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Seasonal changes in adrenocortical responses to acute stress in polygynous male bush warblers (*Cettia diphone*)

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Abstract

The adrenocortical response to acute stress as measured by increase in plasma levels of corticosterone following capture, handling, and restraint over an hour was estimated in free-living male bush warblers at different times of the breeding season on their breeding ground in Chichibu, Honshu, Japan. Initial plasma levels of corticosterone showed a seasonal change, being moderate in April, highest in May to July and declined in late August. In contrast, the stress response was suppressed at the early stage of the breeding season, April and May, and just after the breeding season, late August. In June, July, and early August, the response was obvious although the initial levels of corticosterone were high. These results are different from those of monogamous passerine birds so far studied in which adrenocortical response is obvious at the early stage of breeding season and the response is suppressed later stage when the male is involved in parental care. The results suggest that during a course of the breeding season, male bush warblers that take a polygynous breeding strategy may decrease the amplitude of the adrenocortical response to acute stress at the early stage of the breeding season so as to allow establishment and defense of a territory. The birds became more sensitive to acute stress later the breeding season when they already had females incubating, feeding hatchlings or even fledging. This change of stress response is likely to be a reflection of polygynous breeding strategy of the species.

Keywords: Bush warblers; Adrenocortical response; Acute stress; Polygyny; Corticosterone

1. Introduction

The adrenocortical responses to stress have been studied in a variety of viewpoints and have become a broad concept ranging from clinical to basic medicine, and from laboratory experiments to daily life. Although the importance of stress responses in an ecological viewpoint is obvious, its hormonal control mechanisms still remain unclear. If stressful conditions become chronic, continued high levels of glucocorticoid hormones may lead to inhibition of reproduction, severe debilitation, and even to death. However, in free-living animals, stressful conditions can be avoided by escaping the situation. In fact, the initial rise in corticosterone secretion in birds may trigger facultative physiological and behavioral responses related to emergency activities (e.g., Wingfield et al., 1998). These facultative patterns could potentiate survival directly in the face of unpredictable environmental events, and most importantly, avoid deleterious effects of chronic stress. Corticosterone apparently has an important role in modulating behavior and physiology such as suppression of reproduction and territorial behaviors, increased foraging and irruptive escape-like behavior, mobilization of glucose, and reduced energy expenditure by increased night restfulness (see Astheimer et al., 1992; Silverin, 1998; Wingfield, 1994; Wingfield et al., 1995b, 1998). Field data showing elevated circulating levels of corticosterone in avian populations following severe weather provide additional evidence (Wingfield, 1985; Wingfield and Farner, 1993).

In recent years, it has become evident that many avian populations are able to modulate their sensitivity to stress either seasonally or within populations, and that this modulation has ecological importance (Wingfield, 1994; Wingfield et al., 1995b). In birds breeding in an arctic and

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sub-arctic areas where the breeding season is short, elevated levels of corticosterone may influence territorial as well as parental behavior negatively resulting in reproductive failure. Thus in these species, adrenocortical responses are suppressed while nesting to cope with severe conditions (Silverin and Wingfield, 1998; Silverin et al., 1997). However, other environmental factors that may influence the response are not well studied so far. To understand a role of the stress response in ecological contexts, more studies are required using various species with different reproductive strategies.

Bush warblers (*Cettia diphone*) occur along eastern rim of the Eurasian continent and on the Japanese islands. They are either residents or short-distance migrants on Honshu (main) Island. In early spring, males begin to sing in wintering sites, such as bushes, parks, and backyards in lowland areas. Most, if not all, birds migrate to highland areas and breed in bamboo bushes or grass meadows. Males sing from late March to August in the breeding area and emigrate back to the wintering area in September to October.

Male bush warblers are very territorial and hold territory during the whole breeding season defending it with territorial songs. Males may have more than one nest on their territories at the same time if the resources are abundant indicating a polygynous breeding strategy. Male–female interaction is very rare including parental care (Hamao, 1992; Haneda and Okabe, 1970).

We have studied two free-living populations (Honshu and Hokkaido) of male bush warblers to compare the stress response in different habitats (Wingfield et al., 1995a). The latter population breeds in more severe habitats in northern island of Japan (Furano, Hokkaido) and was expected to show a suppressed adrenocortical stress response. However, the initial levels of corticosterone and the response to the acute stress of the Furano population were higher than those of a population at Chichibu (central Honshu). We concluded that stress modulation may not be a simple consequence of shorter breeding season and severer climate, but rather other ecological bases we do not know yet are involved. Even though we only collected the samples in mid-June to early July and did not know the responses at other breeding stages, we noticed relatively high levels of corticosterone in both populations compared to those reported so far in other passerine species (Wingfield et al., 1992, 1994a,b, 1995b). We also observed clear seasonal changes in baseline concentrations of corticosterone and found high levels of corticosterone from May to July (Wada et al., 1999).

In this study, thus we attempted to follow changes in degree of responses to acute stress during an entire breeding season in a successfully breeding population of male bush warblers in Chichibu (Honshu). Indication was that the seasonal changes in degree of stress response as well as the initial levels were enormously different among the breeding stages. The stress response was suppressed at the early stage of breeding and the post-breeding stage and was high with elevated initial levels in late May to early August. The data also suggest that stress response was suppressed during territory establishment and this suppression disappeared even though the basal levels of corticosterone increased, as the stage of reproduction proceeded. This change in stress response may be a reflection of polygynous breeding strategy of the species.

2. Materials and methods

2.1. Animals and study site

The study site was in “Forest areas 28, 29” and their vicinity (elevation 1100–1200 m) of the University of Tokyo Forest at Chichibu (35° 55′ N and 138° 52′ E), Honshu Island, Japan. The area consists of mountain forest of deciduous and coniferous trees in which forest beds are covered with dense bamboo grass, *Pseudosasa purpurascens*. The climate at Chichibu is that of the Pacific side of Japan, cool winters with little snow fall, and warm, humid summers.

The breeding biology of bush warblers in this area is described elsewhere (Wada et al., 1999) and mentioned only briefly here with unpublished observation obtained in later seasons (1998 and 1999). Male bush warblers wintering at lower elevation arrive in the study area in late March and establish territory after territorial dispute. Thereafter, a male advertises his ownership by singing, but actual fighting is rare (Hamao, 1992). A female arrives later, in early April to mid-April and mates with the owner of a territory. Bush warblers have a polygynous breeding strategy and more than one female nesting on a territory (Hamao, 1992). The male does not participate in nest building, incubating, or feeding of young (Hamao, 1992; Haneda and Okabe, 1970) and remains reproductively active until mid-August. While males are singing, females build a nest in April to early May and lay eggs. Female’s brood patch is maximum in late May to early June indicating females are incubating around this time. Fledglings can be captured at early July and thereafter. In mid- to late-August, plasma testosterone levels in males become basal and males cease singing. They depart the area to wintering ground in September to October, juveniles leaving later.

2.2. Sampling procedures and capture stress protocol

Male bush warblers were captured with Japanese mist nets during our visits to the study site from April to August, 1995 and from March to August, 1996. Serial samples were also collected from five juvenile males in October, 1995.

To assess the adrenocortical response to acute stress, the pattern and degree of increase in circulating corticosterone following capture, handling, and restraint are good indicators and widely applied to free-living birds as well as other vertebrates. We applied this method as follows. Birds were attracted into a mist net by playing tape-recorded songs. After capture, the bird was removed from the net within 5 min and blood samples (50–100 μl) were collected from the wing vein into heparinized capillary tubes after venipuncture and designated as the initial sample (time 0 after capture). Then the bird was kept in a cloth bag and additional samples (30–50 μl) were collected at 5, 10, 30, and 60 min later. After all the samples were taken, the bird was released at the same spot where it was captured. Capillary tubes were sealed with molding clay and stored on ice until return to the station. Here the blood was centrifuged, and the plasma was harvested and stored in a refrigerator. Samples were brought back to the laboratory in an ice cool container and stored at −20 °C until assayed.

Each bird was banded with unique combination of plastics color rings, and body mass was measured with Pesola scale to the nearest 0.1 g between the initial and 5 min blood sampling.

2.3. Hormone assay

Without any extraction, plasma levels of corticosterone were estimated by a direct radioimmunoassay method (see for detail Wada et al., 1999) almost identical to that described by Wingfield et al. (1992). All the samples of each year were assayed using 10 μl of plasma, and were run in a single assay in duplicate. Intra-assay variations and inter-assay variation were 12.19 and 23.2%, respectively.

2.4. Statistics

Spearman rank correlations were used to compare corticosterone levels as a function of date, time of day when data were collected and exposure time to song playback. Data were analyzed using repeated measures analysis of variance (ANOVA) and ANOVA and Dunnett's test as post-hoc test using StatView ver. 5.0 (SAS International) running on Windows2000. Differences were considered significant when $P < 0.05$. Hormone concentrations throughout the text are the means ± SEM.

3. Results

3.1. Sample collection

We collected serial samples from 28 adult male birds in 1995 and 42 in 1996. Since birds were captured by playback protocol, the duration of exposure to playback was different in each bird as well as time of day and date of year (Fig. 1). To validate data handling described below, correlations between capture time and initial plasma levels of corticosterone were analyzed by Spearman rank correlations. Highly significant correlation was detected between the initial levels of corticosterone and capture date of year in both 1995 ($\rho = -0.498$, $z = -2.589$, $P = 0.0096$) and 1996 ($\rho = -0.590$, $z = -3.779$, $P = 0.0002$) (Fig. 1 top). However, no significant correlation was detected between the initial levels of corticosterone and time after playback ($\rho = 0.113$, $z = 0.586$, $P = 0.558$ for 1995; $\rho = -0.180$, $z = -1.153$, $P = 0.249$ for 1996) (Fig. 1 bottom) indicating that the exposure time to conspecific songs did not influence baseline levels of corticosterone in this experimental design. There is no correlation between the initial levels and capture time of day in 1995 ($\rho = 0.123$, $z = 0.640$, $P = 0.522$) but significant correlation in 1996 ($\rho = 0.357$, $z = 2.287$, $P = 0.022$) (Fig. 1 middle). However, if the data of 1995 and 1996 were combined, the correlation between basal corticosterone levels and the capture time of day was no longer significant ($n = 70$, $\rho = 0.033$, $z = 0.272$, $P = 0.7857$). Since there were significant differences in the initial values of corticosterone and capture date of year and no differences between corticosterone levels and time after playback, it is rational to combine 2 year data according to month.

3.2. Adrenocortical responses to the capture stress protocol

Fig. 2 shows changes in plasma corticosterone concentrations following capture, handling, and restraint over an hour in relation to different time of year. Repeated measures ANOVA revealed that there were monthly differences in stress response.

It is clearly shown that adrenocortical response was suppressed in April ($P = 0.0960$) and late August ($P = 0.5603$). Initial levels of corticosterone in April were higher than those of late August, but the increase was blunt and no significant increase was detected (Fig. 2). In late August, initial levels of corticosterone became low (Wada et al., 1999), and the adrenocortical response to acute stress was almost none.

Significant increases were found in May, June, July, and early August (Fig. 2). Typical profiles of stress response curve were found in June, July, and early August although the degree of the responses was low in early August. If P-values of each month were presented, they follow as May (0.0080) > early August (0.0025) > June (0.0002) > July (less than 0.0001). Since the response curve in May was not so obvious and the P-value was largest in the significant months, the data of May was divided into three parts, early, middle, and late May,

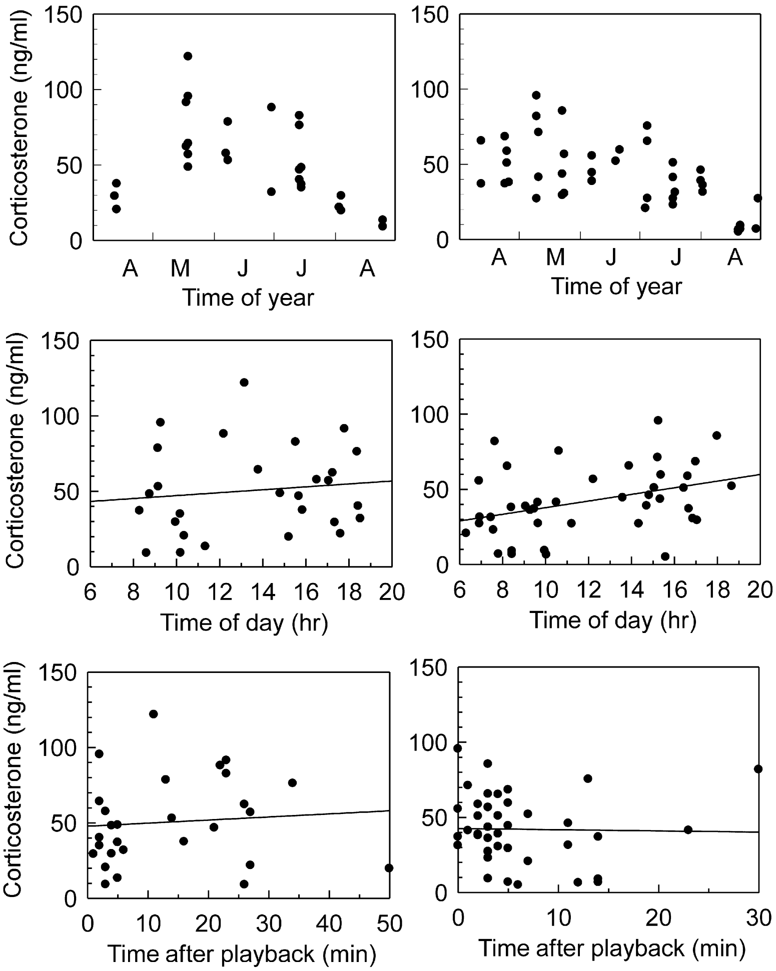

Fig. 1. Initial plasma levels of corticosterone plotted as a function of date of year (top) of capture, time of day (middle) of capture, and exposure time to the playback (bottom) in male bush warblers sampled at Chichibu in 1995 (left column) and 1996 (right column).

and response curves were redrawn (Fig. 3). As shown in the figure, the stress responses in early and middle May is no more significant, $P = 0.1742$ and $P = 0.9658$, respectively, but in late May ($P = 0.0067$).

The adrenocortical response to acute stress in juvenile males sampled in October, 1995 showed a significant increase ($P = 0.0030$) (Fig. 4).

3.3. Initial levels and maximum increases in corticosterone

Fig. 5 shows the monthly means of the initial levels of corticosterone and maximum increase after acute stress. The maximum values were found mostly in 30 or 60 min after the initial sampling.

Initial plasma levels of corticosterone differed significantly among the months. Significant differences were detected in April, May, June, and July compared to late August as control using Dunnett's test as post-hoc after ANOVA. The levels of corticosterone were moderate in April, highest in May, and then decreased gradually to early August. They became the lowest in late August.

Maximum increases in corticosterone levels generated during the capture stress protocol also differed significantly among the months. Significant differences were detected by the post-hoc test in May, June, and July compared with late August. However, the maximum increases were not significantly large in early August and April (Fig. 5).

4. Discussion

4.1. Seasonal changes in stress response in bush warblers

The present study showed that adrenocortical response to acute stress in bush warblers was different dependent on the time of year. It was apparent that the response was different depending on month. We could not precisely tell the reproductive status of each bird captured and exposed to stress response protocol, but we could suppose the reproductive stages during breeding season in this area. At the early stages of the

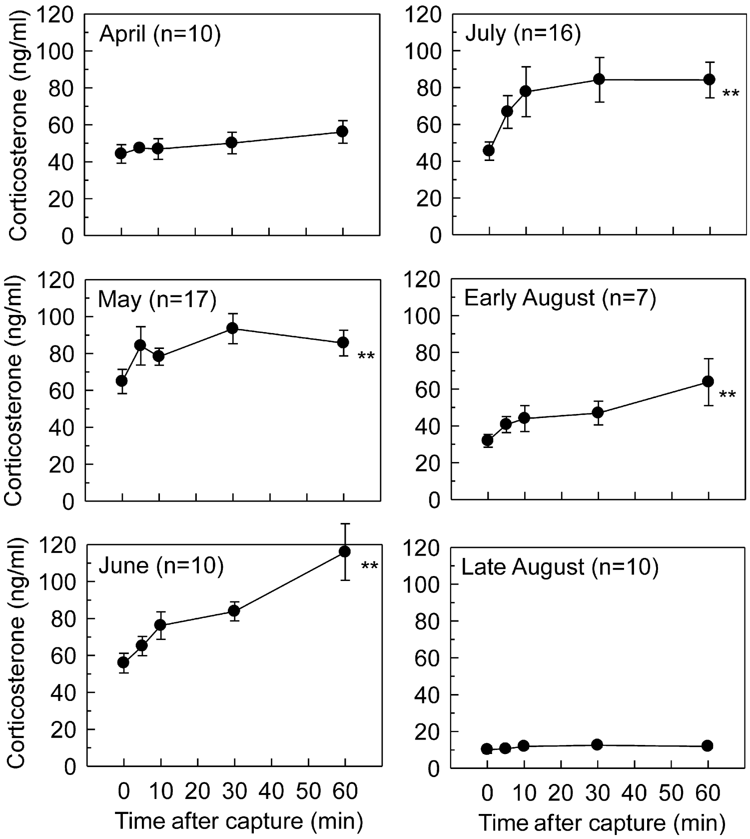

Fig. 2. Increases in plasma levels of corticosterone following capture, handling, and restraint in male bush warblers from April to late August. Each point is a mean and vertical bars the standard error of the mean. Sample sizes are designated in each graph. $^{**}P < 0.01$ with repeated measures ANOVA.

annual reproductive cycle, i.e., April, early May, and mid-May, male birds did not show the typical adrenocortical response to acute stress of capture, handling, and restraint. However, in late May, June, July, and early August, the stress response protocol induced a significant increase in the circulating levels of corticosterone. In late August, the stress response completely disappeared and the initial levels of corticosterone became low.

These results clearly explain a question that arose in a previous study (Wingfield et al., 1995a). We measured adrenocortical responses to acute stress in two different populations of this species expecting to see a difference of the response between the two different environments; one is Honshu Island where the climate is mild and the other is Hokkaido Island where the climate is severe and the breeding season much shorter. Since Silverin et al. (1997) has shown that the northern population of nesting willow warblers (*Phylloscopus trochilus*) suppresses the adrenocortical response to acute stress compared to the southern population in Sweden, we expected a similar result in this species. However, we found a great adrenocortical response to acute stress in male bush warblers at Furano, Hokkaido, the northern population, as well as a marked increase in the levels of plasma corticosterone after acute stress in Chichibu (Honshu) population. June and July data in the present study were similar to the previous data at the same time of year in Chichibu.

In recent years, it has become clear that many avian populations are able to modulate their adrenocortical responsiveness to stress. Seasonal changes are marked and have been documented in detail in white-crowned sparrows (*Zonotrichia leucophrys gambelii*) (Romero and Wingfield, 1998; Romero et al., 1997). Observation points are limited in the birds at migration, breeding, and wintering, the data indicate that the stress response is clearly observed in the birds at breeding, but it is very weak in birds at migrating and wintering stages. Schwabl et al. (1991) also observed suppressed stress responses in garden warblers (*Sylvia borin*) during migration. Thus it is not surprising that in avian species responsiveness to stress changes seasonally, but the stages when the response was suppressed were different in polygynous bush warblers from monogamous passerine species.

Why are there differences in suppression of stress responsiveness between willow warblers and bush warblers? It is possible that different populations of the willow warblers modulate it according to the habitats

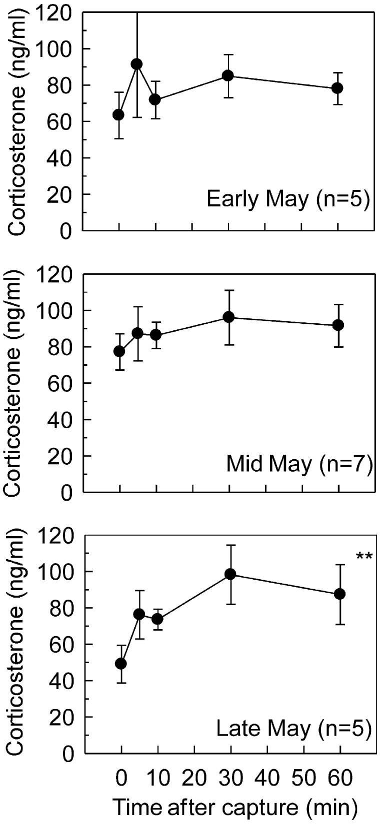

Fig. 3. Increases in plasma levels of corticosterone following capture, handling, and restraint in male bush warblers captured in May and the data were divided into three stages, early, mid, and late May. Each point is a mean and vertical bars the standard error of the mean. $^{**}P < 0.01$ with repeated measures ANOVA.

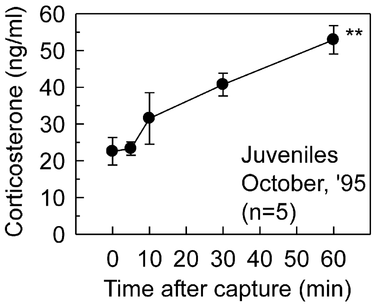

Fig. 4. Increases in plasma levels of corticosterone following capture, handling, and restraint in juvenile male bush warblers in October 1995. Each point is a mean and vertical bars the standard error of the mean ($n = 5$). $^{**}P < 0.01$ with repeated measures ANOVA.

whereas bush warblers modulate it according to stages of breeding. The differences between willow warblers and bush warblers could be due to the differences in breeding strategy. In willow warblers, only females incubate but both males and females feed young. On the other hand, in bush warblers, females incubate and feed young but males do not show any parental care. If the stress response is intrinsic and it has been suppressed in a certain stage of reproduction to cope with environmental stressors for better fitness, there may have been no selective pressure in polygynous male bush warblers during the parental phase. Rather, selective pressure may act at the early stage of breeding.

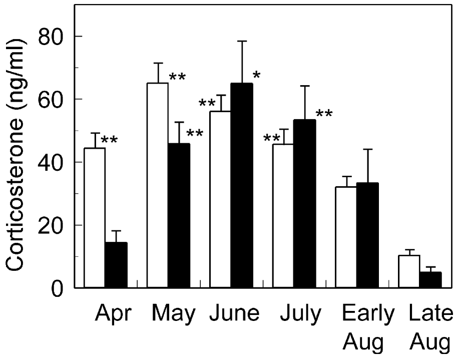

Fig. 5. Comparisons of initial levels (open column) and maximum levels (filled column) of corticosterone following capture and handling. Bars are monthly means and vertical lines the standard error of the mean. Sample sizes are same as Fig. 2. $^{*}P < 0.05$ and $^{**}P < 0.01$ with ANOVA and Dunnett's test as a post-hoc test.

4.2. Ecological consequences of the stress response

Apart from the seasonal changes, many environmental factors could contribute differently to modulate the adrenocortical responses to stress in different populations and at different stages of breeding. In arctic species, some appear to have a smaller increase in corticosterone response to stress, e.g., in snow bunting, *Plectrophenax nivalis* and redpoll, *Carduelis flammea*, at Barrow, Alaska (Wingfield et al., 1994a,b). The Lapland longspur, *Calcarius lapponicus*, breeding on the north slope of Alaska also appears to have a low magnitude of response to the capture stress protocol. However, after a three day snow storm in June, the amplitude of increase in plasma levels of corticosterone following capture and handling was almost an order of magnitude higher than before the storm (Astheimer et al., 1994). Clearly the sensitivity of the hypothalamo–pituitary–adrenal axis to acute stress can be modulated both up and down within a short period to allow maximum adaptation to unpredictable fluctuations in the environment.

In some species such as black-throated sparrows (*Amphispiza bilineata*), cactus wrens (*Campylorhynchus brunneicapillus*), and curve-billed thrashers (*Toxostoma curvirostre*) living in the Sonoran desert, Arizona, significant increases in circulating corticosterone following capture are reduced in summer when the ambient temperature is extremely high (it often exceeded the average maximum temperature of 36.9 °C and sometimes reached to 40–50 °C). On the other hand, in Inca doves (*Scardafella inca*) and Abert's towhees (*Pipilo aberti*), which lived in more shady riparian and suburban habitat with constant access to water, the adrenocortical response is similar both in summer and winter (Wingfield et al., 1992). These data indicate the response in desert species is suppressed in the breeding season and reactivated in winter after breeding has ceased.

4.3. Stress response and polygynous breeding strategy

Apart from the severe conditions for breeding such as in sub-arctic and arid habitats, there might be other cases in which the adrenocortical response is suppressed for reproductive success. As we stated, the bush warbler is polygynous and males provide no parental care (Hamao, 1992; Haneda and Okabe, 1970). Plasma testosterone levels in June and July are high in bush warblers (Wada et al., 1999) which are typical for polygynous species; higher than would be expected for monogamous passerines in which males show parental care in these months (Wingfield et al., 1990). As is shown here, in bush warblers, the adrenocortical response was suppressed in the early stages of breeding season. It is plausible that these species suppress the adrenocortical response at the early stage so that they can compete and establish the territory in a relatively limited area with rich food resources. Although the bush warbler is polygynous and males provide no parental care, they do mate-guard when a potential mate is receptive (there are always unmated males around the territory who could also mate with a receptive female). These stages roughly correspond to April through May.

On the other hand, after the female is incubating and no longer receptive, the male may shift his territory slightly and try to attract another female. This may be the reason why the adrenocortical response to acute stress becomes high in June and July. Potentials to increase corticosterone in response to acute stress may be permissive for a territory shift due to corticosterone effects on mobility (Breuner et al., 1998). If this is true, the females should show suppression of the adrenocortical response to stress in June and July as well as the early stage of the breeding season. It is already shown in willow warblers that there are differences in stress response between males and females (Silverin et al., 1997). Our observations in 1998 and 1999 also showed that there were differences in corticosterone concentrations between males and females in bush warblers at the same study site; circulating corticosterones were low through the breeding season and no obvious changes exist in females (unpublished observations).

There were also clear seasonal differences in initial levels of circulating corticosterone, relatively high in April, peaked in May, gradually decreased through June to early August and declined to the lowest level in late August (Fig. 5). This pattern was roughly parallel to that of circulating testosterone (Wada et al., 1999). It is interesting that high concentrations of testosterone and corticosterone are parallel in early breeding season suggesting mutual interaction between the two hormones. Higher testosterone may suppress adrenocortical response at the early breeding stages in this species and decreases of testosterone levels in June and thereafter may recover the stress response. No response in late August should be due to exhaust after keeping high corticosterone levels during the breeding season. It is worth noting here that the response in juveniles in October was very similar to those of monogamous species so far studied (Fig. 4). This may also support the idea that suppression of the adrenocortical response and high testosterone plasma levels in the early stages of breeding season are characteristic of adult mature males.

The climate in the study area is not severe and food resources are abundant, which is indicated in increase in body mass during the early stages of breeding season (Wada et al., 1999). The data suggest that the suppression of the adrenocortical response at the early stages and the release of the suppression at later stages in the bush warblers are thus specific to their breeding strategy, i.e., polygynous breeding which is an adaptation to dense bushes with high rates of predation and brood parasitism.

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