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Plasma levels of Androgen, Progesterone and gonadal development of breeders and helpers in the Jungle Babbler *Turdoides striatus*

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Abstract – We examined the proximate causes of delayed breeding and helping (allo-parental) behaviour by measuring plasma testosterone and progesterone concentrations in female breeders, male breeders, and helpers in co-operatively breeding Jungle Babblers. No significant difference was noted in the body and gonadal weight of breeders and helpers females. Also testosterone levels in the blood plasma did not change significantly between breeding duo and helpers. This could be related to the fact that the reproductive activities (maintaining the territory, defending the nest etc.) are performed by all members of the flock. The progesterone levels and the size of oviduct were comparatively higher in breeding than in non-breeding females. In helper females, the level of this hormone was intermediate. This result suggests that helpers share all breeding activities (including parental, allo-parental behaviour) but subdued oviducal development prevents them from egg formation and egg laying.

Riassunto – *Testosterone, Progesterone e sviluppo delle gonadi in riproduttori e negli aiutanti al nido in* Turdoides striatus. In questo studio sono state misurate le concentrazioni di testosterone e progesterone nel sangue e le dimensioni corporee e delle gonadi di individui riproduttori e di aiutanti al nido in *Turdoides striatus*. Nessuna differenza significativa è stata rilevata per le dimensioni del corpo e delle gonadi in femmine riprodutrici e in femmine aiutanti al nido. Anche i livelli di testosterone nel sangue non differiscono tra i due gruppi. Ciò potrebbe essere in relazione al fatto che alcune attività riproduttive (es.: difesa del territorio e del nido) sono effettuate similmente dai diversi individui. Le concentrazioni di progesterone sono risultate più elevate nelle femmine che nei maschi. Nelle femmine aiutanti, i livelli di questo ormone nel sangue e le dimensioni dell'ovidotto sono risultati intermedi tra le femmine riproduttrici e quelle non riproduttrici. Questo risultato suggerisce che le femmine aiutanti al nido condividono tutte le attività riproduttive (includendo le cure parentali), ma non possono deporre uova a causa del ridotto sviluppo dell'ovidotto.

INTRODUCTION

Co-operative breeding has been described in nearly 300 species of birds (Brown 1987). This behaviour involves that some adults, termed "helpers", remain reproductively dormant and help to raise the young of breeding pairs to whom they are often, but not always related (Dawson and Mannan 1991, Walters 1990). Many co-operative breeders live under severe ecological constraints, hold year round territories, are non-migratory and live in tropical or subtropical climates. This ecological conditions promotes co-operative breeding. Cooperatively breeding species display all combinations of mating systems, ranging from monogamy to polygynandry. In majority of the cases, a monogamous breeding pair is assisted by adult progeny from previous breeding seasons. For example, Jungle Babbler (*Turdoides striatus*) occurs in groups that consist of a single breeding female, a dominant male breeder, and up to 3 subordinate, non breeding helpers, most of which are females. In these systems, the evolution of cooperative breeding involves two distinct phenomena: the young remain on their natal territory, rather than dispersing, and they express allo-parental behaviour (Brown 1987, Emlen 1982a, Emlen 1982b). The altruistic behaviour demonstrated by the helpers has its own benefits for both, the helpers as well as for the breeding pair. This assumption predicts that helpers significantly increase the reproductive success of the breeding pair and that helpers are closely related to the recipients of their aid. Helpers may gain future indirect benefits by enhancing breeder survivorship

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through benefits of group living, such as increased predator detection and increased foraging efficiency. Helpers may also enhance breeder survivorship by reducing the breeder's energy expenditure during the breeding season. Breeders that reduce nestling provisioning in the presence of helpers may use their surplus energy and time on other equally demanding activities, such as foraging and territory defence. The helper also gains certain future direct fitness benefits i.e., improved prospect of surviving to breed, increased future possibility of breeding and enhanced future reproductive success.

In contrast to the many studies of cooperatively breeding species that have closely examined the evolutionary reasons for delayed breeding and alloparental behaviour (Brown 1987, Koenig and Mumme 1990, Emlen 1991, Cockburn 1998), few physiological studies focus on proximate mechanisms underlying cooperative breeding behaviour. In vertebrate co-operative breeders, the allo-parental behaviour is recognized to be hormonally mediated. Progesterone plays a role in the initiation of parental behaviour in many birds (Silver *et al.* 1978). Progesterone may act with prolactin to stimulate parental care (Silver *et al.* 1978, Balthazart 1983). Elevated progesterone levels prior to expression of allo-parental behaviour might sensitize target tissues to the subsequent action of prolactin. Conversely, testosterone, that is necessary for stimulation of sexual behaviour, suppresses parental behaviour. The courtship displays and parental care in male birds are generally thought to be mutually exclusive.

The purpose of the present study is to obtain basic physiological information on breeding of Jungle babbler a social/co-operative bird of a semi-arid subtropical region of India. Variations in the levels of testosterone and progesterone, and gonadal weight of breeders, non-breeders and helpers are considered. Blood samples were collected for the measurement of circulating hormones, testosterone (T) and progesterone (P).

MATERIALS AND METHODS

The birds were procured from local supplier and were maintained in an aviary under standard animal house conditions. They were provided with food and water given *ad libitum*. Birds received unrestricted natural light. Before sacrificing, the birds were weighed individually in an open pan balance. The number of birds used for hormonal studies was 10 each for male breeders and non-breeders (in duplicate sets), while for females the number was 12 each for breeders, helpers and non-breeders (in duplicate sets).

The reason for the sacrifice of these birds was to understand the biochemical physiology in depth and to explore the feasibility of incorporating the bird in the agricultural pest management (as bio-control agents). The study carried out has been funded by ICAR (Indian Council of Agricultural Research) due to the importance of the bird in IPM (Integrated Pest management) approach. The objective of the project was to assess the relationship of carbohydrate, protein and lipid metabolism along with the histology, histochemistry and reproductive/ breeding physiology including hormonal interaction during different seasons.

The gonads were removed from the body and freed from the tissue fluid. The weights of left and right testis were recorded separately to the accuracy of 1mg. The male birds with larger breeding testes were found from April to November; during this period some males were in non-breeding state too. However, from December to February no males were found with developed testes. In female Jungle Babblers along with the ovarian weight, the oviducal weight was also recorded. Female Jungle Babblers show a prolonged breeding phase from March to December when breeding ovaries are present. Along with the breeding and non-breeding females, a distinct group of females with large sized ovaries but underdeveloped oviduct were found and were considered as helpers (e.g., Khan *et al.* 2001).

Before sacrificing, blood was collected in the heparinised test tubes from the ventricles of the anesthetized birds and later centrifuged for 60 minutes at 3000 rpm. After centrifugation, plasma was collected in Eppendorf tubes and stored at -4°C. The separated plasma fraction (10 µl) was used for quantitative measurements of progesterone and testosterone (by EIAgen kit, Biochem; Italia) in both male and female Jungle Babblers.

The EIAgen Testosterone/Progesterone kit

To evaluate testosterone/progesterone content in blood plasma, a micro plate solid phase enzyme immunoassay kit was used. The EIAgen testosterone/progesterone kit contains: a testosterone/progesterone micro plate, testosterone/progesterone calibrators, testosterone/progesterone conjugates, washing solution, TMB H_2O_2 HS, stop solution (H_2SO_4). The solid phase enzyme immunoassay for testosterone/progesterone is a competitive type immunoassay wherein HRP labelled testosterone/progesterone competes with the testosterone/progesterone present in the sample (10 µl) for a fixed and limited number of antibody sites immobilised on the wells of the microstrips. Once the competitive immunoassay reaction has occurred, the wells are washed and the HRP- testosterone/progesterone fraction bound to the antibody in the solid phase is measured by adding the chromogen/substrate solution which is converted to a blue compound. After 15 minutes of incuba-

tion, the enzyme reaction is stopped with H_2SO_4, which also changes the solution to a yellow colour. The absorbance of the solution is measured photometrically at 450 nm and is inversely related to the concentration of the testosterone/progesterone present in the sample (10 µl). Calculations of the testosterone/progesterone content in the sample are made by reference to a calibration curve.

Calculations of results for testosterone/progesterone

To calculate the mean absorbance of calibrators and samples (A), the absorbance of the chromogen blank (Ac) is subtracted from the absorbance of all the samples. This is considered as the corrected value. Corrected values of the sample are divided by the corrected absorbance of the zero calibrator (Ao) and multiplied by 100 (A-Ac/ Ao-Ac x 100). The respective testosterone/progesterone values are plotted on the logit log or semi log graph paper and the concentration of testosterone/progesterone in the samples are determined by the interpolation from the calibration curves.

Statistical methods

Statistical evaluation of the data for males was done by the Student's *t*- test (unpaired); data for females were compared by one way ANOVA (post hoc test: Bonferroni multiple comparison test). All results are expressed as mean ± SE. The analyses were done using Graph Pad Prism version 3.0 for Windows (Graph Pad Software, San Diego California, USA).

RESULTS

Males

The average body weight of breeding males was 61.4 ± 2.27 g while that of non-breeding males was non-significantly lower, being 56.77 ± 2.24 g (Tab. 1, Fig. 1). The mean testicular weight (left and right testis combined) in the breeding males was 205.00 ± 14 mg and in the non-breeding males was 13.00 ± 1 mg (Tab. 1, Fig. 1). The testosterone levels in the breeding and the non-breeding males were 0.76 ± 0.17 ng/ml of blood plasma and 0.21 ± 0.040 ng/ml of blood plasma respectively (Tab. 2, Fig. 3) whereas the progesterone levels were 0.3 ± 0.025 ng/ml of blood plasma and 0.15 ± 0.054 ng/ml of blood plasma in the breeding and non-breeding males respectively (Tab. 2, Fig. 3).

Females

There was no difference in the mean body weight of breeding and helper females, 58.66 ± 4.5 g and 58.14 ± 1.86 g respectively. In non-breeding females the body weight was

Table 1. Body and Gonad weight in breeding and non-breeding males and body, gonad and oviducal weight in breeding, non-breeding and helper female of Jungle babblers – *Peso del corpo e delle gonadi in maschi riproduttori e non riproduttori di* Turdoides striatus. *Peso del corpo, delle gonadi e dell'ovidotto in femmine riproduttrici, non riproduttrici e nelle aiutanti al nido.*

	Males		**Females**		
	Body wt (g)	**Testes wt** (mg)	**Body wt** (g)	**Ovary wt** (mg)	**Oviduct wt** (mg)
Breeding	61.4 ± 2.27	205.0 ± 14.0	58.66 ± 4.50	72.66 ± 9.39	181.66 ± 30.17
Non-breeding	56.77 ± 2.24	13.0 ± 1.0	54.0 ± 2.47	9.0 ± 1.27	8.71 ± 2.87
Helpers	------	------	58.14 ± 1.86	65.71 ± 6.03	47.57 ± 8.30

Table 2. Progesterone and Testosterone levels (ng/ml) in blood plasma of male and female Jungle babblers – *Concentrazioni di Progesterone and Testosterone (ng/ml) nel sangue di maschi e femmine di* Turdoides striatus.

	Males		**Females**	
	Progesterone	Testosterone	Progesterone	Testosterone
Breeding	0.30 ± 0.025	0.76 ± 0.17	1.13 ± 0.066	0.65 ± 0.050
Non-breeding	0.15 ± 0.054	0.21 ± 0.040	0.16 ± 0.042	0.18 ± 0.049
Helpers	-----	------	0.7 ± 0.00	0.63 ± 0.033

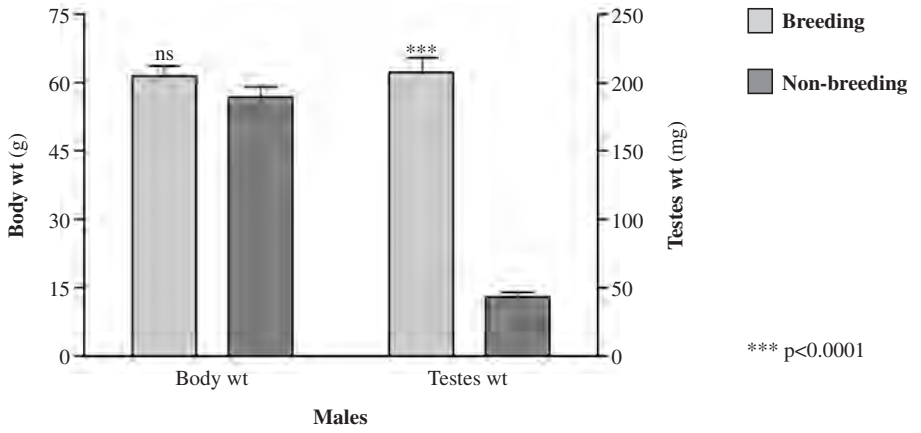

Figure 1. Body weight and testes weight in breeding and non-breeding male Jungle babblers – *Peso del corpo e dei testicoli in maschi riproduttori e non riproduttori di* Turdoides striatus.

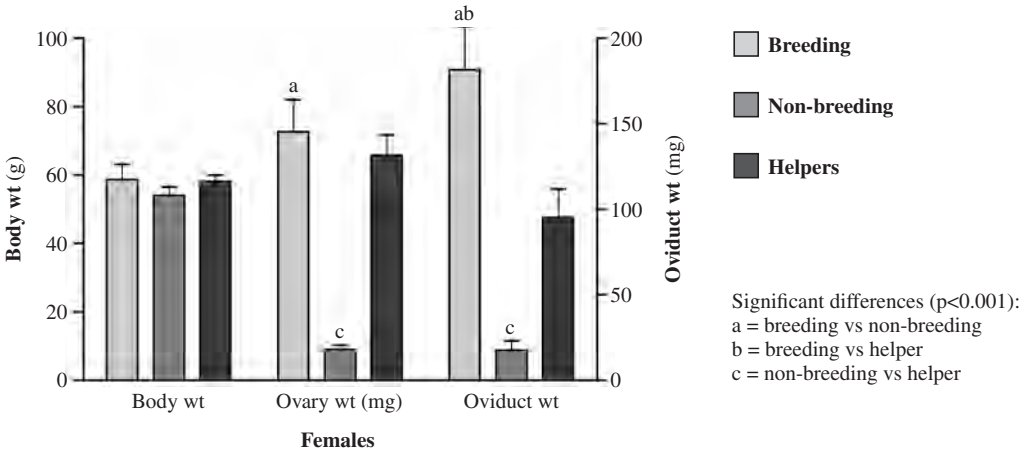

Figure 2. Body, ovary and oviduct weight in breeding, non-breeding and helper female Jungle babblers – *Peso del corpo, dell'ovario e dell'ovidotto in femmine riproduttrici, non riproduttici e nelle aiutanti al nido di* Turdoides striatus.

non-significantly lower, being 54.0 ± 2.47 g (Tab. 1, Fig. 2). The mean weight of the ovaries of the breeding females was 72.66 ± 9.39 mg that was significantly higher than the non-breeding ones, 9.0 ± 1.27 mg, while in the helper females the ovary weight was 65.71 ± 6.03 mg (Tab. 1, Fig. 2). The weight of the oviduct in breeding females was 181.66 ± 30.17 mg whereas it was significantly lower in non-breeding females, 8.71 ± 2.87 mg; intermediate values were found in helper females, 47.57 ± 8.30 mg (Tab. 1, Fig. 2). The testosterone levels in the breeding and the non-breeding females were 0.65 ± 0.050 ng/ml of blood plasma and 0.18 ± 0.049 ng/ml of blood plasma respectively; in this case helper females showed levels similar to breeding ones, 0.63 ± 0.033 ng/ml of blood plasma (Tab. 2, Fig. 4). A similar pattern was found for progesterone, with 1.13 ± 0.066 and 0.16 ± 0.042 ng/ml of blood plasma respectively in breeding and non-breeding females, with the intermediate value of 0.7 ± 0.00 ng/ml of blood plasma in helper females (Tab. 2, Fig. 4).

DISCUSSION

In co-operatively breeding birds, helpers delay their own reproductive efforts to help a breeding pair rear offspring. Numerous studies have found evidence that "helpers" directly improve the survival and present or future reproductive success of breeders (Emlen 1991). Helpers can increase the condition (Hatchwell *et al.* 1999) or survival of the young they rear (Emlen and Wrege 1988). Alternative-

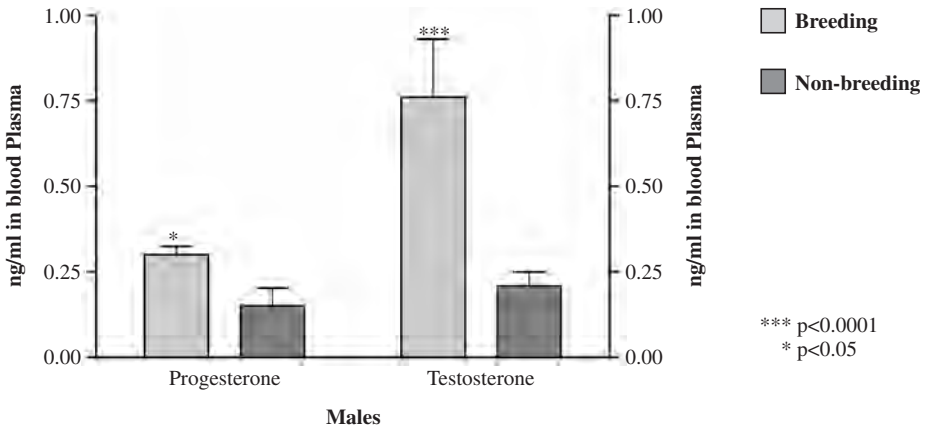

Figure 3. Hormonal levels in breeding and non-breeding male Jungle babblers – *Concentrazioni ormonali in maschi riproduttori e non riproduttori di* Turdoides striatus.

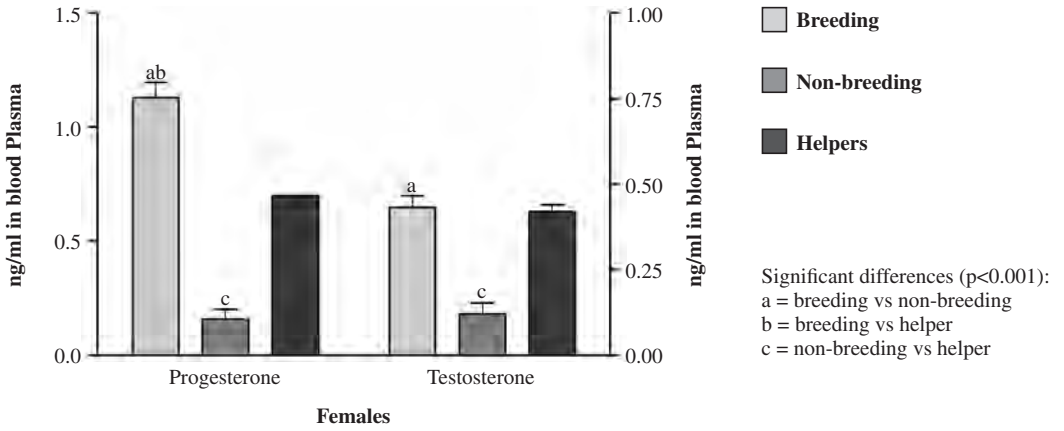

Figure 4. Hormonal levels in breeding, non-breeding and helper female Jungle babblers – *Concentrazioni ormonali in femmine riproduttrici, non riproduttici e nelle aiutanti al nido di* Turdoides striatus.

ly helpers can reduce the workload of the parents they help through "load lightening" (Crick 1992). This can increase the probability that the parents survive to breed again (Koenig and Mumme 1987; Reyer 1984; Russell and Rowley 1988), or increase their future productivity, by decreasing inter-birth interval or increasing productivity per litter (e.g. for the grey crowned babbler *Pomatostomus temporalis* see Brown 1978). In the Arabian babbler *Turdoides squamiceps*, helpers have been shown to exert a strong, positive influence on breeding success (Wright 1998).

The mechanism which allow otherwise mature birds to forgo breeding and yet still exhibit many breeding behaviour, such as feeding nestlings and nest defence include: helpers are denied access to breeding opportunities (Mumme *et al.* 1983; Emlen and Wrege 1986; Reyer *et al.* 1986) and due to sexual immaturity (poor physical and physiological conditions) or lack of appropriate stimuli, individuals do not produce adequate levels of reproductive hormones to render them reproductively competent (Reyer *et al.* 1986).

We observed that there is no difference in body weights between breeding and helper females. When the energy costing activities like incubating the eggs and feeding the young ones are shared not only by the parents but by all the members of the flock, no predisposition of fat will be required especially in case of females, and thereby their body weight and that of the helper females probably remain the same during the breeding state. Though there is no difference in the ovarian weight and body weight of breeding females and helpers, in the latter the oviducal weight was lower probably under the influence of subdued production of progesterone from the ovary retarding the

full growth of the oviduct. Helpers had intermediate progesterone levels to that observed in breeding and the non-breeding individuals (Table 1).

Androgens and their metabolites play an essential role in the induction and maintenance of aggressive and reproductive behaviour in birds. Estrogen, progesterone (in synchrony with prolactin) and androgen are involved in the regulation of aggressive nesting, courtship, copulatory, parental and allo-parental behaviour during the different stages of reproductive cycle in co-operatively breeding birds.

Jungle babblers though have a feeding territory (Andrews 1968) don't show nesting territory and all individuals of the flock take part in parental care. This is reflected in breeding males having non-significantly high testosterone levels as compared to the females in breeding state. Reproductive behaviour in males of most avian species is strongly correlated with elevated plasma T concentration (Wingfield and Farner 1993), while low concentration of reproductive hormones appears to be the proximate bases of sexual inactivity in some avian co-operatively breeding species (Reyer *et al.* 1986; Mays *et al.* 1991; Schmidt *et al.* 1991; Schoech *et al.* 1991; Schoech *et al.* 1996; Poiani and Fletcher 1994; Khan *et al.* 2001).

The helper females show plasma testosterone almost equivalent to breeding females indicating their equal role in breeding activities (especially defensive acts). Testosterone mediates a negative correlation between parental behaviour and aggression in several seasonally breeding mammalian species (Trainor and Marler 2001). This could be true for birds too. In Bank Myna *Acridotheres ginginianus*, a colonial nester, where all the males of the colony are involved in colony defence, rise and fall in the testosterone levels occur sharply from non-breeding to breeding and back in non-breeding phase whereas in the related species of the same family Sturnidae, Brahminy myna *Sturnus pagodarum* which is an individual hole nester, the rise and fall in the testosterone levels has been reported to be gradual i.e. the testosterone levels maintained for longer period (reports from our lab, unpublished). In Jungle babblers, where the whole flock is involved in defending a single nest, low levels of testosterone compared to other birds are noted. In this species non-significant differences in the plasma testosterone levels are observed in the breeding males, breeding females as well as in the helper females suggesting that the nest defence, taking care of the eggs, incubation and protecting and feeding the young ones is a combined flock activity.

There exists a positive correlation between progesterone concentration and follicular development (Silver *et al.* 1978). In females, the seasonal variation of progesterone is synchronous with the laying activity. In helper females intermediate levels of progesterone i.e. higher than breeding males but lower than breeding females supports their role in the parental activities. Oviduct development is influenced by the progesterone which induces the development of tubular glands in the magnum region of the oviduct (Hutchison 1975). Low levels of progesterone in helpers lead to immature oviduct, therefore no egg laying could be carried out by the helper females but the levels of progesterone are enough to express allo-parental behaviour (Khan *et al.,* 2001).

In Harris hawks *Parabuteo unicinctus*, all helper females appear to be physiologically unprepared for breeding, based on very low levels of LH, T and E, whereas these hormones were elevated in breeders (Mays *et al.* 1991). The physiological inhibition could result from stress due to dominance by the breeder of the same sex to assure its genetic parentage (Reyer *et al.* 1986). An adult helper female that is capable of reproduction may pose a greater threat to the α-female or to the group stability because two or more laying females would increase the number of chicks to be raised. On the other hand, physiological inhibition could occur due to the presence of opposite sex, presumably as a result of selection to avoid inbreeding.

In the present study, moderately increased levels of progesterone are observed in males which can be related to its social breeding habits where all the individuals are involved in incubation.

CONCLUSIONS

Babblers are known to exhibit co-operative breeding activities. In co-operative breeding, the individuals in the group forage peacefully together and defend the same territory. Helpers participate in defending territories, constructing and maintaining nest, incubating eggs, feeding and brooding nestlings and feeding fledglings (Walters 1990, Jackson 1994). This reflects that the burden of energy expenditure is shared equally by all the individuals in a group and that they rely on daily food supply rather than storing the food. Therefore, the physical status of the pair which is in the breeding state is nearly similar to that of the individuals in non-breeding state and hence they do not show significant differences in the body weight during breeding and the non-breeding phase. Further, when hormonal profiles are compared, the helpers show a condition between breeding and non-breeding females suggesting their equal involvement in all the reproductive activities except egg laying. The behavioural interaction of the helpers with other birds in the group (which might prevent inbreeding or

allow the helpers to remain in their natal territory) could be proximate cause for their hormonal suppression. The sacrifice of the helpers to forgo their breeding may be because these birds live under severe ecological constraints and this promotes co-operative breeding.

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