-tracked. Mean snout-vent lengths (SVL) were 982 mm (range 902-

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1038 mm) and 929 mm (range 774-1120 mm) for melanistic and striped individuals, respectively, and mean body masses (BM) were 159 g (range 110-200 g) and 156 g (range 102-207 g) for melanistic and striped individuals, respectively.

In each month of June, September, October, and November 2003, each individual was radio-tracked for 6 to 13 consecutive days. Number of individuals tracked differed among days (three to six individuals per day) because the time of the surgery differed among individuals and I temporarily lost signals of some individuals. I received the pulse of each transmitter using a portable receiver (LA12-Q, AVM Ltd., California) and a hand-held three element Yagi antenna once per hour from 0800 to 1700 h almost every day during each survey. I did not observe behaviour of the radio-tracked individuals and their occupied microhabitats except for a few cases. Because the radio-tracked individuals dispersed over a large area (distance that was measured along the road was approximately 2 km between the most distant individuals), it was almost impossible to determine the exact location of all individuals every hour.

3-2-4. OPERATIVE ENVIRONMENTAL TEMPERATURES

Operative environmental temperature (T_e: Bakken & Gates, 1975; Bakken, 1992) was measured using physical models of the snakes

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(Peterson, Gibson & Dorcas, 1993). To determine suitable materials and colouration of models, several types of models and dead melanistic and striped *E. quadrivirgata* were exposed to the sun, and their temperatures were recorded every 1 min for 2 h during the middle of a clear day. By comparing temperature profiles among them, I selected a physical model made of a hollow aluminum pipe (30 cm long, 3.2 cm diameter, 1.5 mm wall thickness) that was painted with dark gray (Creative Color Spray, No. 01 Country Blue: Asahipen Corp., Japan) and red colour spray paints (Creative Color Spray, No. 45 Ruby Red: Asahipen Corp., Japan) for models of melanistic and striped snakes, respectively. These final models predict T_b of average-sized adult snakes quite well (mean and maximum thermal discrepancy between the model and snake were 0.75 and 1.8°C for melanistic and 0.83 and 3.9°C for striped, respectively; correlation between the two readings, both $r^2 > 0.90$, $P < 0.0001$).

Both ends of the model were sealed with the rubber stoppers, and a small hole was drilled in the center of the stopper to allow entry of a thermocouple probe from a TR52 Data-Logger (T & D Inc., Japan). The sensor tip of the probe was positioned in the center of the lumen of the model.

I placed six models (three dark gray and three red coloured

models) in the study site. My aim was to identify T_es that were potentially available for snakes within their normally used area, and to clarify how snakes respond to these thermal habitats to regulate T_b with considering its availability. Thus, each dark gray coloured model was placed haphazardly with respect to biotic and abiotic features (e.g. substrate type, exposure to the sun, distance from the road, under or above litter) in a terrestrial habitat where a signal of a melanistic individual was received and where having a possibility being used by the snake. Thus, place of model was not an exact point where the snake occupied. Temperature data for habitats that *E. quadrivirgata* rarely occupied (e.g. aquatic and arboreal habitats) were not sampled. To collect temperature data for habitats that were potentially available to snakes as many as possible, each model was moved to new place almost every day after the last telemetry session in a day (i.e. 1700 h), and was remained at the same place for 24 h. Similarly, each red coloured model was placed haphazardly in a habitat where a signal of a striped individual was received. Thus, I obtained T_es for six different positions each day. Temperatures of the models were recorded every 15 min using the data-loggers.

Discrepancy between available T_b and T_e become larger as mass of an animal increase and as the rate of movement increase, that is, the larger the animal and the shorter the time spent in a particular

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thermal microhabitat, the less likely the animals are to reach equilibrium (Seebacher & Shine, 2004). However, I did not correct T_e because mass of the radio-tracked snakes was not so heavy (less than 210 g) and movements were not so frequent (compared to diurnal heliothermic lizards).

I used maximum, minimum, and median T_es to evaluate the thermal quality of habitats that snakes were normally used. All possible temperatures available to a snake in a given day are difficult to sample because I used a small number of models. Thus, maximum and minimum hourly T_es were those recorded during a monthly survey period rather than average of daily maxima and minima. I used median rather than mean to represent average thermal quality of habitat because distributions of T_es for both colour morphs were non-normal in most months. In addition, discrepancy between median and mode (T_e was rounded to the nearest whole number) was small (e.g. mean discrepancy of monthly T_e, 0.9°C; range 0.1-2.0°C), and thus median T_e could well represent potentially available average thermal habitat for snakes. I assumed that if snakes occupied habitats randomly within their normally used area, it was highly possible that their T_b profiles were similar to T_e profiles of average thermal habitat.

Median hourly T_es in each month for each colour morph were

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calculated based on the following number of records: three (or two for 0800 and 1700 h) x number of models (usually three) x days of survey. For example, median hourly T_e at 1200 h for melanistic morph in July was calculated from the T_es that were recorded at 1145, 1200, and 1215 h by each of the three dark gray coloured models during 11 days, and thus based on 99 (3 x 3 x 11) records. I did not use T_es that lagged 30 min from T_b recordings in any analyses (e.g. T_es that were recorded at 1130 or1230 h for calculation of median hourly T_e at 1200 h) based on an assumption that these T_es did not contribute to recorded T_b. Median monthly T_es for each colour morph were re-calculated by the same way that the hourly T_es were calculated. That is, monthly median was calculated from all T_es obtained in a given month with exclusion of T_es that lagged 30 min from T_b recordings.

3-2-5. INDICES OF THERMOREGULATION

I used thermoregulation indices developed in recent years to compare the extent of thermoregulation between melanistic and striped individuals (Hertz *et al.*, 1993; Christian & Weavers, 1996; Blouin-Demers & Weatherhead, 2001). I calculated the accuracy of T_b, that is d_b, as deviations of T_b from T_{set} (after Hertz *et al.*, 1993). If T_b is below T_{set}, d_b is the difference between the lower bound of T_{set}

and T_b, and if T_b is above T_{set}, d_b is the difference between the upper bound of T_{set} and T_b. For a T_b within T_{set}, d_b equals zero. Mean hourly d_bs for each individual were deviations of mean hourly T_bs of each individual from T_{set}. Similarly, mean monthly d_bs for each individual were deviations of mean monthly T_bs (average of mean hourly T_bs) of each individual from T_{set}. Mean hourly and monthly d_bs for each morph were means of these individuals' d_bs of each morph.

Similarly, I calculated the thermal quality of the habitat, that is d_e, as deviations of T_e from T_{set} (Hertz et al., 1993). It indicates how closely available T_es in a habitat match T_{set} (a large d_e means that the animal must thermoregulate carefully if it is to maintain its T_b within T_{set}). I used median T_e to calculate d_e to identify degree of deviation of average thermal habitats' quality. Hourly d_es for each colour morph were deviations of median hourly T_es of each colour morph from T_{set}. Similarly, monthly d_es for each colour morph were deviations of median monthly T_es of each colour morph from T_{set}.

From measures of d_b and d_e, I calculated the effectiveness of thermoregulation as $E = d_e - d_b$ (Blouin-Demers & Weatherhead, 2001). Positive values of E indicate that the animal thermoregulates to some extent, whereas negative values of E indicate that the animal avoids thermally favourable habitats (Blouin-Demers & Weatherhead, 2001). When the animal does not thermoregulate and selects

microhabitat randomly with respect to T_e, E will tend toward zero (Blouin-Demers & Weatherhead, 2001). Mean hourly Es for each morph were means of individuals' hourly Es of each morph. Mean monthly Es for each individual were calculated as mean monthly d_e minus mean monthly d_b, and mean monthly Es for each morph were means of these individuals' Es. I calculate d_e from median value, and thus positive values of E suggests that snakes do not thermoregulate using most available thermal habitats. To facilitate comparisons with previous studies, I also reported the Hertz index (Hertz *et al.*, 1993), which was calculated as $1 - (d_b/d_e)$.

Additionally, I calculated the thermal exploitation index (E_x), by dividing the time in which T_bs are within T_{set} by the time available for the animal to have its T_b within T_{set} (Christian & Weavers, 1996). I calculated total durations that maximum and median T_es exceeded the lower bound of T_{set}. These were regarded as the time available for the snake to have its T_b within T_{set} using of thermally extreme and average habitats.

3-2-6. MICROHABITAT USE

To obtain the information of microhabitat use by the snake, I radio-tracked three additional snakes (two melanistic and one striped individuals) in July and September 2004. The focus of this

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survey was an examination of microhabitat use, and thus I did not use the T_b data of these three individuals in the following analyses.

I categorized microhabitats used by the radio-tracked snakes into two types based on a distance to the nearest sunlit site (large gap: Endler, 1993) from the snake. If distance to the nearest sunlit site from the snake was approximately less than 10 m, the microhabitat was categorized as forest gap, and if the distance was more than 10 m, it was categorized as shaded forest. Because of a topographical constraint (steep and thickly vegetated study site) and a high propensity of *E. quadrivirgata* react to human approach, I had to abandon close approaches to visually confirm the exact location of the radio-tracked snakes on many occasions. However, I regarded my estimation of the location was accurate in most cases because the received pulse of the transmitter was almost as strong as that when direct observation was made.

I radio-tracked each individual 2-3 times/day. Intertracking interval was set at more than 2 h (usually 3 h), and each individual was almost equally tracked various times of the day during a survey period. Successive observations in a day may not be independent for some species such as sit-and-wait foragers because they often occupy a same place for a long period (e.g. May *et al.*, 1996). However, because *E. quadrivirgata* is a diurnal active forager (Ota, 1986; Mori,

1989) and the snakes frequently moved during intertracking

periods, I regarded each observation as an independent point for

statistical analyses. A total of nine and seven day surveys were

conducted in July and September 2004, respectively.

3-2-7. STATISTICAL ANALYSES

Statistical analyses were performed with the data averaged for each

individual over the period appropriate for each specific analysis

(hour, month). I checked normality using Shapiro-Wilks test and

homogeneity of variance using Bartlett's test before parametric tests

were conducted. If necessary, I transformed the data to meet the

assumptions of parametric tests. I used non-parametric tests if

transformation did not improve non-normal distribution of the data.

Mean monthly T_bs, d_bs, and Es were analyzed using two-factor

ANOVA with morph and month as fixed-effects factors and subject as

a random-effects factor. Significance of statistical tests was accepted

at $\alpha = 0.05$. Data were presented as mean $\pm$ 1 SE.

3-3. RESULTS

3-3-1. TEMPERATURES SELECTED IN THE LABORATORY

A total of 68 T_b readings from 34 individuals (31 melanistic and 3

striped individuals) were used to determine T_{set} of the population.

Selected T_b did not differ between the first and the second measurements (paired t-test, d.f. = 66, t = -0.11, P = 0.91), and thus I pooled the two measurements to determining T_{set}. Median of T_b was 30.2°C, and 25% and 75% quartiles were 28.0 and 31.6°C, respectively. Thus, I considered T_{set} of the population as 28.0-31.6°C.

3-3-2. THERMAL QUALITY OF HABITATS

In July, nearly 50% of T_es were higher than the lower bound of T_{set} (i.e. 28°C) in both dark gray and red coloured models (Table 3-1). The percentage that T_es were within T_{set} drastically decreased in September (Table 3-1). T_es did not differ between the two colour models in July, September, and October (Mann-Whitney U-test, July, Z = 0.54, P = 0.59; September, Z = 1.25, P = 0.21; October, Z = -1.18, P = 0.24), whereas T_es were higher in red coloured (i.e. striped) models than in dark gray coloured (i.e. melanistic) ones in November (Z = 4.08, P = 0.001).

In July, median hourly T_es exceeded the lower bound of T_{set} after the midday and were maintained within T_{set} in 60% of the time of a day in both colour models (Fig. 3-1A). In September to November, median hourly T_es never exceeded the lower bound of T_{set} (Fig. 3-1B, C, and D). Maximum hourly T_es were higher in striped morphs than in melanistic morphs in September (Wilcoxon signed-rank test, T = 8,

$P = 0.047$), whereas the maximum T_es did not significantly differ in the other months (July, $T = 15$, $P = 0.20$; October, $T = 26$, $P = 0.88$; November, $T = 13$, $P = 0.14$).

Median monthly T_es never exceeded the lower bound of T_{set} in any month (Table 3-2). Two-factor ANOVA (month and morph as factors) revealed that month had significant effects on median monthly T_es ($F_{3,3} = 307.3$, $P = 0.0003$), whereas colour did not ($F_{1,3} = 0.33$, $P = 0.60$).

Mean hourly d_es varied from 0 to 2.2°C in July (Fig. 3-2A). After 1200 h, almost all d_es were 0°C in both colour models (Fig. 3-2A). Mean hourly d_es varied from 1.8 to 4.2°C in September, 6.5 to 10.7°C in October, and 7.5 to 11.2°C in November (Fig. 3-2B, C, and D). Mean hourly d_es did not significantly differ between the two colour models in July and October (July, $T = 0$, $P = 0.06$; October, $T = 2$, $P = 0.09$). In September, mean hourly d_es were significantly higher in striped models than in melanistic ones ($T = 1$, $P = 0.01$), whereas the d_es were significantly higher in melanistic models than in striped ones in November ($T = 0$, $P = 0.005$).

Mean monthly d_es varied from 0.2°C in July to 10.0°C in November (Fig. 3-3). Mean monthly d_e was calculated from monthly T_e (i.e. 28 - mean monthly T_e), and thus statistical analysis was omitted (see result for monthly T_e).

3-3-3. FIELD BODY TEMPERATURES OF RADIO-TRACKED SNAKES

I obtained a total of 1614 T_b measurements (890 and 724 for melanistic and striped individuals, respectively) from seven snakes during 40 days (mean 23.1 d/snake, range 13-35 d). In July, 44.3% and 49.6% of T_bs were higher than the lower bound of T_{set} in melanistic and striped individuals, respectively (Table 3-1). Intermorph differences of this value became larger in September and October (Table 3-1).

I calculated the time that mean hourly T_b was within T_{set} for each individual. In July, T_b of melanistic individuals was within T_{set} for 58.1% of the day on average, whereas the corresponding value for striped individuals was 61.6%. Mean hourly T_bs of both melanistic and striped individuals gradually increased in the morning, reaching the lower bound of T_{set} at approximately 1130 h, and then T_bs were maintained within T_{set} throughout the day (Fig. 3-1A). In September, mean hourly T_bs of melanistic individuals were relatively stable throughout the day (Fig. 3-1B). On the other hand, those of striped individuals gradually increased, and became relatively stable until the evening, keeping T_b above median T_e (Fig. 3-1B). In October and November, mean hourly T_bs never reached the lower bound of T_{set} (Fig. 3-1C and D). Mean hourly T_bs of both melanistic and striped

individuals peaked in the middle of the day and were relatively stable until the evening in October (Fig. 3-1C), whereas those in November were relatively stable throughout the day, being lower than median T_es (Fig. 3-1D). Mean hourly T_bs did not significantly differ between melanistic and striped individuals in July ($T = 9$, $P = 0.11$), whereas the T_bs were significantly higher in striped individuals than in melanistic individuals in the other months (September, $T = 5$, $P = 0.038$; October, $T = 6$, $P = 0.0498$; November, $T = 1$, $P = 0.007$). ANOVA indicated that month had significant effects on the mean monthly T_bs, whereas the other factors and the interaction between month and morph did not (Table 3-3).

3-3-4. EFFECTIVENESS OF THERMOREGULATION

Mean hourly d_bs varied from 0.2 to 1.7°C in July, 0.5 to 2.9°C in September, 5.7 to 11.0°C in October, and 8.0 to 12.2°C in November (Fig. 3-2). Striped individuals exhibited lower values than melanistic individuals most of the time (Fig. 3-2). Mean hourly d_bs are almost identical between melanistic and striped individuals in July (six out of ten d_b values was tie), whereas the d_bs were significantly higher in melanistic individuals than in striped individuals in the other months (September, $T = 2$, $P = 0.04$; October, $T = 2$, $P = 0.0498$; November, $T = 1$, $P = 0.007$).

Mean hourly d_b of striped individuals was highly correlated with hourly d_e in July, September, and October (all, $r^2 > 0.91$, $P < 0.0001$), whereas no significant correlation was obtained in November ($r^2 = 0.06$, $P = 0.49$) (Fig. 3-4). In melanistic individuals, mean hourly d_b was highly correlated with hourly d_e in July ($r^2 = 0.97$, $P < 0.0001$) and October ($r^2 = 0.79$, $P = 0.0006$), whereas no significant correlations were obtained in September ($r^2 = 0.14$, $P = 0.28$) and November ($r^2 = 0.20$, $P = 0.19$)(Fig. 3-4). Intermorph differences of the relationships between mean hourly d_b and d_e were prominent in September, as T_bs of melanistic individuals were mostly constant irrespective of the changes of T_es.

Mean monthly d_bs varied from 0°C in July to 11.5°C in November (Fig. 3-3). Because d_b and T_b are interrelated, a two-factor ANOVA showed a result similar to the T_b data. That is, month had significant effects on mean monthly d_bs ($F_{3, 6} = 28.89$, $P = 0.0006$), whereas the other factors and the interaction between month and morph did not (morph, $F_{1, 6} = 0.22$, $P = 0.65$; subjects, $F_{5, 6} = 1.74$, $P = 0.26$; month x morph, $F_{3, 6} = 0.013$, $P = 0.99$).

Mean hourly Es did not significantly differ between melanistic and striped individuals in July ($T = 2$, $P = 0.13$) and November ($T = 15$, $P = 0.38$), whereas the Es were significantly higher in striped individuals than in melanistic individuals in the other months

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(September, $T = 5$, $P = 0.02$; October, $T = 0$, $P = 0.005$; Fig. 3-5). Both melanistic and striped individuals exhibited positive Es in September and negative Es in November (Table 3-4). Although striped individuals tended to have higher values of mean monthly E than melanistic individuals (Table 3-4), two-factor ANOVA indicated all factors and the interaction had no significant effects on the E (morph, $F_{1, 6} = 0.08$, $P = 0.79$; month, $F_{3, 6} = 0.89$, $P = 0.50$; subjects, $F_{5, 6} = 1.63$, $P = 0.28$; morph x month, $F_{3, 6} = 0.06$, $P = 0.98$). The Hertz index (Hertz et al., 1993) indicated the occurrence of careful thermoregulation by both melanistic and striped individuals in July (Table3-4).

3-3-5. DEGREE OF THERMAL EXPLOITATION

In July, both melanistic and striped individuals exhibited relatively high E_x values, whereas almost all E_x values were zero in the other months (Table 3-5). Striped individuals exhibited higher E_x values than melanistic individuals (Table 3-5). Average time when maximum hourly T_e exceeded the lower bound of T_{set} was longer in striped morph than in melanistic morphs (Fig. 3-1 and Table 3-5). I calculated percentage of the time that mean hourly T_bs exceed median hourly T_es. Differences between melanistic and striped individuals were pronounced in September and October, when the

index for melanistic individuals was approximately a half of that of striped individuals (Fig. 3-6).

3-3-6. MICROHABITAT USE

Microhabitat use in each month did not significantly differ between the two melanistic individuals (Fisher's exact tests, July, $P = 0.354$; September, $P = 0.058$), and thus I combined them. Striped individual used the forest gap predominantly: it used the shaded forest in 0% and 7.7% of the total observations in July and September, respectively (Table 3-6). Melanistic individuals used the shaded forest in 29.4% and 12.1% of the total observations in July and September, respectively (Table 3-6). Differences of microhabitat use between melanistic and striped individuals were statistically significant in July ($P = 0.008$), but not in September ($P = 0.562$). When the data of the two months were combined (microhabitat use did not differ between the two months in both melanistic and striped individuals), statistically significant intermorph differences in microhabitat use were detected ($P = 0.019$).

3-4. DISCUSSION

3-4-1. THERMAL ENVIRONMENTS AND THERMOREGULATION

Thermal environment in early summer in the study site seems

benign because the snakes are able to maintain their T_b within T_{set} during the midday to evening period (over 50% of the time during the day) by using average thermal habitats. Thermal environments of the study site are relatively severe for *E. quadrivirgata* in autumn and early winter. For example, only < 8% of T_es reached the lower bound of T_{set}, and median hourly T_es never exceeded this boundary during this time. Hourly d_e reached 4.2°C and 11.2°C in the morning in September and November, respectively. Monthly d_es became higher as season progressed, and reached 10°C in November.

Maximum hourly T_es were higher in the striped morph than in melanistic morph, especially in September (Fig. 3-1), indicating that habitats striped individuals normally used included warmer microhabitats such as forest gaps than those used by melanistic individuals. Although I have no quantitative data on the availability of each microhabitat, forest gaps were considerably less abundant than shaded forest in terms of overall area. Mean hourly T_bs of striped individuals were higher than median hourly T_es in most of a day in September and October. Mean hourly T_bs of striped individuals were usually higher than those of melanistic individuals in any month (Fig. 3-1). As a result, mean hourly d_bs of striped individuals were usually smaller than melanistic individuals in any month (Fig. 3-2). Mean hourly Es of striped individuals were higher

than melanistic individuals in September and October (Fig. 3-5). Furthermore, the period during which mean hourly T_bs exceeded median hourly T_es was longer in striped individuals. These facts suggest that striped individuals make more thermoregulatory efforts than do melanistic individuals.

In contrast with striped individuals, mean hourly d_bs of melanistic individuals were relatively constant in September regardless of the change of hourly d_es. This constancy of the d_bs irrespective of changes in d_e suggests that melanistic individuals increase thermoregulatory investment only when thermal quality of habitats is low. They do not make a greater effort to achieve T_bs close to T_{set}, and accept thermoconformity when the thermal quality of habitats is high. These patterns are partially consistent with lizard thermoregulatory behaviour: the effectiveness of thermoregulation (i.e. $E = d_e - d_b$) decreased with increasing thermal quality of the habitat, that is, a slope < 1 for equation regressing d_b on d_e (Blouin-Demers & Nadeau, 2005). On the other hand, striped individuals seem to always make thermoregulatory efforts according to changes in the d_es.

In September, maintenance of T_b within T_{set} will be difficult to achieve using average thermal habitats. Presumably, the snakes satisfy their thermoregulatory demands by using more thermally

favourable microhabitats. In October, both melanistic and striped individuals exhibited thermoconformity (Fig. 3-4C). Despite the fact that 135-390 min per day was potentially available for the snakes to attain T_b within T_{set} by using thermally extreme microhabitats in October and November, neither melanistic nor striped individuals appeared to take advantage of these thermal habitats. Use of a particular habitat for thermoregulation should be beneficial when the associated costs are low (Huey & Slatkin, 1976) or disadvantages of thermoconformity are higher than costs of thermoregulation (Blouin-Demers & Nadeau, 2005). Costs of thermoregulation become high as, for example, the time to search for thermally suitable microhabitats increases. Thus, the rarity of thermally suitable microhabitats within their normally used area (i.e. higher costs are required for thermoregulation) leads the snakes to accept thermoconformity at these times. In November, the correlation between mean hourly d_b and d_e was low and the d_b was relatively constant in both melanistic and striped individuals. This figure may indicate occupancy of relatively stable thermal environments for hibernation.

Mean monthly Es for melanistic and striped individuals were positive in July and September. Specifically, striped individuals exhibited the highest value (1.4) in September, indicating active

thermoregulation by this morph. Hertz index values (Hertz *et al.*, 1993) indicate careful thermoregulation by both melanistic and striped individuals in July. This result is attributable to the prevalence of thermally suitable environments rather than the consequence of careful thermoregulation by the snake: when thermal environments are suitable, snakes may be able to maintain their T_b within T_{set} even if they are thermoconformers (see Blouin-Demers & Weatherhead, 2001 for more detailed discussion).

Overall, it is evident that both melanistic and striped *E. quadrivirgata* behaviourally regulate their T_b. However, striped individuals always regulate their T_b more actively and precisely (with respect to T_{set}) than melanistic individuals.

3-4-2. THERMAL SUPERIORITY OF MELANISM

Contrary to the expectation that melanistic individuals will be precise thermoregulators, the results suggest that striped individuals are apparently more active and precise thermoregulators than melanistic individuals. Nonetheless, this would indicate, thermal superiority of melanistic individuals over striped individuals.

In September, and also partially in October, melanistic individuals seem to modify thermoregulation strategy in

consideration of the thermal environments (Fig. 3-4B and C). These features may represent efficient thermoregulation of melanistic individuals. As mentioned above, striped individuals tend to use thermally favourable but rare microhabitats such as forest gaps more frequently than do melanistic individuals. Owing to this effort, striped individuals would be able to maintain their T_b at a comparable level to melanistic individuals.

Restriction of activities to the vicinity of a rare microhabitat to satisfy thermoregulatory demand in striped individuals poses serious constraints on time available for other activities such as foraging and mate searching, and also limits resources (e.g. food, mate) available to them compared to melanistic individuals. Considering the fact that heating rate is slower in striped individuals than in melanistic individuals under an experimental condition (chapter two), activity of striped individuals may be spatio-temporally constrained due to their thermal inferiority. Actually, activity of striped individuals in the study site is low in winter, (chapter one), suggesting that the annual activity period of striped individuals is shorter than that of melanistic individuals.

However, if food resources are abundant in forest gaps, and striped individuals select this habitat actively, we cannot regard their habitat use as a consequence of thermal constraint. This

possibility seems unlikely because the proportion of stomach that contained food is significantly lower in striped individuals than in melanistic individuals (chapter one). It may suggest that distribution of food resources is not biased toward forest gaps. Thus, habitat use of striped individuals may not be a consequence of active selection to satisfy demands other than thermoregulation. Alternatively, striped individuals may waste more time in thermoregulation than melanistic individuals, and thus the former cannot use food resources sufficiently nonetheless these resources are abundant in their selected habitat. Thus, I conclude that striped individuals are spatio-temporally constrained due to their thermal inferiority, and that melanistic individuals are superior in thermoregulation compared to striped individuals.

GENERAL DISCUSSION

I found that *E. quadrivirgata* on Yakushima Island exhibits peculiar features on diet, body sizes, and morph frequency compared to main-island populations. Main-island populations of *E. quadrivirgata* eat mainly anuran prey (Fukada, 1992; Kadowaki, 1992), whereas the snakes on Yakushima Island heavily rely their diet on scincid lizard. Geographic differences of diet would reflect differences of abundance of prey animals among the study sites.

Body sizes of *E. quadrivirgata* on Yakushima Island were smaller than those of the main-island population, and the ratio of melanistic individuals was remarkably high. Numerous studies showed the importance of colour and body size on thermal aspects of ectotherms (e.g. Watt, 1968; Gibson & Falls, 1979; Brakefield & Willmer, 1985; Stevenson, 1985; Stewart & Dixon, 1989; Forsman, 1995b, 1997; De Jong *et al.*, 1996; Forsman *et al.*, 2002; Gross *et al.*, 2004). I showed that body size as well as colour plays an important role on thermal aspects of *E. quadrivirgata*. That is, melanistic individuals of *E. quadrivirgata* heated faster than striped individuals and that intermorph difference in heating rates was larger in small size snakes than in large size snakes. Considering these facts, it may be possible that small body size helps maintain the prevalence of melanism on Yakushima Island.

A high proportion of melanistic morphs in dwarf populations of *E. quadrivirgata* also occurs on Oh-shima Island, located off the south coast of central main-island (Hasegawa & Moriguchi, 1989; Goris & Maeda, 2004). The body size of snakes is geographically highly plastic, and has primarily been considered to be a direct phenotypic response to local prey type and size (Schwaner, 1985; Hasegawa & Moriguchi, 1989; Forsman, 1991; Kohno & Ota, 1991; Mori, 1994; chapter one). Thus, the body size trend and the origin and maintenance of colour dimorphism within a population must be governed by independent mechanisms, but a secondary linkage between small size and a high frequency of melanism may exist on the basis of thermal advantage. Similarly to *E. quadrivirgata* in the present study, melanism usually prevails in species of ladybird beetles small in body size (Stewart & Dixon, 1989), although interpretation of this observation contrasts with that presented here (i.e. advantage of rapid heating in small snakes vs. disadvantage of overheating in large ladybird beetles). From the perspective of evolutionary biology, direct and indirect links between morphology, physiology, behaviour, and fitness give a fruitful area for future study (Willmer, 1991; Garland & Losos, 1992).

I quantitatively evaluated thermoregulation of free-ranging *E. quadrivirgata* by radiotelemetric survey. Based on this survey and

the results of heating experiment, I concluded that melanistic individuals were superior in thermoregulation compared to striped individuals. Theoretically, there are four different possible means by which striped individuals may manage their relative thermal inferiority. First, striped individuals would maintain a level of thermoregulatory accuracy similar to that of melanistic individuals and accept a suboptimal T_b for activities. Second, they would devote the time required and restrict other activities to the vicinity of a specific habitat to attain a T_b comparable to melanistic individuals. Third, they would adopt a thermoconforming strategy. Fourth, they would lower T_{set}. The first possibility is rejected by the field data: field active T_bs of striped individuals are not lower than those of melanistic individuals (chapters one and three). As shown in chapter three, the present study supports the second possibility. Thermoregulatory effort shown by striped individuals is inconsistent with the third possibility (chapter three). In the present study, I could not make direct comparison of T_{set} between the two morphs due to a small sample size of striped individuals used in the experiment. Circumstantial evidences (i.e. field active T_bs are not lower in striped individuals, striped individuals do make thermoregulatory effort; chapters one and three) are at least inconsistent with the fourth possibility.

In the adder, frequency of melanism is significantly higher in females than in males (Luiselli, 1992, 1993; Forsman, 1995a), whereas there are no significant sexual differences in this frequency in *E. quadrivirgata* (chapter one). This interspecific difference may reflect a differential advantage of 'being melanistic' between viviparous and oviparous snakes (see also Introduction of chapter three). Based on a heating experiment under laboratory conditions, Bittner *et al.* (2002) suggested that if melanism does confer a selective thermal advantage in the garter snake, it is restricted to larger individuals. The garter snake is viviparous, and females attain larger body sizes than males, as with the adder. Bittner (2003) also showed that juvenile snake clay models were attacked more frequently than adult snake clay models irrespective of colour. I showed that melanistic individuals of *E. quadrivirgata* heated faster than striped individuals and that intermorph difference in heating rates was larger in small size snakes than in large size snakes (chapter two). These facts, together with interspecific difference of the ontogenetic timing of melanization, suggest that reproductive mode, foraging mode, and body sizes including direction of sexual size dimorphism must be important key features that should be considered when investigating the adaptive significance of melanism in snakes from the thermal aspects. Obviously, these features

influence various behaviours, and in turn influence susceptibility to predators. Thus, these features must be also important to consider when we investigate the adaptive significance of melanism in snakes from other aspects.

In my study, I verified a part of premises for the adaptive advantage of melanistic snakes. To elucidate the mechanisms of maintenance of melanistic/striped colour dimorphism in *E. quadrivirgata*, and explain the prevalence of melanistic individuals on Yakushima Island, further studies from various aspects are necessary.

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Table 1-1. The numbers of the two color morphs of *Elaphe*

quadrivirgata on Yakushima Island observed in different years.

Figures include six melanistic road-killed individuals.

Recaptures within same years are excluded.

	1981	1998	1999	2000	1998 - 2000
Melanistic	22	30	32	37	95
Striped	17	6	3	5	13

Table 1-2. Prey items obtained from stomachs of

Elaphe quadrivirgata on Yakushima Island.

Thirty-four stomachs contained at least one prey

item out of 120 stomachs examined.

N = total number of prey; % = frequency of

occurrence of prey.

Prey	N	%
Eumeces japonicus	23	53.5
Takydromus tachydromoides	16	37.2
Gekko yakuensis	2	4.7
Gloydius blomhoffii	1	2.3
Unidentified fragments	1	2.3

Table 1-3. Mean snout-vent length (SVL) and body mass (BM) of *Elaphe quadrivirgata* on

Yakushima Island and in Kyoto (data from Fukada, 1992). Immature individuals (see text for definition)

and recaptures are excluded. Fresh road-killed individuals are included. Gravid females are excluded

from the calculation of mean BM. Figures in parentheses exclude gravid females. N = sample size.

Locality	Sex	N	SVL (mm)			BM (g)		
			Mean	SE	Range	Mean	SE	Range
Yakushima	Males	36	827.6	22.4	531-1074	113.6	7.4	30.0-210
	Females	31 (29)	742.4	16.6	544-938	91.3	6.3	39.4-160
Kyoto	Males	—	1077.7	—	—	300	—	—
	Females	—	864.2	—	—	250	—	—

Table 1-4. Composition of the two colour morphs of hatchling

Elaphe quadrivirgata on Yakushima Island and their mothers.

[male, female]

| Mother (ID) | Hatchlings | | % of |
	Melanistic	Striped	melanistic
Striped (113)	0	5	0
Striped (117)	2	2	50
Melanistic (76)	1	2	33.3
Melanistic (154)	0	4	0
Melanistic (156)	3	0	100
Melanistic (157)	4	0	100
Melanistic (163)	1	2	33.3
Melanistic (209)	4	0	100
Melanistic (211)	2	1	66.7
Total	17 [8, 9]	16 [8, 8]	51.5

Table 1-5. Summary of data for body temperature (T_b),

air temperature (T_a), and substrate temperatures (T_s) for

Elaphe quadrivirgata on Yakushima Island (all in °C).

Recaptures are included. Values are given as mean ± 1 SE.

Ranges are in parentheses. Sample size = 116.

T_b	T_a	T_s
27.4 ± 0.33	25.2 ± 0.31	26.7 ± 0.42
(18.1-34.6)	(15.4-32.3)	(15.5-42.5)

Table 2-1. Mean ± 1 SE of parameter values of the von Bertalanffy equation

fitted to body temperature data during heating for melanistic and striped morphs

of *Elaphe quadrivirgata*. Ranges are given in parentheses. N = sample sizes.

Morph	N	Equilibrium temperature (°C)	Heating coefficient (min^{-1})
Melanistic	13	50.3 ± 3.4 (40.3-86.5)	0.0304 ± 0.0038 (0.0085-0.0656)
Striped	14	53.4 ± 3.3 (38.9-79.8)	0.0238 ± 0.0035 (0.0071-0.0470)

Table 3-1. Percentage of body and operative environmental temperatures (T_b and T_e, respectively) which were higher than the lower bound of the set-point range (28.0°C) in melanistic and striped *Elaphe quadrivirgata* on Yakushima Island. Sample sizes are shown in parentheses.

Morph		Month			
		July	September	October	November
Melanistic	T_b	44.3 (203)	2.4 (328)	5.9 (239)	0 (120)
	T_e	47.5 (924)	6.1 (772)	7.9 (896)	1.8 (504)
Striped	T_b	49.6 (117)	16.4 (324)	12.9 (203)	0 (80)
	T_e	46.9 (924)	6.6 (1102)	6.8 (616)	4.2 (336)

Table 3-2. Monthly mean body and median operative environmental temperatures (T_b and T_e, respectively) of

radio-tracked melanistic and striped *Elaphe quadrivirgata* on Yakushima Island. Numbers in parentheses indicate

the total number of the radio-tracked snakes (snake day). N = number of radio-tracked snakes or T_e measurements.

T_b is followed by ± 1 SE.

Morph		July (34)		September (58)		October (50)		November (20)	
		N	Mean or Median	N	Mean or Median	N	Mean or Median	N	Mean or Median
Melanistic	T_b (°C)	2	28.2 ± 0.1	2	26.1 ± 1.1	3	19.1 ± 1.1	2	16.6 ± 3.6
	T_e (°C)	924	27.8	772	25.2	896	19.4	504	18.0
Striped	T_b (°C)	2	28.5 ± 0.2	3	26.6 ± 0.4	3	19.8 ± 2.4	2	18.1 ± 1.7
	T_e (°C)	924	27.8	1102	25.2	616	19.1	336	18.9

Table 3-3. Summary results of two-factor ANOVA for the

effects of month, morph, and subjects nested within morphs

on body temperatures of radio-tracked melanistic and

striped *Elaphe quadrivirgata* on Yakushima Island.

Predictor	d.f.	S.S.	F	P
Month	3, 6	181.11	10.87	0.008
Morph	1, 6	1.34	0.24	0.64
Subjects [Morph]	5, 6	42.47	1.53	0.31
Month x Morph	3, 6	0.62	0.04	0.99

Table 3-4. Monthly changes of effectiveness of thermoregulation (E,

followed by ± 1 SE) for radio-tracked melanistic and striped *Elaphe*

quadrivirgata on Yakushima Island. E is an index proposed by

Blouin-Demers & Weatherhead (2001), and was calculated as $E = d_e - d_b$.

Hertz index is an index proposed by Hertz *et al.* (1993) and was calculated

as $1 - (d_e/d_b)$. d_e is deviation of operative environmental temperature

from set-point range of *E. quadrivirgata* from Yakushima Island, and

represents thermal quality of habitats. d_b is deviation of body

temperature from the set-point rage, and represents accuracy of body

temperature.

Month	Melanistic		Striped	
	E	Hertz index	E	Hertz index
July	0.2	1	0.2	1
September	0.85 ± 1.1	0.30 ± 0.4	1.40 ± 0.4	0.50 ± 0.4
October	-0.33 ± 1.1	-0.04 ± 0.1	0.73 ± 2.4	0.08 ± 0.3
November	-1.45 ± 3.6	-0.15 ± 0.4	-0.80 ± 1.7	-0.09 ± 0.2

Table 3-5. The time that maximum and median hourly operative environmental

temperatures (T_es) for melanistic and striped *Elaphe quadrivirgata* on Yakushima

Island exceeded the lower bound of set-point range (T_{set}) between 0800 and 1700 h.

Thermal exploitation index (E_x) was calculated as the time in which snake's T_bs are

within T_{set}, divided by the time available for the animal to have its T_b within T_{set}

(Christian & Weavers, 1996).

Month	Melanistic				Striped			
	Maximum T_e		Median T_e		Maximum T_e		Median T_e	
	Time (min)	E_x	Time (min)	E_x	Time (min)	E_x	Time (min)	E_x
July	480	0.65	330	0.95	480	0.69	300	1.11
September	360	0	0		465	0.07	0	*
October	270	0	0		390	0	0	
November	135	0	0		210	0	0	

* Nevertheless of median T_es did not exceeded the lower bound of T_{set}, mean T_b of

striped individuals exceeded it by 30 min.

Table 3-6. Number of locations of radio-tracked melanistic and
striped *Elaphe quadrivirgata* in two microhabitat categories on
Yakushima Island. Microhabitats were categorized into two types
based on a distance to the nearest sunlit site from the snake
(see text for definitions). Number of direct observations of the snake
are given in parentheses.

Month	Morph	Microhabitat	
		Forest gap	Shaded forest
July	Melanistic	24 (6)	10 (3)
	Striped	18 (1)	0
September	Melanistic	29 (3)	4 (1)
	Striped	12 (3)	1

Appendix. I present dietary data obtained after the 2000 survey.

Numbers of prey items were shown. Percentage of each item was given in parentheses. [the numbers of stomachs containing at least one prey, the total numbers of stomachs examined]

Prey	Melanistic [64, 253]		Striped [6, 40]	
	Male	Female	Male	Female
Eumeces japonicus	40 (69.0)	12 (46.2)	1 (20.0)	1 (33.3)
Takydromus tachydromoides	12 (20.7)	11 (42.3)	1 (20.0)	1 (33.3)
Gekko yakuensis	4 (6.9)	2 (7.7)	2 (40.0)	0
Gloydius blomhoffii	1 (1.7)	0	0	0
Hyla japonica	1 (1.7)	0	0	0
Egg (species unidentified)	0	1 (3.8)	1 (20.0)	0
Unidentified flagments	0	0	0	1 (33.3)
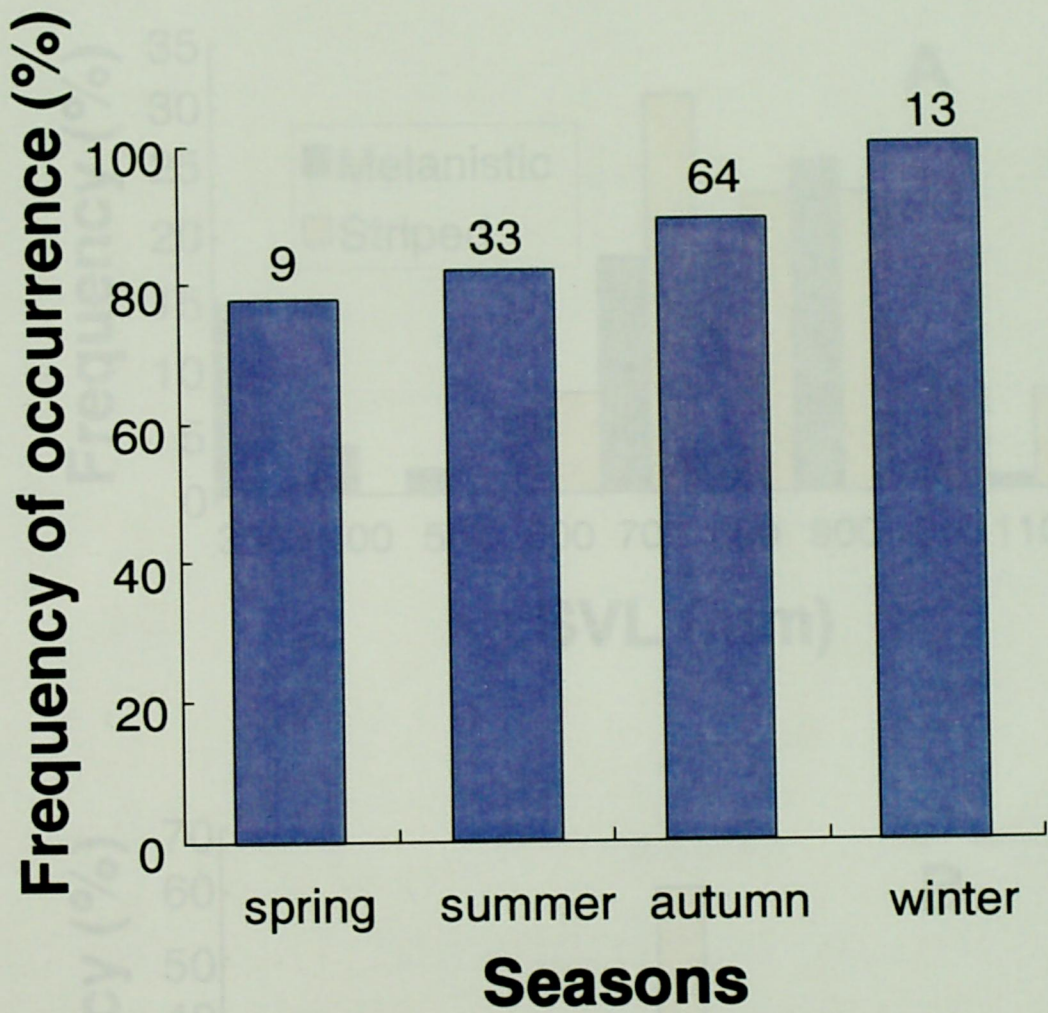
Figure 1-1. Seasonal variation in frequency of occurrence of melanistic morph of *Elaphe quadrivirgata* on Yakushima Island. Data representing spring, summer, autumn, and winter were obtained during May, June-August, September-October, and November-December, respectively. Numerals above bars denote sample sizes.
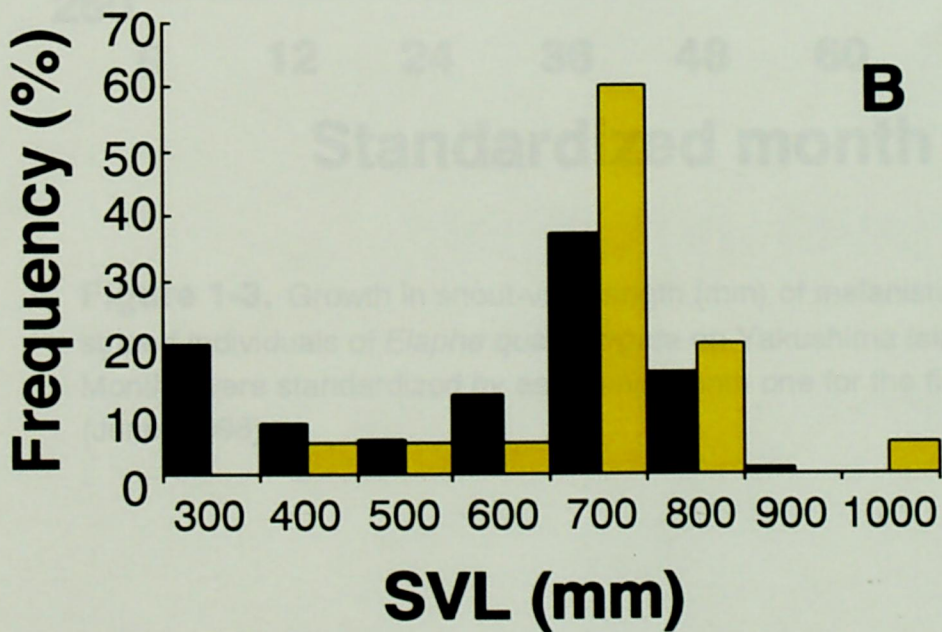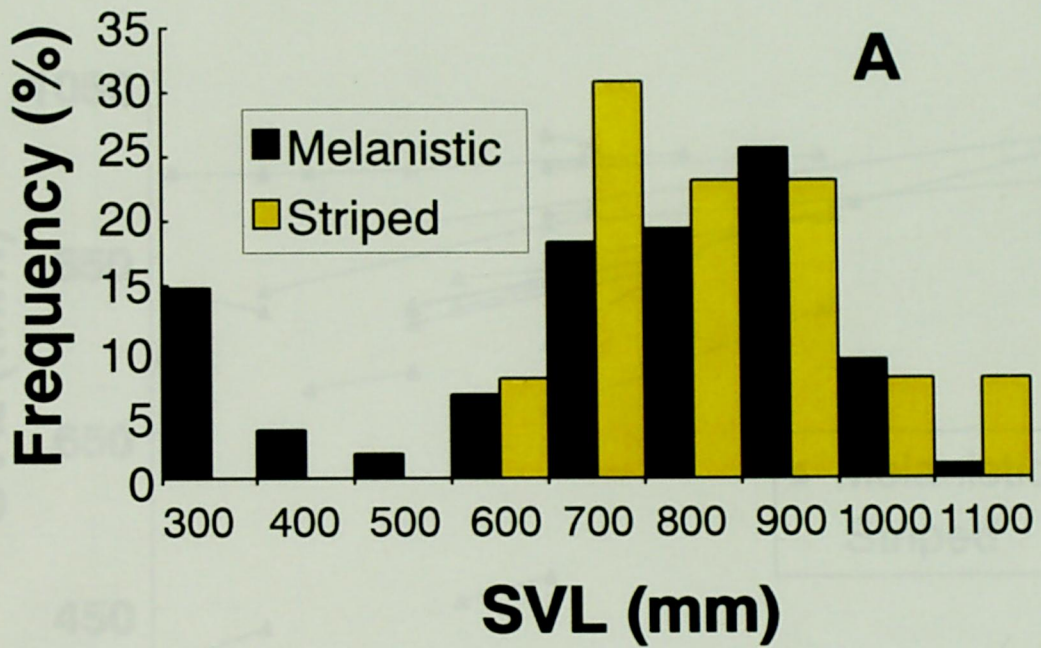
Figure 1-2. Size frequency distribution of melanistic and striped morphs of *Elaphe quadrivirgata* on Yakushima Island. (A): males; (B) females.
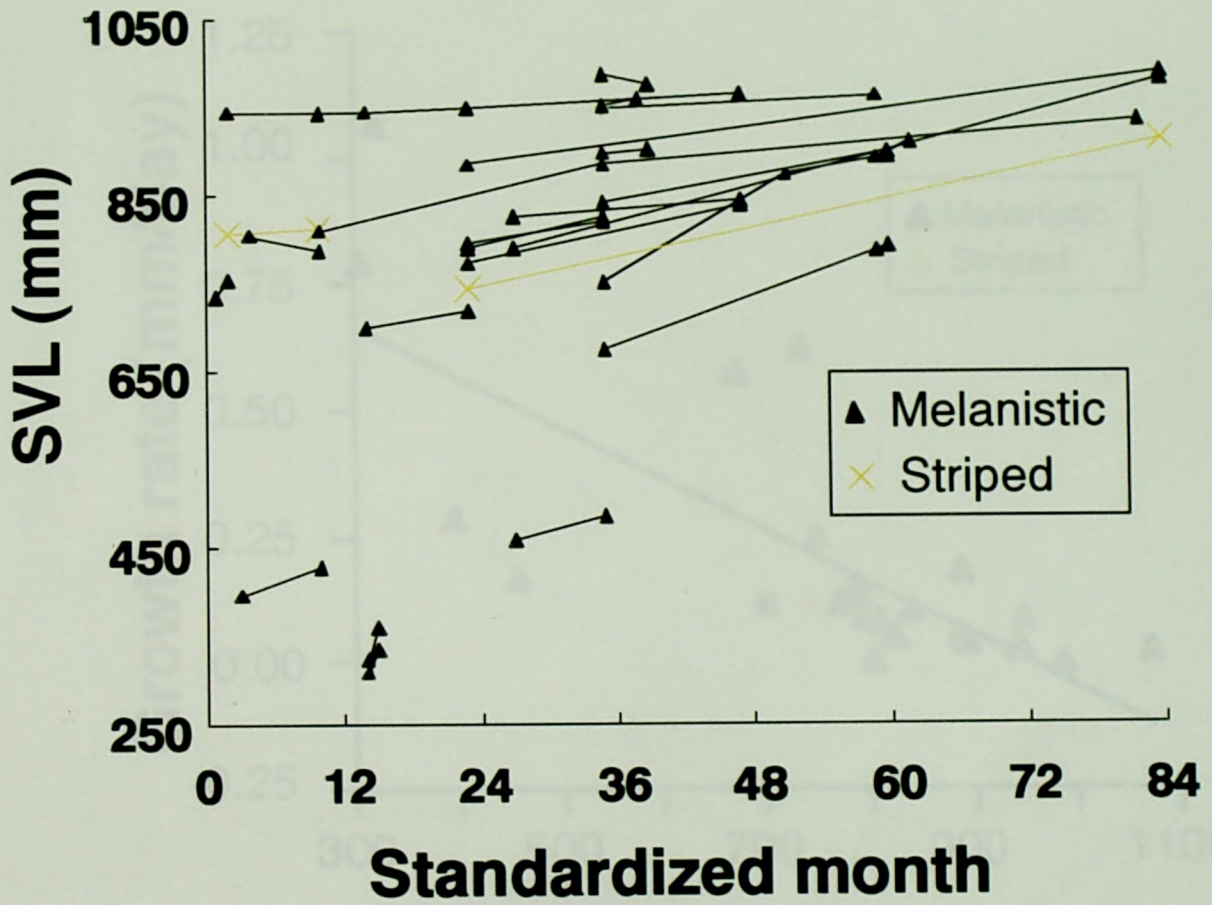
Figure 1-3. Growth in snout-vent length (mm) of melanistic and striped individuals of *Elaphe quadrivirgata* on Yakushima Island. Months were standardized by assigning month one for the first survey (June, 1998)
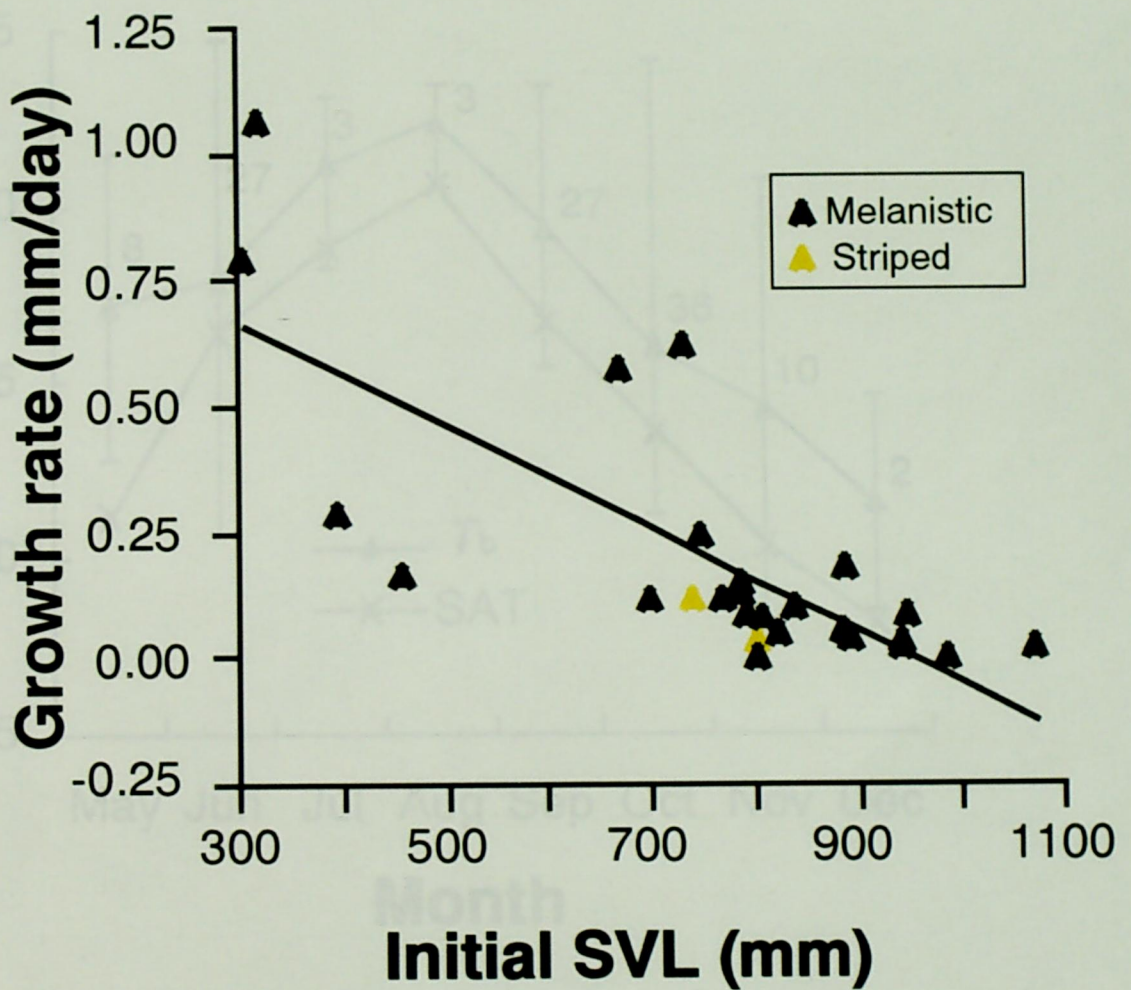
Figure 1-4. Relationship between growth rate in snout-vent lenght (SVL) and SVL at first capture.
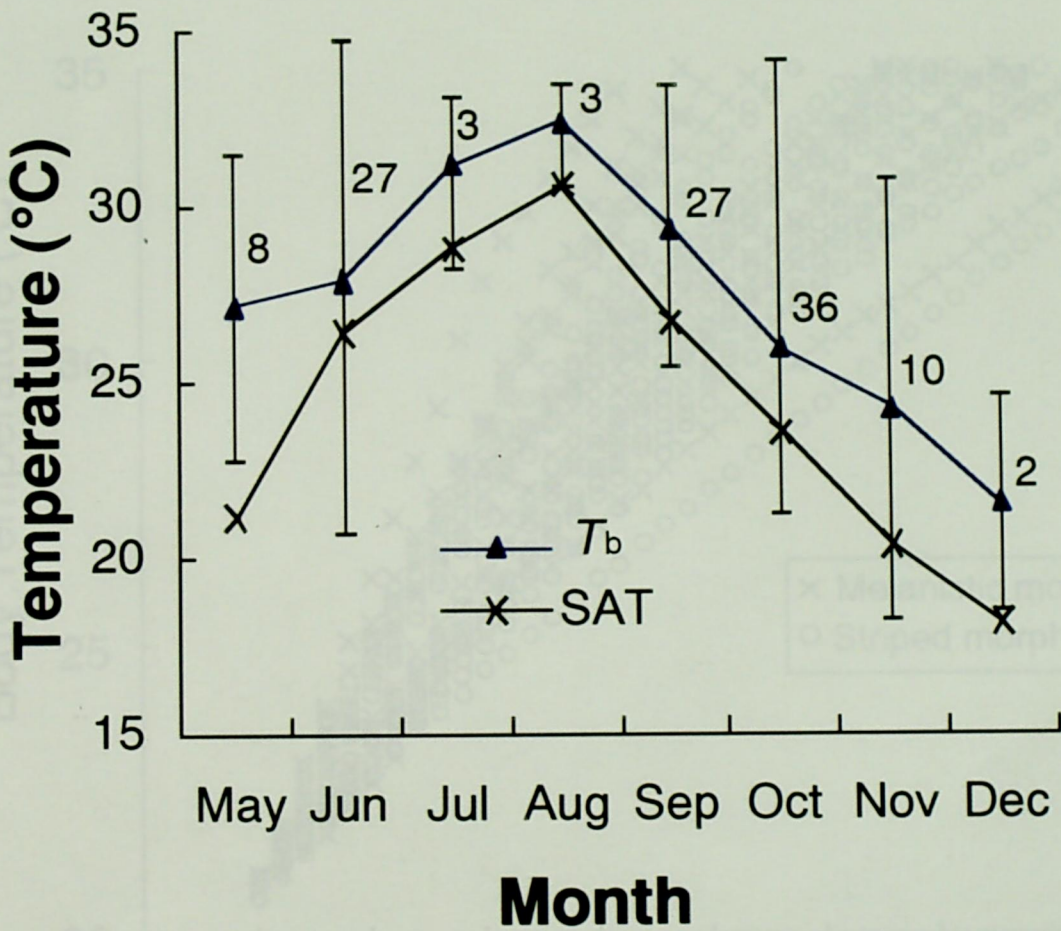
Figure 1-5. Monthly mean body temperatures (T_b) in *Elaphe quadrivirgata* and standard air temperature (SAT) on Yakushima Island. Vertical bars indicate ranges, and numerals beside them denote sample sizes.

Figure 2-1. Plots of body temperatures (T_b) against time during the presumed basking stage (from the beginning of a trial until T_b reaching 35°C) for 27 individuals of *Elaphe quadrivirgata* (13 melanistic and 14 striped morphs). Regression line for each individual was not presented (all, $r > 0.96$, $P < 0.001$).
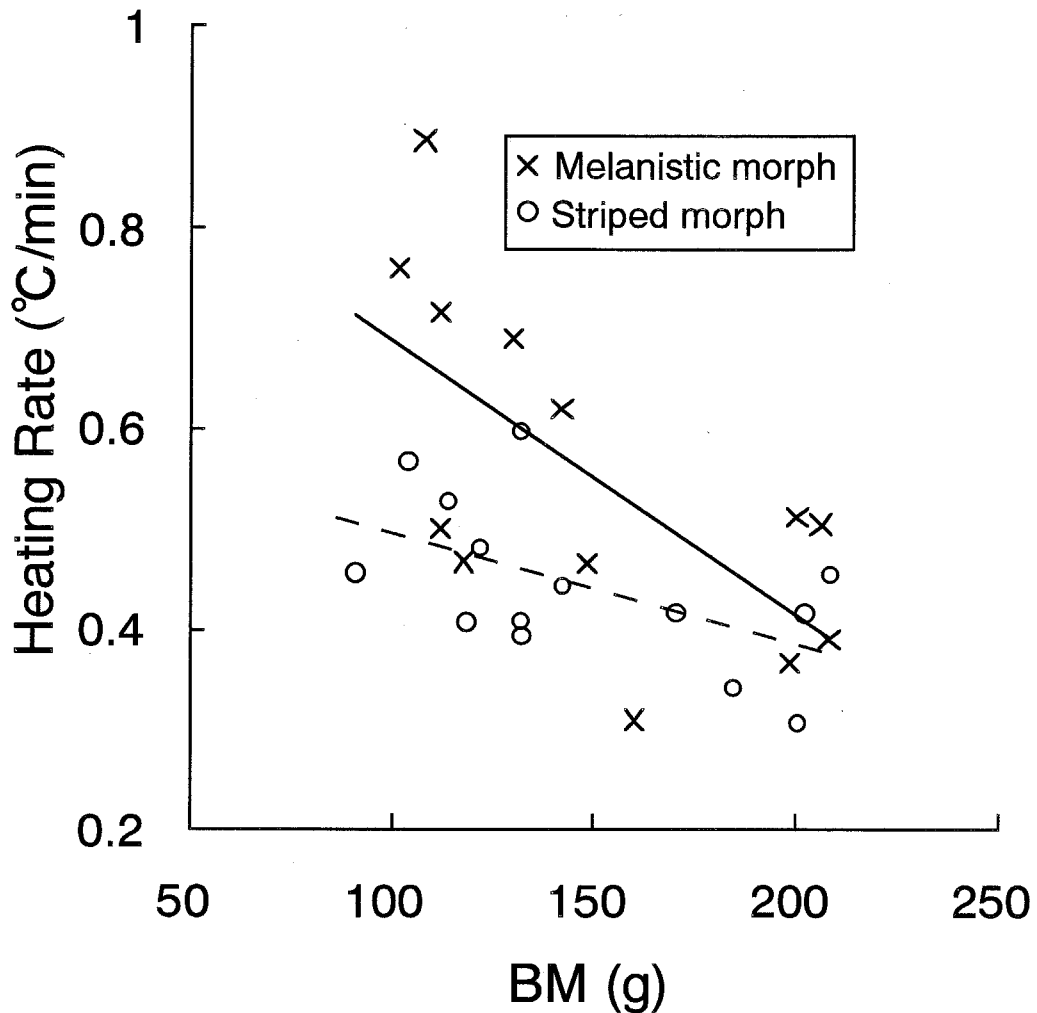
Figure 2-2. Relationships between body mass (BM) and heating rate during the presumed basking stage (from the beginning of a trial until T_b reaching 35°C) for melanistic and striped morphs of *Elaphe quadrivirgata*. Solid and dashed lines show least squares regression lines fitted to melanistic and striped morphs, respectively. Regression equation for melanistic morph: Heating rate = 0.95962 − 0.00272 BM (r^2 = 0.425). For striped morph: Heating rate = 0.60976 − 0.00113 BM (r^2 = 0.300).
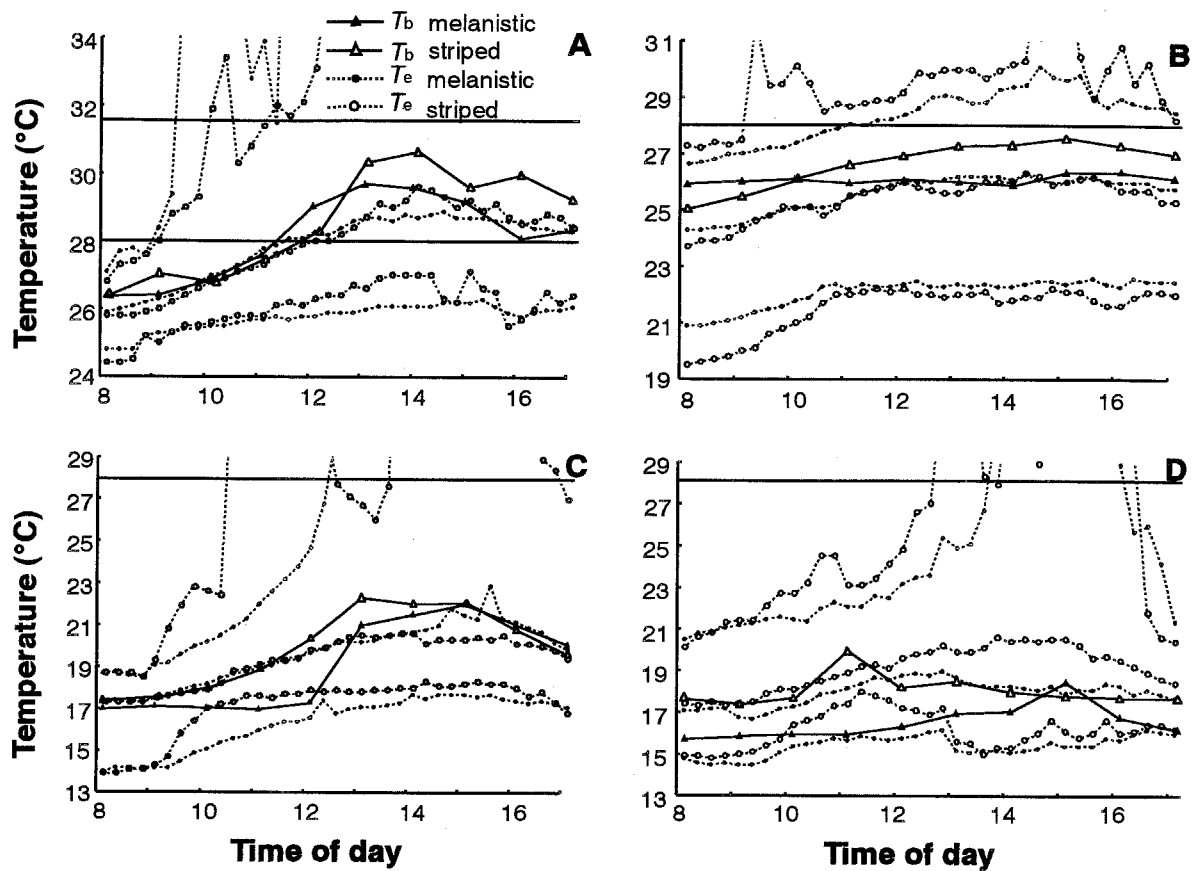
Figure 3-1. Mean body and operative environmental temperatures (T_b and T_e, respectively) of radio-tracked melanistic and striped *Elaphe quadrivirgata* on Yakushima Island in (A) July, (B) September, (C) October, and (D) November. For T_e, upper, middle, and lower dotted lines indicate maximum, median, and minimum T_es, respectively. The solid horizontal lines in (A) show the upper and lower bounds of set-point range. Only the lower bound is shown for (B), (C), and (D). Note that the scale of the Y-axis differs among months.
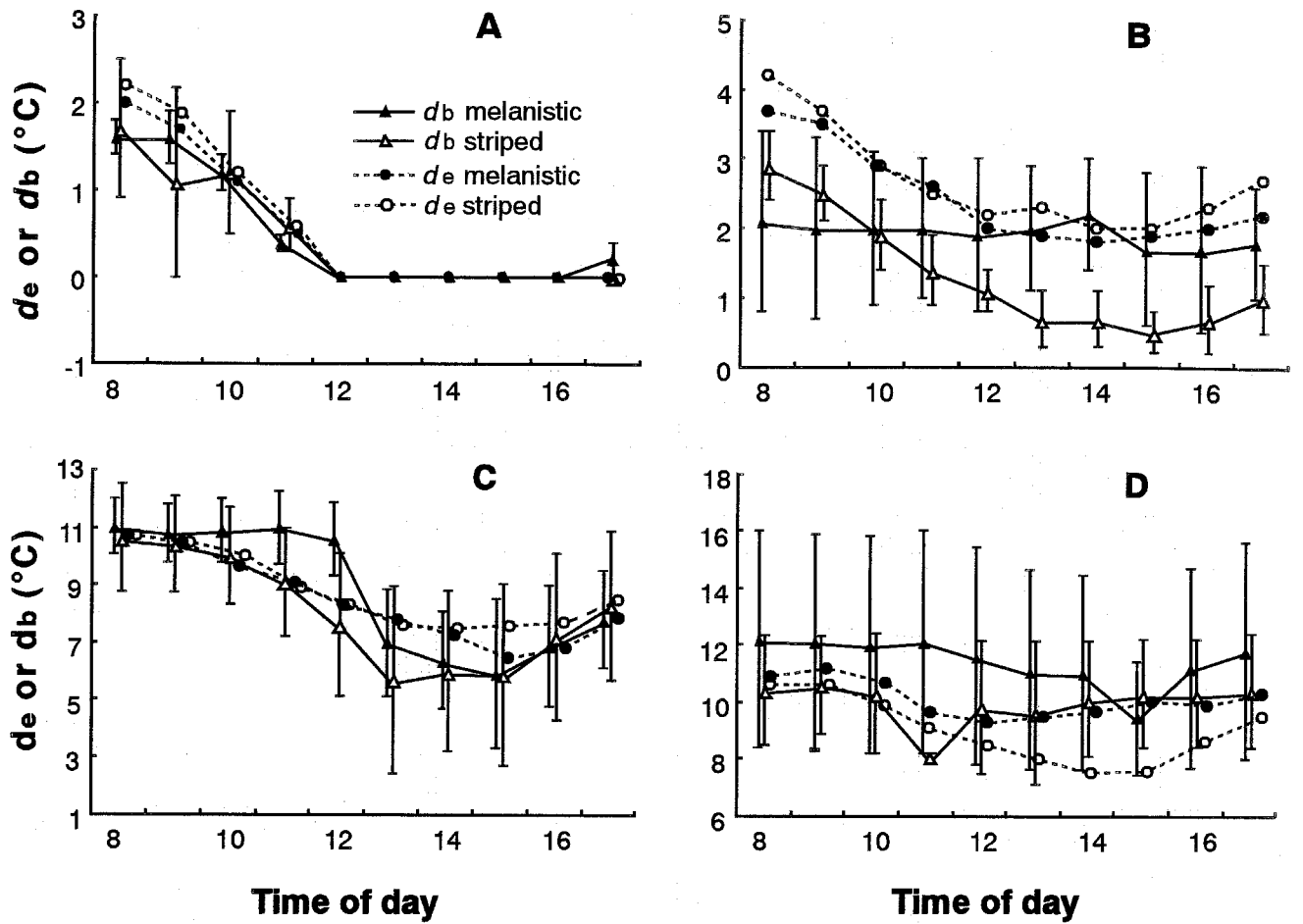
Figure 3-2. Daily changes of deviations of mean body and median operative environmental temperatures from set-point range (d_b and d_e, respectively) in radio-tracked melanistic and striped *Elaphe quadrivirgata* on Yakushima Island in (A) July, (B) September, (C) October, and (D) November. If T_b (or T_e) is within T_{set}, value of d_b (or d_e) equals zero. Vertical bars show ± 1 SE. Note that the scale of the Y-axis differs among months.
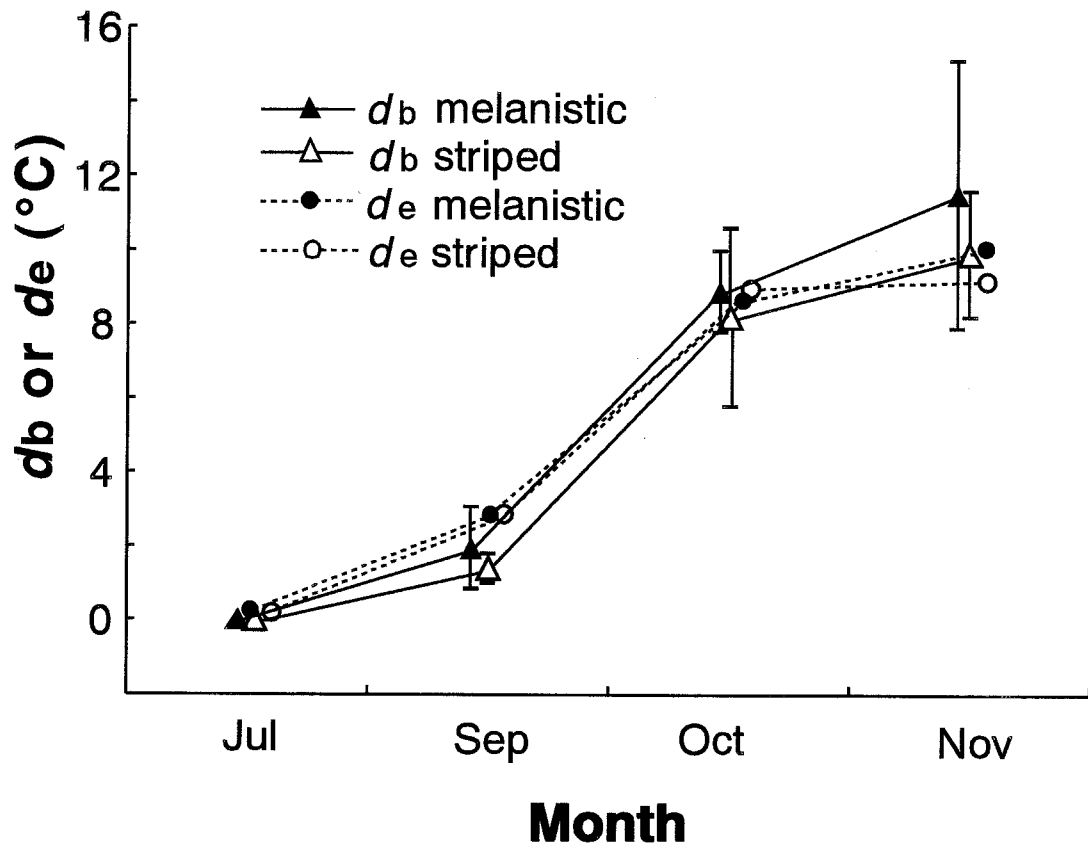
Figure 3-3. Monthly change of deviations of mean body and operative environmental temperatures from set-point range (d_b and d_e, respectively) in radio-tracked melanistic and striped *Elaphe quadrivirgata* on Yakushima Island. Vertical bars show ± 1 SE.
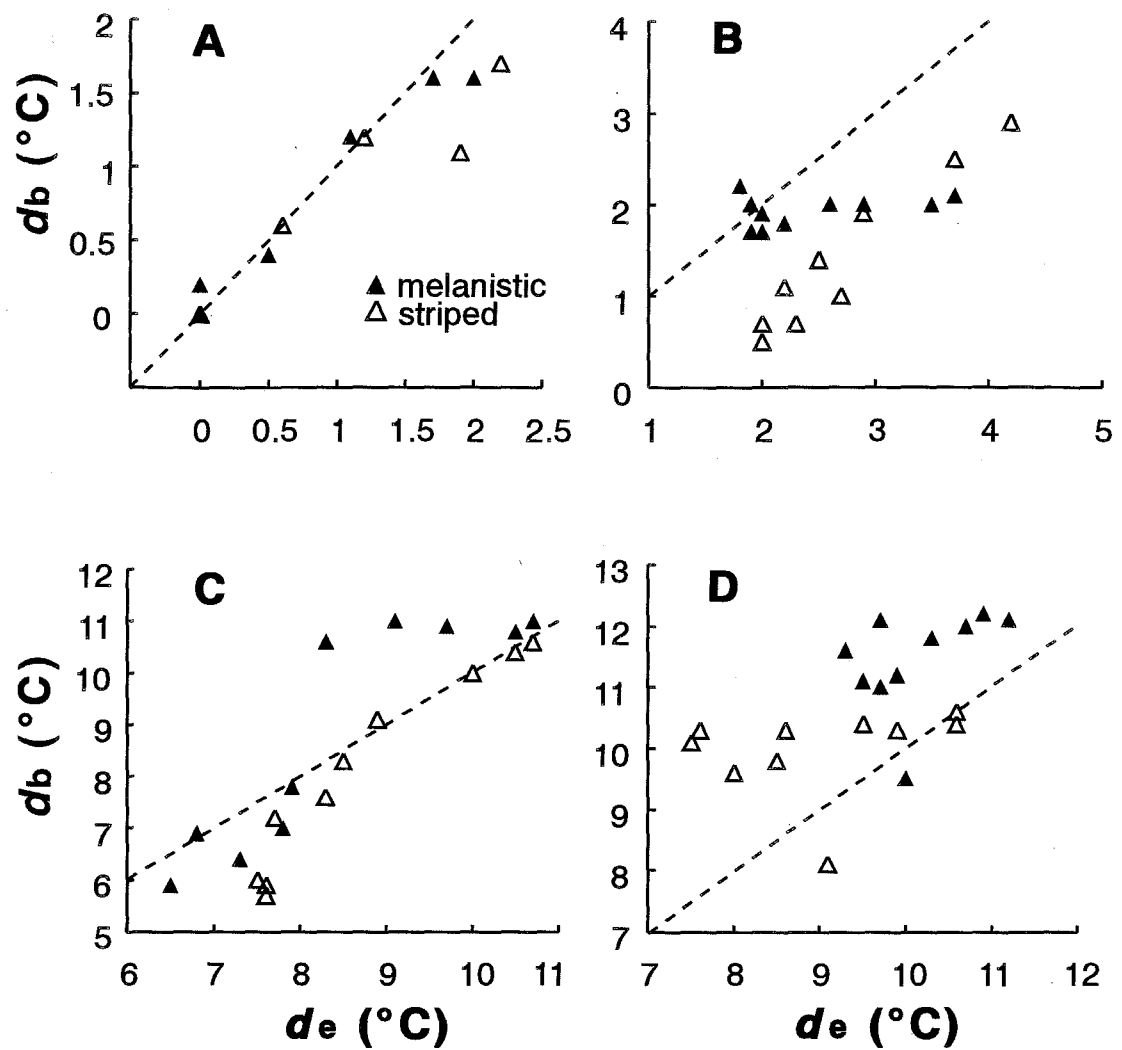
Figure 3-4. Accuracy of body temperature (d_b) against thermal quality of habitat (d_e) in radio-tracked melanistic and striped *Elaphe quadrivirgata* on Yakushima Island in (A) July, (B) September, (C) October, and (D) November. Each point indicates the hourly mean value of a given month. Dashed line indicates where d_b equals d_e.
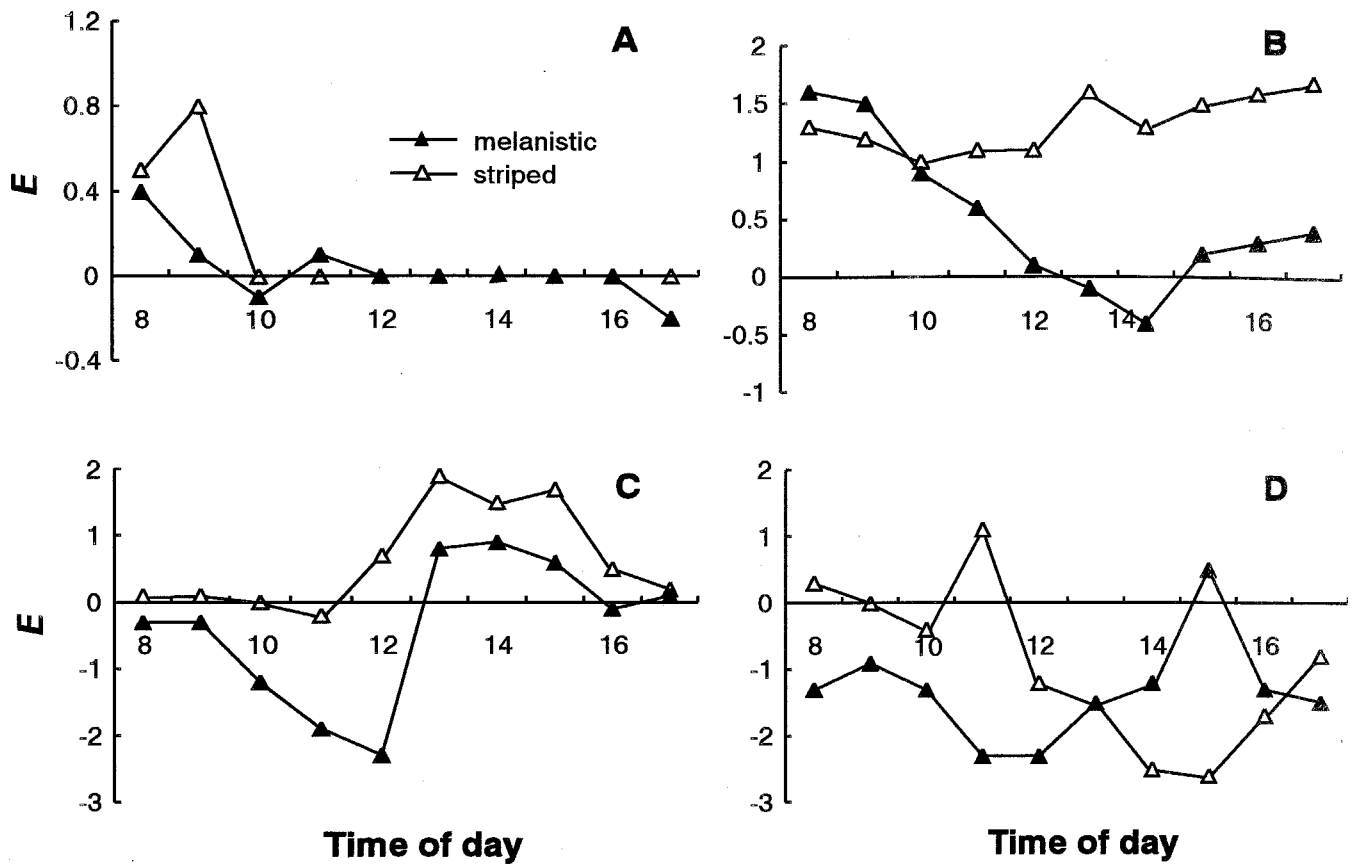
A

1.2
0.8
E 0.4
0
-0.4

▲— melanistic
△— striped

8 10 12 14 16

B

2
1.5
1
0.5
0
-0.5
-1

8 10 12 14 16

C

2
1
E 0
-1
-2
-3

8 10 12 14 16

D

2
1
0
-1
-2
-3

8 10 12 14 16

Time of day

Time of day

Figure 3-5. Hourly changes of index of the thermoregulation effectiveness (*E*) of radio-tracked melanistic and striped *Elaphe quadrivirgata* on Yakushima Island in (A) July, (B) September, (C) October, and (D) November. Note that the scales of the Y-axis differs among months.
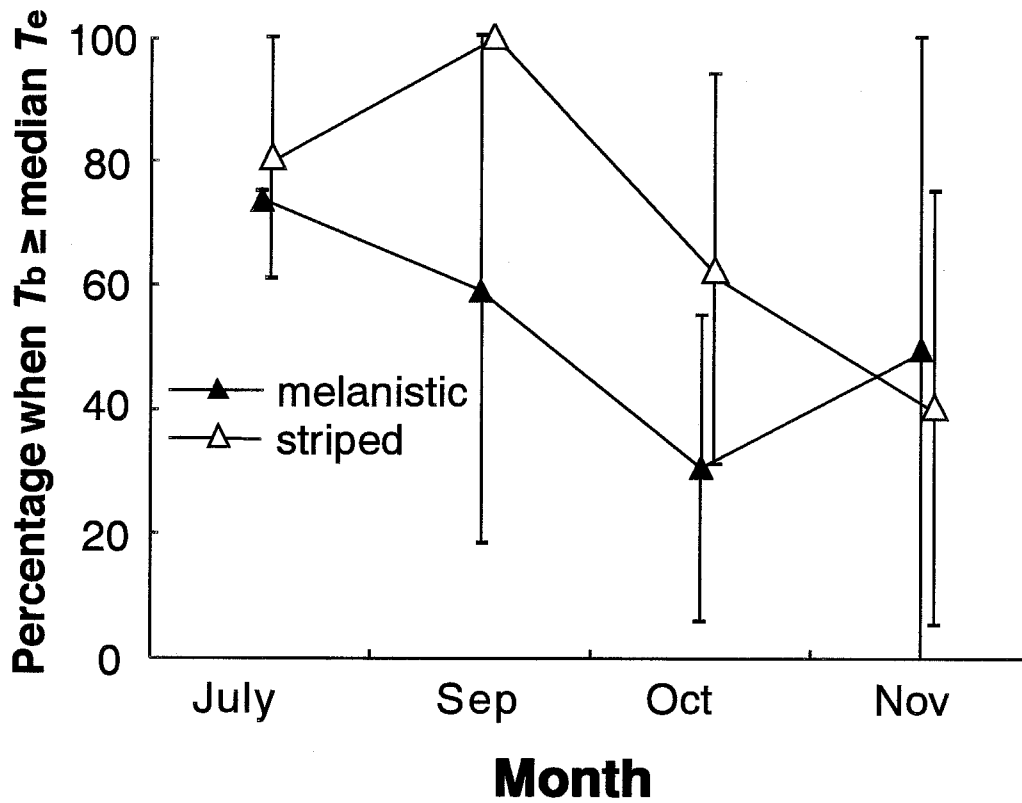
Figure 3-6. Percentage of the time when mean hourly body temperatures (T_b) were equal to or higher than median hourly operative environmental temperatures (T_e) in radio-tracked melanistic and striped *Elaphe quadrivirgata* on Yakushima Island. Data were collected between 0800 and 1700 h. Vertical bars show ± 1 SE.