DIET ANALYSIS OF THE RED-HEADED TROGON AND ORANGE-BREASTED TROGON IN RELATION TO SEASONAL ARTHROPOD ABUNDANCE AND AVIAN PHENOLOGY

JAMES SCOTT STEWARD

A THESIS SUBMITTED IN PARTIAL FULFILLMENT
OF THE REQUIREMENTS FOR
THE DEGREE OF MASTER OF SCIENCE
(ENVIRONMENTAL BIOLOGY)
FACULTY OF GRADUATE STUDIES
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ACKNOWLEDGMENTS

My sincere thanks to the many people that helped with this Thesis. Firstly I would like to thank Assistant Professor Philip D. Round, my major advisor for all his help and guidance through out. Assistant Professor John Milne, my co-advisor for his advice on all entomological and statistical aspects of the thesis as well as kindly providing me room and the use of equipment in his lab. I am grateful to all members of my thesis advisory committee, Assistant Professor Philip D. Round, Assistant Professor John Milne, Assistant Professor Amara Naksathit, Mr Andrew Pierce and Associate Professor Vijak Chimchome, the chair in the thesis defence, for their suggestions and comments on the thesis.

In the field I am indebted to Andrew Pierce and Wangworn Sankamethavee for sharing all their expertise, data and knowledge of the study area and species. I would also like to thank all the staff and students from the Gibbon, Hornbill and Bird project that I met working within Khao Yai National Park, with special thanks to Mr Somsak Likhitrattanapisal, Mr Korakoch Pobprasert, Ms. Jitwadee Khunwongsa and Ms. Phetprakhai Wonkson.

I am thankful to Professor Warren Y. Brockleman and his students for establishing the Mo Singto Forest Dynamics plot and allowing me to share their accommodation and facilities

For providing permission to work and accommodation within the park I'm grateful to Khao Yai National Park and Khao Yai Training Centre, Training Division, Department of National Parks, Wildlife and Plant Conservation (DNP).

This work was financially supported by the TRF/BIOTEC Special Program for Biodiversity Research and Training grant BRT_351006.

Finally I would like to thank my parents for all their support and interest in the project and their kind financial assistance throughout my studies.

James Scott Steward

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ABSTRACT

The relationship between arthropod availability and the timing of avian breeding was investigated at Khao Yai, National Park, Thailand. The diets of Red-headed Trogons (*Harpactes erythrocephalus*) and Orange-breasted Trogons (*Harpactes oreskios*) were studied by means of nest cameras and direct observation. Monthly food availability was estimated by canopy pan traps and sweep netting. Breeding data was collected from 2003–2009. Both species' diets were found to be similar (Orthoptera, Lepidoptera larvae and Phasmatodea made up 81% and 87% of Orange-breasted Trogon and Red-headed Trogon diets, respectively), but timing of breeding differed. Orange-breasted trogons started breeding earlier and the season lasted for 2–3 months, Red-headed Trogons started later and the season spanned 5–6 months. Cross-correlation analysis showed that the timing of breeding of both species was linked to food availability, but in different ways. Red-headed Trogons timed breeding one month in advance of food peaks, and Orange-breasted Trogons five months in advance of food peaks. A compromise between nest competition and avoidance of the lean season is discussed as the likely reason for the difference in the timing of breeding.

KEY WORDS: FOOD AVAILABILITY/ HARPACTES ERYTHROCEPHALUS/
HARPACTES ORESKIOS/ORANGE-BREASTED TROGON/
RED-HEADED TROGON/TIMING OF BREEDING

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LIST OF ABBREVIATIONS

ABBREVIATION	**TERMS**
cm	centimetre
dbh	diameter at breast height
DVR	Digital video recorder
F	Female
g	Gram
ha	hectare
km^2	square kilometre
l	litres
M	Male
m	metre
mg	milligrams
min	minute
mm	millimetre
MST	Mo Singto Forest Dynamics Plot
OBT	Orange-breasted Trogon
RHT	Red-headed Trogon
VMD	Video motion detection

CHAPTER I
INTRODUCTION

1.1. Background and justification

The timing of breeding in temperate birds has been largely explained by the food hypothesis; that breeding is timed to coincide with peaks in food availability (Perrins, 1991, van Noordwijk et al., 1995). In temperate areas the dramatic seasonal changes in food availability are well documented and easy to observe as the seasons change. Tropical areas have a much more constant climate and the timing of breeding has not always proved as easy to explain. In some studies food has still proved to be important to the timing of breeding (Fogden, 1972, Poulin et al., 1992) and in others the timing of breeding appeared to be influenced by other factors such as climate (Skutch, 1950, Young, 1994) or nest predation (Morton, 1971).

One of the largest hurdles in studies of the effect of food on Southeast Asian forest birds is that basic data are lacking (Sodhi, 2002). The large amount of fieldwork already undertaken (Gale, 2009, Pierce et al., 2004, 2007, Pierce, 2009, Sankamethawee, 2009) on the 30 ha Mo Singto Forest Dynamics Plot (Brockelman, 1998) (hereafter MST) provided a unique opportunity for further studies into aspects of avian ecology. Large amounts of new breeding data are available for many species of birds. However there was little information on how this was correlated, if at all, with seasonal fluctuations in food supply.

This study focused on how variations in food availability affected the timing of breeding of the two trogon species present in the study area, the Red-headed Trogon, *Harpactes erythrocephalus*, and the Orange-breasted Trogon, *Harpactes oreskios*. Trogons were selected for the study for several reasons. Both species are largely insectivorous. This almost sole reliance on a single type of food resource simplifies the study of the relationship between food availability and phenology without the need to consider variations in alternative food resources such as fruit or nectar. Both trogon species are relatively easily detected and were estimated to be present in the study area at sufficient densities for practicable study (0.18 individual per ha and 0.28 individuals per ha for Orange-breasted Trogon and Red-headed Trogon respectively, Round et al., 2005). The observed tendency of trogons to feed on, and provision nestlings with, large arthropods (Skutch, 1959, Andrew Pierce and Wangworn Sankamethavee, unpub. data) also made them well suited for making unobtrusive diet observations. The two species share many similar traits in terms of selection of nest sites, diet, foraging techniques and area, and general behaviour. However, preliminary analysis of data collected since 2003 suggested that the timing and duration of their breeding differed, with Orange-breasted Trogon breeding earlier than Red-headed Trogon (Khao Yai Avian Diversity Project, unpub. data).

This study of trogons' feeding behaviour, diet, and breeding ecology aimed to investigate the links between food availability and the timing of breeding as well as describe unknown parameters of their general biology.

1.2. Objectives and scope of the study

The objectives of this study were

i) to assess the composition of arthropods in the diets of the Red-headed Trogon (RHT) and Orange- breasted Trogon (OBT)

ii) to collect data on seasonal changes in arthropod food availability relevant to the study species

iii) to examine the relation between seasonal changes in food availability and the timing of breeding

iv) to investigate reasons for the difference in timing of breeding between the two species

v) to investigate detailed differences in the feeding ecology, and other interactions between the two trogon species.

1.3. Hypotheses and predictions

This study structured its hypotheses and predictions similarly to those of Young (1994) who studied the neotropical House Wrens (*Troglodytes aedon*).

It was predicted that:

(1) peak breeding should coincide with food peaks if food for egg production is limiting

(2) peak breeding should be about one month in advance of food peaks if food for provisioning nestlings is limiting.

(3) peak breeding should occur two to five months in advance of food peaks if food for post-reproductive events (post fledging. parental care, juvenile dispersal, and moulting) is important.

These three hypotheses together form the main hypothesis that breeding is timed so that major energetic demands associated with successful reproduction (egg production, provisioning for young or fledgling dispersal) coincide with the peak in food availability

CHAPTER II
LITERATURE REVIEW

2.1. Orange-breasted Trogon and Red-headed Trogon: Species descriptions

2.1.1. Trogons

Both the Red-headed Trogon and Orange-breasted Trogon are members of the avian family Trogonidae, the sole family of the order Trogoniformes, whose main distinguishing characteristic is their unique heterodactyl toe arrangement in which the third and fourth toes are directed anteriorly and digits one and two posteriorly. (In those other non- passeriform bird orders with a similarly x-shaped toe orientation it is digits two and three that are directed anteriorly, and one and four posteriorly—a zygodactylous arrangement). The legs and feet of trogons are relatively short and weak, restricting their movements when perched to shuffles along a branch. The 39 species of trogons show a pan-tropical distribution ranging 35 ° either side of the equator, at elevations from sea level to 3500 m. Eleven species occur in Asia, many more (25) in the Neotropics, with just three species in Africa (Johnsgard, 2000).

Many aspects of the ecology of Trogonidae remain unknown. The author of the most recent review of the family states "I am saddened by the number of times I had to enter 'No information available' in the species accounts" (Johnsgard, 2000). Most published studies on trogons are of the neotropical species (Skutch, 1944, 1948, 1956, 1959, 1962, Gonzalez-Rojas et al., 2007). There is very little published data on the basic natural history of any of the Asian or African species.

Generalised observations of trogons note their arboreal nature and tendency to perch motionless and silent on branches for prolonged periods of time (Lekagul and Round, 1991, Johnsgard, 2000). The African species are considered solely insectivorous; the neotropical quetzals forage predominately on fruit while the remaining trogons eat a mixture of insects and fruit (Johnsgard, 2000). Frugivory has been correlated with body size (Remsen, 1993, Pizo, 2007), with fruit making up a larger percentage of the diet as size increases. Most descriptions of trogons feeding describe the birds scanning their surroundings slowly from a perch before gleaning fruits or insects from vegetation whilst in flight or the "hawking" of insects from the air.

2.1.2. Orange-breasted Trogon and Red-headed Trogon

Much of the scant information available on either Orange-breasted Trogon or Red-headed Trogons is published in regional bird guides and handbooks (e.g., Smythies, 1953, 1981, Ali and Ripley, 1983, Lekagul and Round, 1991, Wells, 1999, Robson, 2000, 2002); and in monographs of the Trogoniformes (Johnsgard, 2000, Forshaw, 2009).

For Orange-breasted Trogons, Robson (2002), reports 26.5–31.5 cm total length. A single adult male weight of 57.3 g was recorded by Wells (1999). Johnsgard (2000) notes wing lengths from various sources ranging from 119–130 mm and tails of 140–185 mm measurements are taken from several different locations and subspecies. Morphometric data of OBT caught during mist netting on the MST are presented in Table 2.1. The scarce information on breeding biology includes observation of many nests in hollow stumps and dead bamboos 2–3 ft from the ground; eggs laid from February–April in Burma (Smythies, 1953), and in Borneo nests in early months of the year (Smythies, 1981). Wells (1999) describes two nests: one shallow unlined depression at the top of a 2 m high stump and the other in the side of a stump at a height of 1.5 m. Eggs were recorded in late January and early April from the Thai-Malay Peninsula. No detailed information on the diet is available (Johnsgard, 2000). Orange-breasted Trogon is said to be solely insectivorous, taking "chiefly bugs and beetles" (Smythies, 1953). Such foods as crickets, locustids, cicadas, beetles, grasshoppers, lizards, ants and fruit are also listed (Smythies, 1981).

Red-headed Trogon is larger (total length of 31–35.5 cm, Robson, 2002). Five adults weighed 75.0 – 86.6 g, with the heaviest a female (Wells, 1999). Johnsgard (2000) noted wing lengths of 131–177 mm, and tail lengths 153–233 mm from a variety of sources and subspecies. All morphometric data of RHT caught during mist netting on MST are presented in Table 2.2. In Burma, eggs were recorded from March to May (Smythies, 1981). Juveniles with parents were noted in March and May in the Thai-Malay Peninsula (Wells, 1999). In India and Nepal breeding was recorded between April–July (chiefly May and June) and nests are described as unlined natural hollows in rotten tree trunks or woodpecker holes, at 1.5–5 m. The clutch-size is 3–4 eggs (Ali and Ripley, 1983). The only dietary items recorded are green grasshoppers, beetles, stick insects and leaves and berries (Ali and Ripley, 1983).

Orange-breasted Trogons are found in lowland and hill forests from southern China throughout south-east Asia (Thailand, Laos, Cambodia, Vietnam, Burma, Malaysia, Sumatra, Borneo) to Java. Red-headed Trogon has a more northerly and westerly distribution, inhabiting forest from north-east India, Nepal, Bhutan, a larger area of southern china, through Southeast Asia to Sumatra (Figure 2.1).

Table 2.1. Morphometrics of OBT caught during mist-netting at Mo Singto Plot (Khao Yai Avian Diversity Project, unpub. data)

Date	Sex	Wing (mm)	Tail (mm)	Weight (g)
11 Feb 06	M	130	180	57.0
11 Feb 06	F	127	181	56.0
23 Apr 06	M	129	183	57.2
11-Nov-07	F	126	168	65
09-Mar-09	M	130	179	54.4
09-Mar-09	F	124	172	56.6

Table 2.2. Morphometrics of RHT caught during mist-netting at Mo Singto Plot (Khao Yai Avian Diversity Project, unpub. data)

Date	sex	Wing (mm)	Tail (mm)	Bill (mm)	Weight (g)
08-Mar-03	F	145	182		
18-Mar-03	F	146	183		93
04-Sep-03	F	150	200		87
04-Nov-03	F	149	185		88
29-Dec-03	F	142	165	21.4	85
03-Feb-05	F	148	-	25	84.5
09-Mar-05	M	148	192		85.5
09-Mar-05	M	146	185		90
30-Mar-05	M	149			89.5
21-Feb-07	M	150	192		90
05-May-09	M	152	192		85

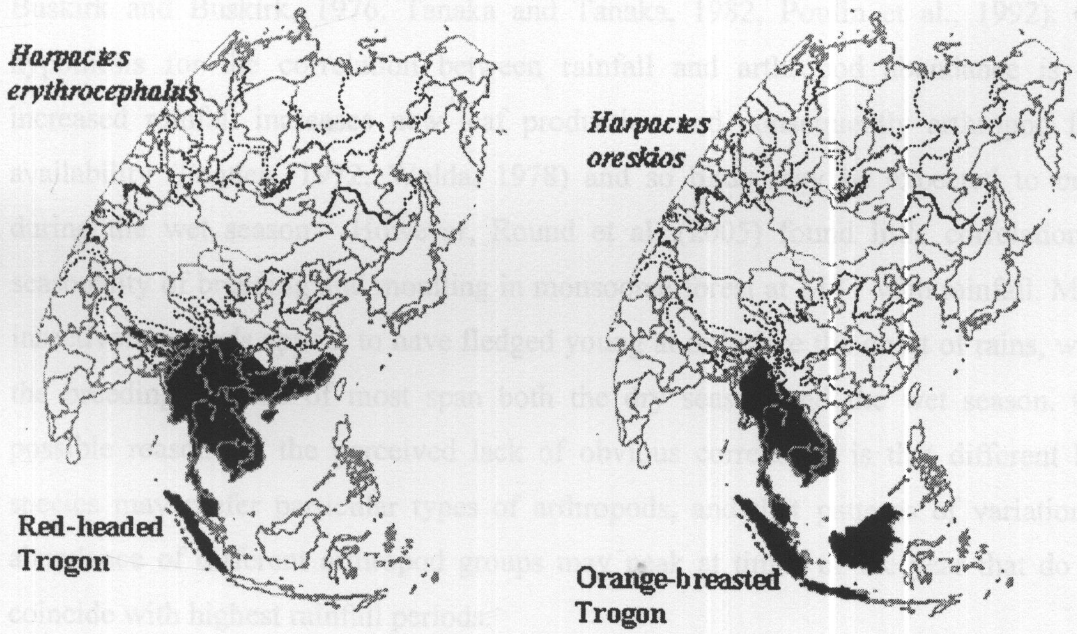

Figure 2.1. Distribution of RHT and OBT

2.2. Timing of breeding

The timing of bird breeding and moult, and what controls it, has been of interest to investigators for more than sixty years. The timing of these two nutritionally costly processes is often explained by the food availability hypothesis: that is, that breeding and moulting occur at times when ample food resources are available to sustain them (Stutchbury and Morton, 2001). It has been well supported in many studies of temperate birds that breeding occurs when food is abundant for raising young (Ewald and Rohwer, 1982, Van Noorwijk et al., 1995). Fewer studies have been done on tropical birds and the longer breeding seasons and less pronounced fluctuations in arthropod abundance mean the timing of breeding is not as easily explained.

Rainfall and general invertebrate abundance are often considered to be related in tropical areas. A marked decrease in arthropod abundance during the dry season seems characteristic of neotropical areas that experience <1500 mm of rainfall per year and have a severe dry season (Janzen, 1973, Wolda, 1978, Poulin et al., 1992). In more humid tropical areas that experience >1500 mm of rainfall per year and have a mild dry season, a less marked reduction has been found (Janzen, 1973, Buskirk and Buskirk, 1976, Tanaka and Tanaka, 1982, Poulin et al., 1992). One hypothesis for the correlation between rainfall and arthropod abundance is that increased rainfall increases new leaf production and consequently arthropod food availability (Fogden, 1972, Wolda, 1978) and so birds may be expected to breed during the wet season. However, Round et al. (2005) found little correlation of seasonality of breeding and moulting in monsoonal forest at MST with rainfall. Many insectivorous birds appear to have fledged young at or before the onset of rains, while the breeding seasons of most span both the dry season and the wet season. One possible reason for the perceived lack of obvious correlation is that different bird species may prefer particular types of arthropods, and that patterns of variation in abundance of different arthropod groups may peak at times of the year that do not coincide with highest rainfall periods.

A general community-wide study by Fogden (1972) of bird populations in equatorial forest in Sarawak (a climate he refers to as the most stable in the world) still found a well-defined breeding season. Due to difficulties of finding nests at his study site, he used records from all over Sarawak to define a December–August breeding season. Estimations of fluctuations in arthropod abundance were made for four groups of insects by observing numbers of flushed insects along a set route. He summarised that the breeding season was timed to avoid the coincidence of the four energetic activities (breeding, parental care of young, moulting and dispersal) with a two month lean period in food availability during October and November.

Young (1994), on the other hand, in a more specific study of a single insectivorous species in Costa Rica, investigated which if any of three major energy demands (egg production, nestling provisioning, nestling dispersal) influenced the timing of breeding. He concluded that rather than breeding being timed so that maximum food availability coincided with the period of feeding nestlings it instead was timed so as to coincide with post- reproductive moult and juvenile dispersal.

CHAPTER III
STUDY AREA

3.1. Khao Yai National Park

Khao Yai National Park, Thailand's first national park, was established in 1962. Situated to the northeast of Bangkok, in the Dongrak mountain range, it spans parts of four provinces: Nakhon Ratchasima, Prachin Buri, Nakon Nayok and Saraburi. The park covers an area of 2168 km^2 between the latitudes of 14° 05′ N and 14° 15′ N and the longitudes of 101° 05′ E and 101° 50′ E. The elevation of the park ranges from 250 to 1400 m above sea level. The four highest peaks within the park are Khao Laem (1326 m) in the northeast, Khao Khieo (1292 m), Khao Rom (1351 m) in the southeast, and Khao Sam Yod (1142) in the west (McClure, 1974). Smitinand (1962) classified the vegetation into five types: mixed deciduous forest (5%), dry evergreen forest (21%), moist evergreen forest (64%), hill evergreen forest (5%) and grassland and secondary.

Khao Yai has a monsoonal climate with three distinguishable seasons (Figure 3.1). The hot season occurs during March-April; the rainy season during May–October and the cool season during November–February

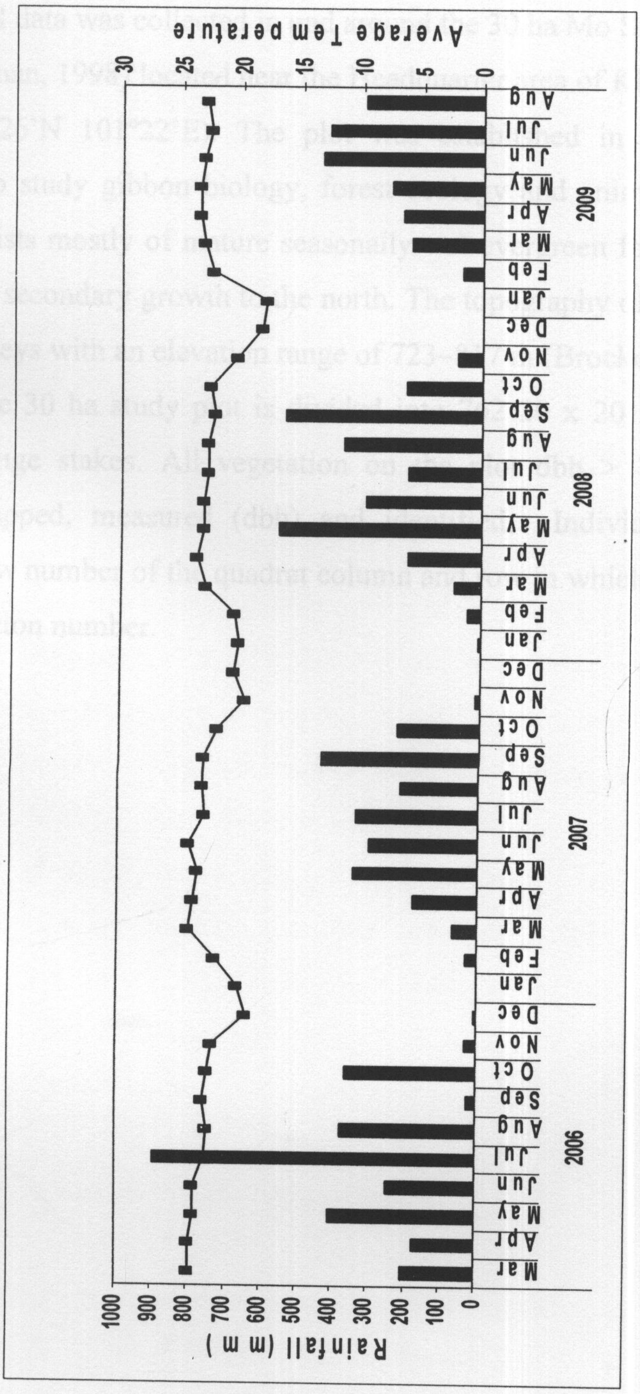

Figure 3.1. Monthly rainfall and average temperature during March 2006–August 2009 from Mo-Singto area of Khao Yai, National Park.

3.2. Mo Singto Forest Dynamics Plot

All data was collected in and around the 30 ha Mo Singto Forest Dynamics Plot (Brockelman, 1998) located near the Headquarter area of Khao Yai National Park, Thailand (14°26'N 101°22'E). The plot was established in 1993 by Dr. Warren Brockelman to study gibbon biology, forest ecology and animal-plant relationships. The area consists mostly of mature seasonally wet evergreen forest with a small area of 40 year-old secondary growth to the north. The topography of the area is a series of ridges and valleys with an elevation range of 723–817 m (Brockelman et al., 2001)

The 30 ha study plot is divided into 762 20 x 20 m squares marked by numbered orange stakes. All vegetation on the plot dbh > 1 cm, is individually numbered, mapped, measured (dbh) and identified. Individual number tags on vegetation show number of the quadrat column and row in which they occur and a 3–4 digit identification number.

CHAPTER IV
METHODOLOGY

To investigate my hypothesis two measures were needed; a measure of monthly food availability and a measure of monthly reproductive effort. The number of eggs laid per month was used to represent reproductive effort and weighted biomass index (see section 4.2.3.2) was used to represent monthly changes in food availability.

4.1. Breeding

Nest data has been collected on the MST since 2003 as part of an ongoing research project (Appendix A and B). Once found, nests were checked (with the aid of a mirror when necessary) every second day or daily around hatch and fledge dates and depending on field worker availability. Nest cards were filled out for any nest found in or around the MST. These recorded nest location, height, type, number of eggs/nestlings and status. More detailed observations of trogons were made from October 2006 until May 2009. In the 2008 and early 2009 breeding season trogon nests were searched for more specifically, initially by attempting to follow birds to nests, but it was found to be more productive to search promising looking rotten stumps for signs of excavations.

4.1.1. Estimates of first egg dates

Nest data were used to extrapolate first egg dates using known incubation and nestling periods (Table 4.1). For example if a RHT nest was found as a full clutch of 2 eggs on 30th March and, after being monitored for 8 days, was predated, 8 days was subtracted from the 18 days incubation period and the mid-point of the remaining 10 days was used to predict a clutch completion date of 25th March. Therefore as RHT lay every other day and begin incubation upon laying the final egg an estimated first egg date would be 23rd March

Table 4.1. Length of nest stages and clutch sizes used to extrapolate first egg dates (Calculated from Khao Yai Avian diversity project unpub. data).

Species	Clutch size (eggs)	Incubation Period (days)	Fledging Period (days)
Orange-breasted Trogon			
Range	2–3	17–18	11–13+
Mean (± SD)	2.4 ± 0.5	17.5 ± 0.7	12[a]
N	17	2	-
Red-headed Trogon			
Range	2–3	17–19	12.5–14
Mean (± SD)	2.6 ± 0.5	18 ± 0.2	13 ± 0.7
N	46	9	5

[a] due to inconclusive fledging data (one full fledging period of 11 days and two predation incidents occurred after 12 and 13 days) 12 days was selected for use as an estimate of OBT fledging period.

4.1.2. Reproductive effort

The total number of eggs laid per month were used as a measure of reproductive effort. Total eggs laid was considered a better measure of reproductive effort than number of nests. This was based on the assumption that a clutch of 3 eggs represented a greater energetic investment in reproduction than a clutch of 2 eggs.

4.2. Food availability

An outline of the methodology used to calculate food availability is summarised in Figure 4.1. In order to establish prey groups' length-weight relationship needed for a regression analysis, a separate arthropods data set of the arthropod groups preyed upon was collected opportunistically on and around the MST (see section 4.3.2.1.).

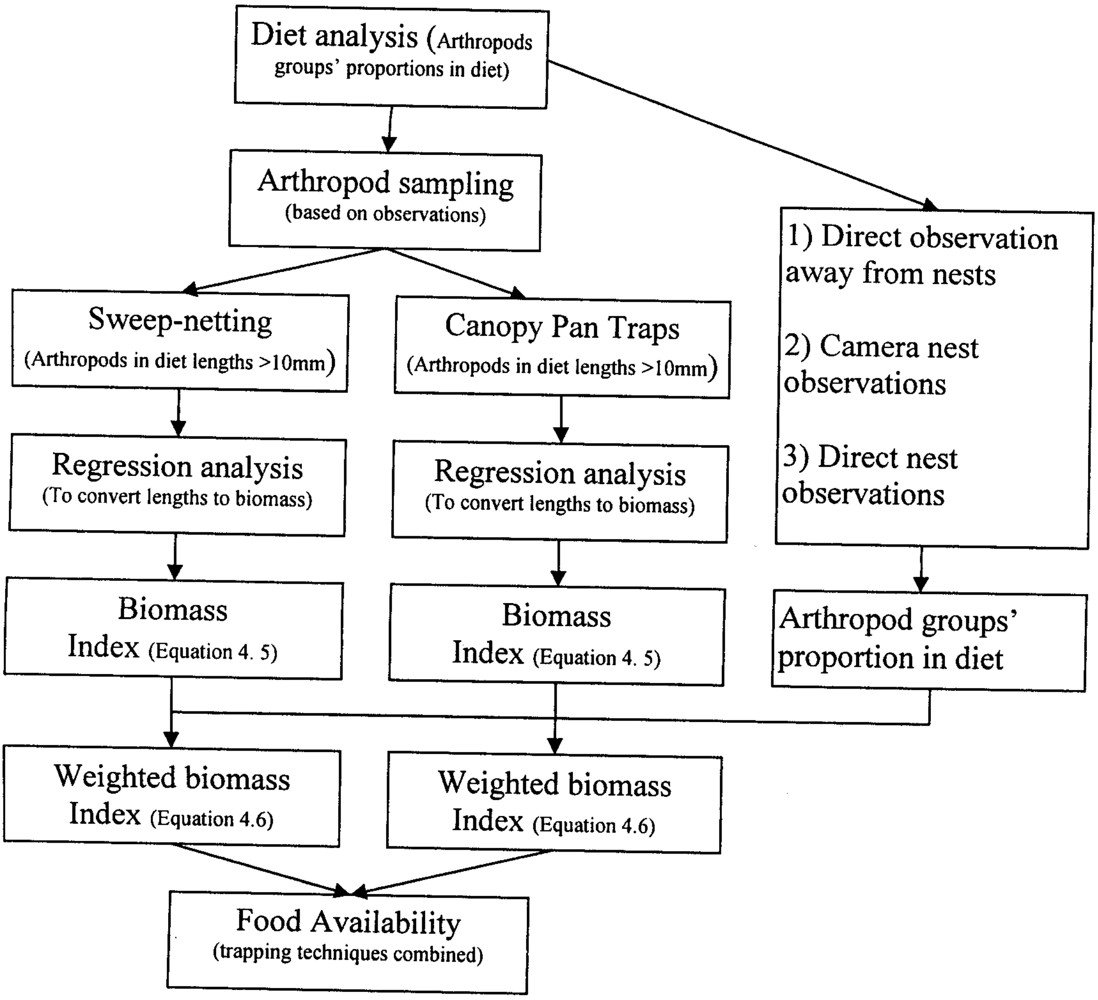

Figure 4.1. Summary of steps in the calculation of food availability

4.2.1. Diet analysis

To assess food availability to an insectivore, it is vital to build up a profile of the various arthropod taxa present in a study area that are preferred by the study species (Cooper and Whitmore, 1990, Young, 1994). Information on arthropods foraged for by the two trogons was collected using digital images captured at nests, direct nest observations and by direct observations of adults.

4.2.1.1 Nest camera observation

A camera system for monitoring nests (as described in Bolton et al., 2007) was used, but with a new model (DV58) of the Memocam Digital Video Recorder (DVR) with a weatherproof design, 2GB SD card storage capacity and low power consumption mode (Figure 4.2). The video motion detection (VMD) feature of the system allowed the capture of images of adult birds feeding nestlings at nests that were located during the 2008 breeding season. Images collected were examined and categorised into three categories; positive identification, tentative identification or alternatively as not identified. The same images were then independently identified using the same system by an entomologist. The two independent identifications were then compared to reach final decisions on each image set.

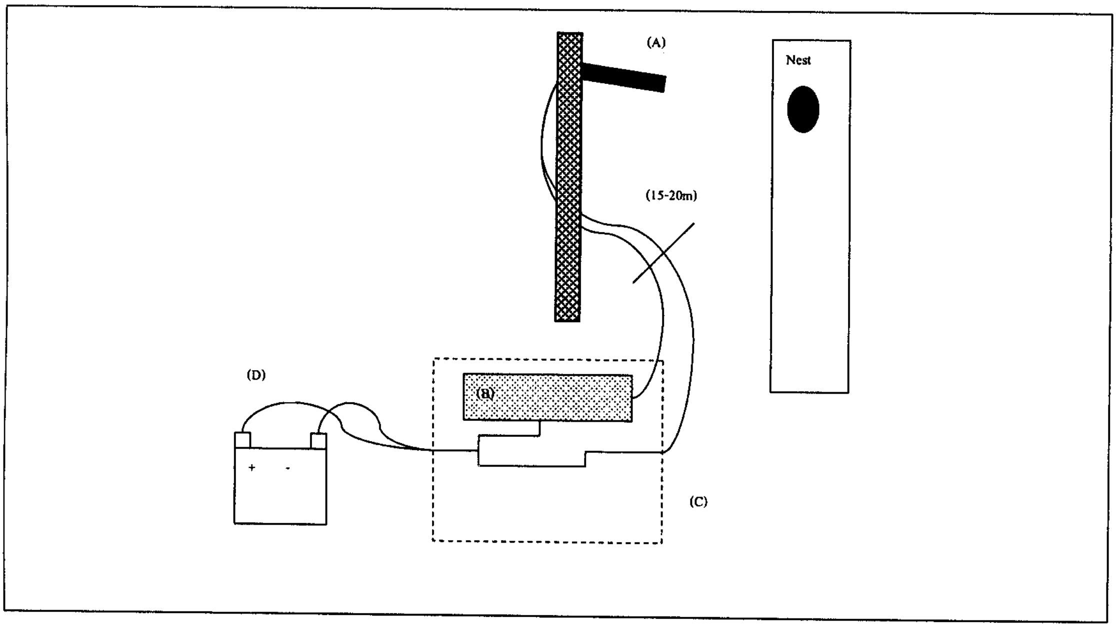

Figure 4.2. Nest camera System (A) Colour Bullet Camera (420 TV lines) attached to vegetation (B) Memocam minature DVR (D-V58/WP) (C) Protective box (D) 12v Battery

4.2.1.2 Direct nest observation

Due to a camera malfunction direct nest observations of two Orange-breasted Trogons' nests that proceeded as far as the nestling stage were also made during the 2009 breeding season. Observations were made through a 60x magnification, 80 mm spotting scope, from behind a sheet blind 15–20 m from the nest. A record of all nest activity was recorded including when possible positive identifications of prey types.

4.2.1.3. Direct observation

Direct observations of adult individuals of both species away from nests were made during October 2007–April 2009. Once a target bird was encountered on the plot it was followed for 180 min or until lost. A record of the bird's height, location (tree number), time, activity (perched, in flight, foraging) and relevant observations on foraging techniques (gleaning, aerial sallies etc.) flock associations and prey type were recorded at 5 min intervals. Height data was used to define the foraging microhabitat and significance in the differences were tested using the Mann-Whitney test performed with SPSS.

4.2.2 Arthropod sampling

As ultimately a measure of food availability was required for comparisons with breeding, arthropod samples were taken monthly in MST before, during and after the breeding season from November 2007 to September 2008. Two techniques were selected for sampling arthropods: sweep-netting the lower vegetation strata and suspending aerial pan traps in higher vegetation strata. A combination of the two was considered the most appropriate method of sampling the potential prey items extensively and exclusively within the microhabitats used by the two trogon species. The definition of food availability for an insectivore used was that suggested by Wolda (1990) "Insect availability is the abundance of potential prey items in the microhabitat used by an insectivore when searching for food." The diet analysis defined potential prey items, and data from direct observations of trogons were used to clearly define the microhabitat used by each species when searching for food. Sweeping was considered an effective method of sampling foliage-dwelling arthropods, but becomes troublesome when sampling vegetation above 3m. Aerial pan traps were therefore used to sample leaf dwelling arthropods in the canopy between 3–15 m.

4.2.2.1 Sweep netting

Using a 456 mm diameter sweep-net with a 119 cm handle the first 3 m of vegetation were swept, along five selected 100 m transects on the plot (Figure 4.3), one time per month. Each 100 m transect was divided into five 20 m sections and 20 equal strength sweeps of vegetation were performed along each 20 m section of the transect resulting in 25 samples per month. (If a sweep did not contact vegetation it was not counted. This often occurred because a constant motion of the sweep net is desirable while moving along a transect in order to reduce escapees from the net). The net and its contents were then placed in a killing jar containing ethyl acetate for 10–15 min. Once suitably stunned the sample was emptied out of the net directly into a killing jar for a further 10–15 min, until all arthropods were killed. Finally leaves, twigs and other pieces of vegetation were removed and the sample was placed into a labelled collecting jar. After returning from the field samples were frozen until they could be sorted in a laboratory to remove remaining vegetation debris, and then preserved in 70 % ethanol.

4.2.2.2 Canopy pan traps

20 large green circular plastic containers (50 cm diameter, 15 cm deep) filled with 5 l of salt water (to preserve captured arthropods) and a small amount of detergent (to reduce surface tension) were suspended at different heights (4.75 –14.55 m) in the canopy depending on the availability of suitable cross-branches. The traps were distributed around the plot area (Figure 4.3) in suitable trees (those with a horizontal branch at a height between 3–15 m, with vegetation above, and clear of

vegetation obstructions below, to facilitate setting and emptying). They were set one time per month for a 7 day period (14th–21st of each month). Insects collected in the salt water solution were washed in fresh water and then preserved in 70% ethanol. Direct observations of trogons confirmed that both arthropod sampling techniques (sweep netting *0.1–3 m and canopy pan traps 4.75–14.55 m) sampled within both* trogon species' foraging microhabitat (RHT 0–15 m, OBT 0–25 m).

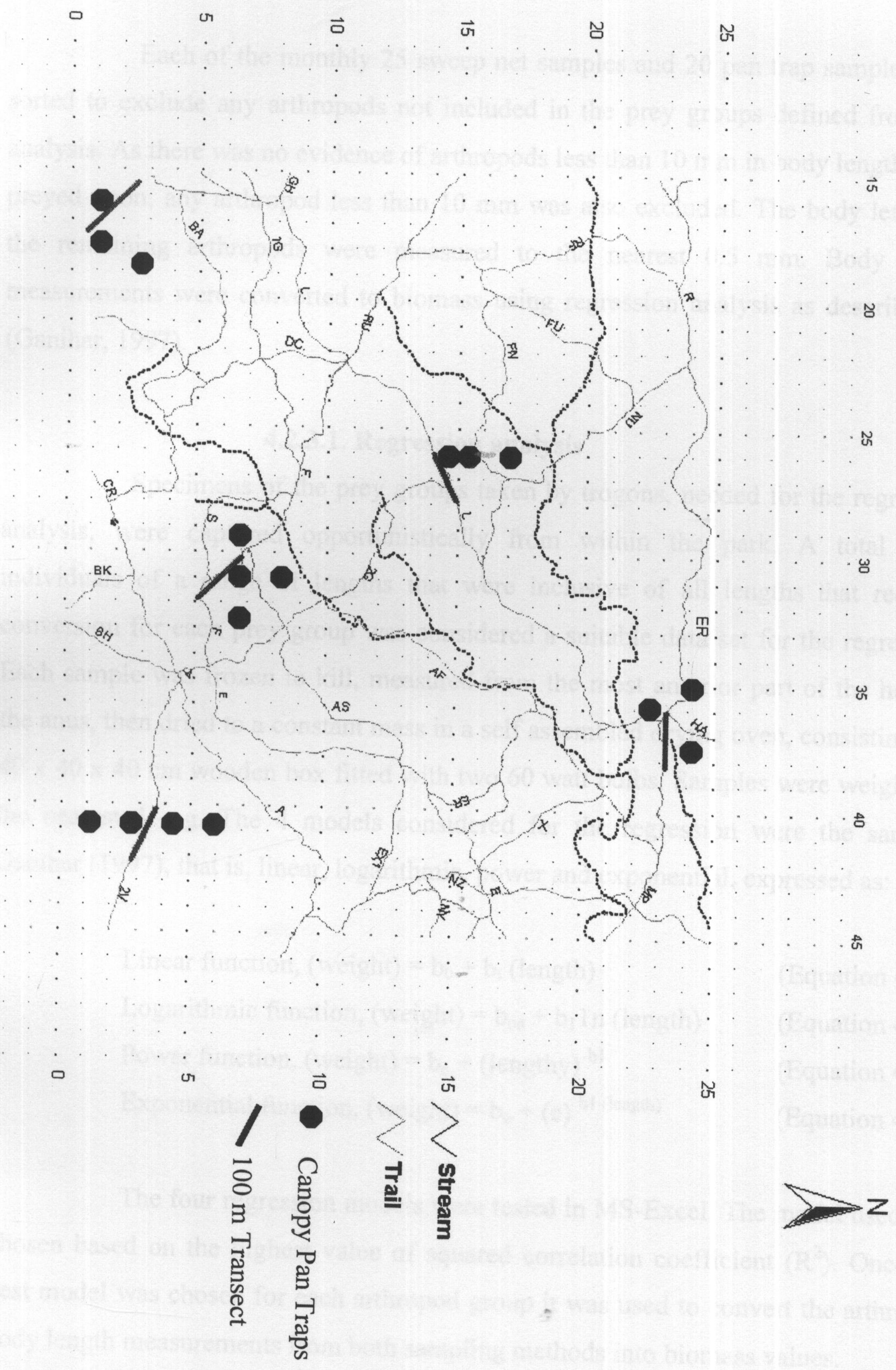

Figure 4.3. Location of 100 m sweep netting transects and canopy pan traps on the Mo Singto Forest Dynamics Plot.

4.2.3. Estimation of monthly available arthropod prey biomass

Each of the monthly 25 sweep net samples and 20 pan trap samples were sorted to exclude any arthropods not included in the prey groups defined from diet analysis. As there was no evidence of arthropods less than 10 mm in body length being preyed upon, any arthropod less than 10 mm was also excluded. The body length of the remaining arthropods were measured to the nearest 0.5 mm. Body length measurements were converted to biomass using regression analysis as described by (Ganihar, 1997).

4.2.3.1. Regression analysis

Specimens of the prey groups taken by trogons, needed for the regression analysis, were captured opportunistically from within the park. A total > 10 individuals of a range of lengths that were inclusive of all lengths that required conversion for each prey group was considered a suitable data set for the regression. Each sample was frozen to kill, measured from the most anterior part of the head to the anus, then dried to a constant mass in a self assembled drying oven, consisting of a 40 x 40 x 40 cm wooden box fitted with two 60 watt bulbs. Samples were weighed to the nearest 1 mg. The 4 models considered for the regression were the same as Ganihar (1997), that is, linear, logarithmic, power and exponential, expressed as:

Linear function, (weight) = $b_0 + b_i$ (length) (Equation 4.1)
Logarithmic function, (weight) = $b_{oa} + b_1 \ln$ (length) (Equation 4.2)
Power function, (weight) = b_o + (lengthy)^{b1} (Equation 4.3)
Exponential function, (weight) = $b_o + (e)^{b1\,(\text{length})}$ (Equation 4.4)

The four regression models were tested in MS-Excel. The model used was chosen based on the highest value of squared correlation coefficient (R^2). Once the best model was chosen for each arthropod group it was used to convert the arthropod body length measurements from both sampling methods into biomass values.

4.2.3.2. Biomass indices.

Once monthly weights were calculated for each trapping method the data was further converted to food availability based on a mathematical approach suggested by Poulin and Lefebvre (1997). Firstly seasonal variation in biomass abundance was calculated per taxon group as a proportion of the summation of that group captured over the whole sampling period with:

$$\text{Biomass index} = \sum_{i=1}^{n} \frac{x_{ij}}{y_i} \qquad \text{(Equation 4.5)}$$

where x_{ij} is the weight of arthropods from group i sampled with a trapping method during the date j, y_i is the weight of arthropods from group i collected during the whole sampling period. This approach takes into account the likely bias of any trapping method to certain taxonomic groups by removing the affect of variation in capture efficiencies of different arthropod taxon. The index reaches it highest values when several different prey groups' biomass are simultaneously high rather than total biomass which may be dominated by only one or two arthropod taxon that are more efficiently sampled by the trapping technique.

Secondly the biomass index is weighted by multiplying each prey group by its relative preference in the bird's diet with:

$$\text{Weighted biomass index} = \sum_{i=1}^{n} p_i \frac{x_{ij}}{y_i} \qquad \text{(Equation 5.6)}$$

where p_i is the proportion of arthropods from group i in the bird's diet. This index reaches its highest values when the biomasses of several prey groups favoured by the bird are high. Because the index is based on the summation of the percent biomass (relative to the whole sampling period) of each prey group sampled, samples from different techniques can be combined.

4.3. Cross-correlation analyses

Cross-correlation, a type of signal analysis based on the correlation between two variables that were measured along the same time series, can be used to uncover relationships between biological phenomena that are separated in time (Young, 1994). In this study cross-correlation was used to examine the three food hypotheses by cross-correlating monthly food levels and reproductive effort. The two variables used in this study were total eggs laid each month and combined weighted biomass index. Lag periods and sinusoidal patterns of positive and negative correlation can be used to address the three hypotheses. The duration of the lag period corresponding to the greatest positive correlation in food and breeding effort will show if food availability and breeding effort coincide or the number of months by which they differ. If food availability proves to be seasonally variable, and breeding is linked to food availability, the cross-correlation will show a sinusoidal pattern of first positive and then the negative correlation. I performed cross-correlation analyses with SPSS.

CHAPTER V
RESULTS

5.1. Breeding Season

A total of 51 RHT nests and 19 OBT nests have been found and monitored by the Khao Yai Avian Diversity Project since 2003. (Appendices A and B; Figure 5.1.). RHT breeding data for 2009 was excluded from the calculation of monthly reproductive effort as nest finding efforts were substantially higher at the beginning of that season compared to the end. In all other years search effort was relatively constant throughout the season.

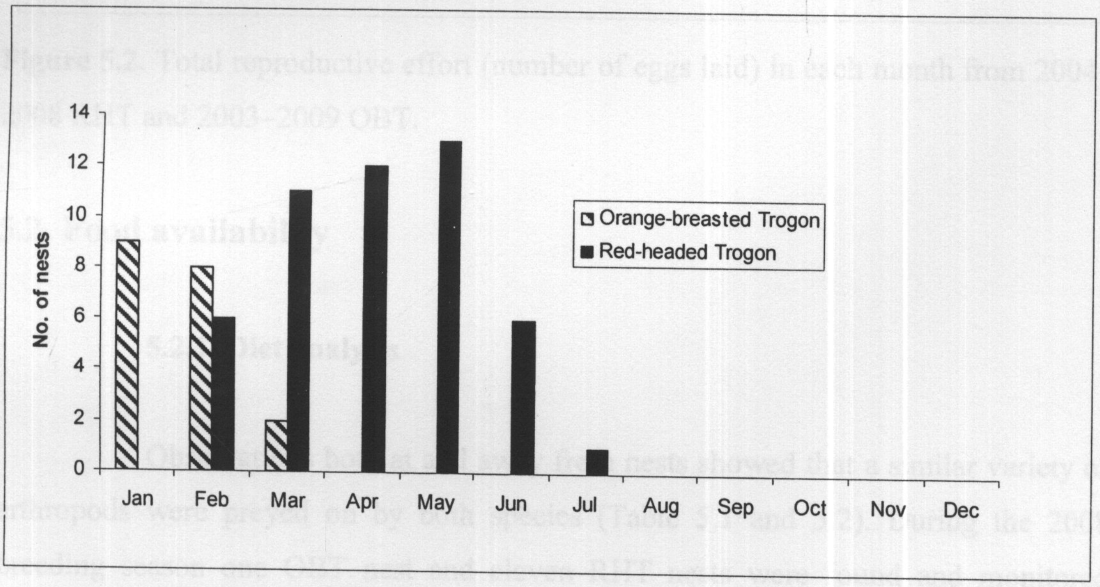

Figure 5.1. Total number of nests found each month from 2004–2008 for RHT and 2003–2009 for OBT based on extrapolated first egg dates
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RHT breeding began in late February or early March, peaked in May and the last eggs were laid in June or in one case early July. OBT started one or two months earlier, with the highest reproductive effort in January and February, and only two nests in March (Figure5.2).

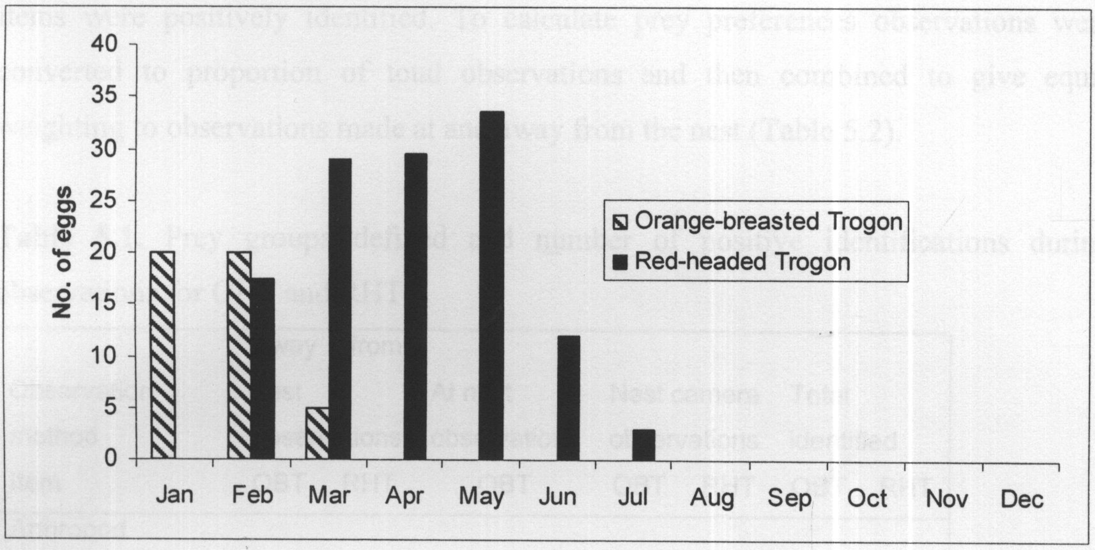


Figure 5.2. Total reproductive effort (number of eggs laid) in each month from 2004–2008 RHT and 2003–2009 OBT.

5.2. Food availability

5.2.1. Diet analysis

Observations both at and away from nests showed that a similar variety of arthropods were preyed on by both species (Table 5.1 and 5.2). During the 2008 breeding season one OBT nest and eleven RHT nests were found and monitored within or near MST. During the 2009 season five OBT nests and four RHT nests were found (unlike other years nest-finding effort was clearly less after April). The camera system was set on three different RHT nests in 2008. The first was predated by a variable squirrel (*Callosciurus finlaysonii*) in the egg stage. At the second nest the camera was set the day after hatching and monitored for 12 days until fledging, resulting in 70 identifiable sets of images. No images were recorded at the final nest due to a camera malfunction. In the 2009 season the two nests that reached the nestling stage were observed directly for a total of 56 hours, 16.5 hours for the first nest and 39.5 hours for the second. A total of 87 arthropods were positively identified. Both nests were depredated before the nestlings fledged.

Away from the nest, during direct observation, 19 OBT and 29 RHT prey items were positively identified. To calculate prey preferences observations were converted to proportion of total observations and then combined to give equal weighting to observations made at and away from the nest (Table 5.2).

Table 5.1. Prey groups defined and number of positive identifications during observations for OBT and RHT.

Observation method	Away from nest observations		At nest observations	Nest camera observations		Total identified	
Item	OBT	RHT	OBT	OBT	RHT	OBT	RHT
Arthropod							
Araneae			2			2	
Coleoptera		1					1
Hemiptera Cicadidae	2	1	12		5	14	6
Lepidoptera adults	1	2	4	1		6	2
Lepidoptera larvae	10	13	9	1	11	20	24
Mantodea		1	3		3	3	4
Orthoptera	5	6	39	2	25	46	31
Phasmatodea	1	6	18	1	26	20	32
Unidentified			16		34		
Unseen			35				
Total no. of prey items identified	19	30	87	5	70	111	100

Table 5.2. Arthropod prey item proportions in diet

Observation	Away from nest		At nest		Combined	
	OBT	RHT	OBT	RHT		
Item	n = 19	N = 30	n = 92	n = 70	OBT	RHT
Araneae			0.02		0.01	-
Coleoptera		0.03			-	0.02
Hemiptera Cicadidae	0.11	0.03	0.13	0.07	0.12	0.05
Lepidoptera adults	0.05	0.07	0.05	0.00	0.05	0.03
Lepidoptera larvae	0.53	0.43	0.11	0.16	0.32	0.30
Mantodea	0.00	0.03	0.03	0.04	0.02	0.04
Orthoptera	0.26	0.20	0.45	0.36	0.35	0.28
Phasmatodea	0.05	0.20	0.21	0.37	0.13	0.29

Diet items were categorised into 8 categories based around taxonomic order. Lepidoptera distinctive life stages were separated and cicadas were grouped at the family level as they were the only family of Hemiptera observed in the diets. RHT were recorded eating fruit in three observations, and frugivory was also inferred from seeds located in the nest, but no record or observations were made of OBT consuming fruit. An RHT was observed once taking a single *Pothos chinensis* (Raf.) Merr. (Family Araceae) berry and on two separate occasion several *Gironniera nervosa* Planch. (Family Ulmaceae) fruits. Additionally the debris collected from the floor of one of three RHT nests contained several seeds, some of which were identifiable as *Cinnamomum subavenium* Miq. (Family Lauraceae) and were thought to have been regurgitated by the adult bird during incubation. Accumulation of regurgitated seeds in the nest cavity has been reported in other trogon species (Skutch, 1959).

5.2.2. Foraging microhabitat

A total of 1177 point observations were made between November 2007 and March 2009, 752 for RHT and 425 for OBT. Foraging height was 0–16m for RHT (mean 5.07 ± 3.4 m SD) and 0–25m for OBT (mean 9.48 ± 4.23 m SD), with OBT feeding significantly higher than RHT (Mann-Whitney U = 67385, Z = -16.54, RHT = 752, OBT = 425, P <0.001).

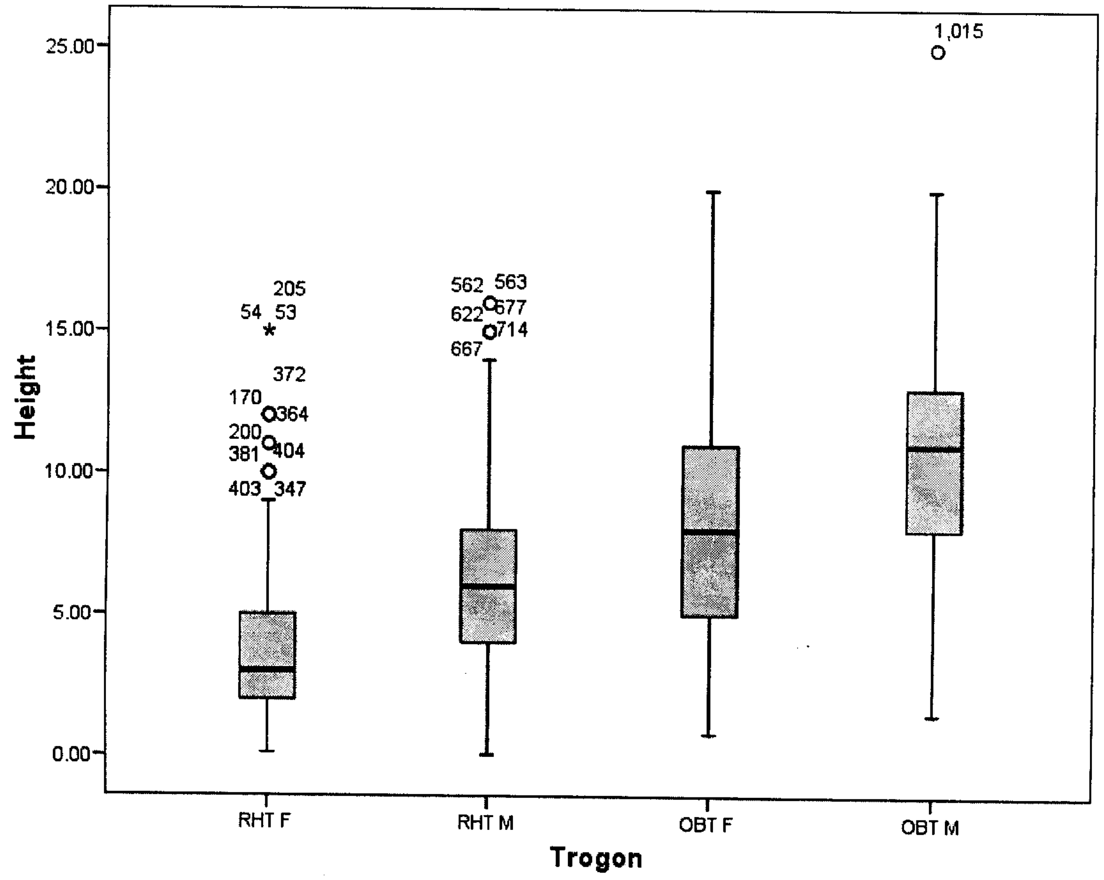


Figure 5.3. Foraging heights of different trogon species and sexes from direct observations. Box and whisker plot demonstrating the differences in foraging observation at different vegetation heights. Females of both species were observed, and foraged, at lower heights than males. The black line in the centre of the box indicates the median value. The shaded box indicates where 50 per cent of the data falls. The whiskers connect the highest and lowest scores that are not considered to be outliers. Outliers and extreme values (shown as circles and star respectively) are those values that are more than 1.5 box- or > 3 box-lengths from the twenty-fifth or seventy-fifth percentile and are therefore not considered as falling inside the range of scores to be displayed in the distribution.

Within each species a significant difference in foraging height between the sexes was also found (Figure 5.3). The mean foraging height in female RHT was 3.89 ± 2.81 m and in male RHT 6.56 ± 3.6 m (Mann-Whitney RHT U = 37752, Z = -10.86, RHTM =333 RHTF = 419). Similarly in female OBT mean foraging height was 8.17 ±

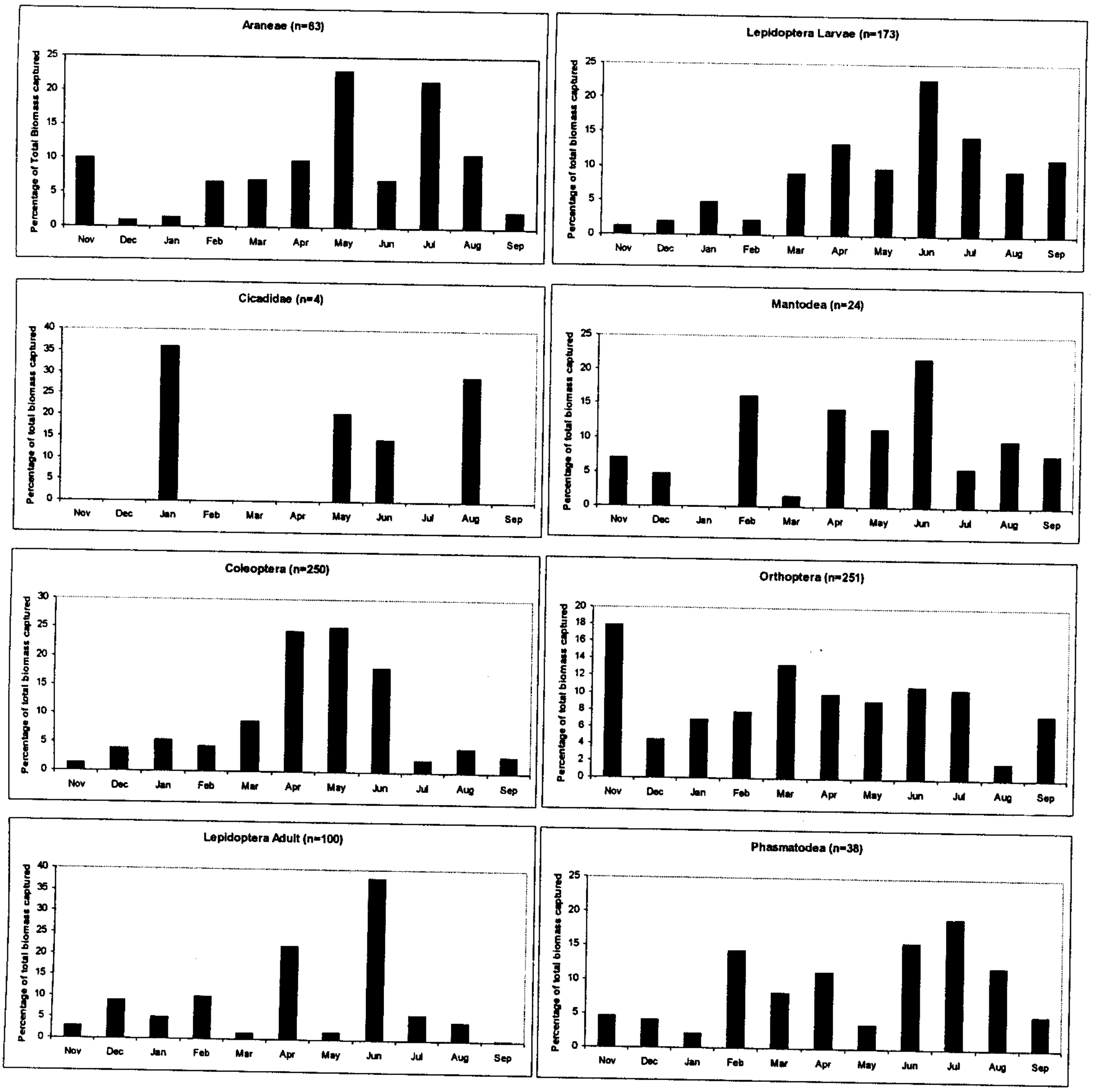
4.15 m and male 10.51 ± 4.02 m (Mann-Whitney OBT U = 14960, Z= -5.84, OBTF = 188, OBTM = 237; $P < 0.001$).

5.2.3. Arthropod sampling

A total of 902 potential prey items were sorted and measured from the arthropod samples. Arthropod lengths were converted to weights using the regression analysis (Table 5.3), based on a data set of 202 specimens (Appendix C). As found by Ganihar (1997) and Brady and Noske (2006) the power model was found to be the best predictor for the majority of taxonomic groups (Appendix D), with the one exception being Mantodea (best predicted with the linear model). The biomass of many of the individual potential prey groups for RHT and OBT showed similar seasonal variations (Figure 5.4). Biomass peaked in the early wet season, with the leanest periods towards the end of the wet season through to the end of the dry season.

Table 5.3. Length-weight regression

Prey category	N	Range of lengths (cm)	Model	B_0	B_1	R^2
Arachnida						
Araneae	23	0.36 – 3.85	Power	0.0269	3.06	0.85
Insecta						
Coleoptera	16	0.95 – 3.3	Power	0.0355	2.0686	0.73
Hemiptera Cicadidae	34	1.69 – 4.7	Power	0.0345	1.793	0.7
Lepidoptera adult	15	1.2 – 3.2	Power	0.0062	3.475	0.84
Lepidoptera larvae	16	0.92 – 5	Power	0.0021	2.9337	0.69
Mantodea	13	1.1 – 6.95	Linear	0.0364	-0.0368	0.91
Orthoptera	55	0.45– 3.39	Power	0.0178	2.9868	0.93
Phasmatodea	30	1.5 – 12.05	Power	0.0007	2.4164	0.87



Araneae (n=63)

Lepidoptera Larvae (n=173)

Cicadidae (n=4)

Mantodea (n=24)

Coleoptera (n=250)

Orthoptera (n=251)

Lepidoptera Adult (n=100)

Phasmatodea (n=38)

Figure 5.4. Seasonal fluctuations in percentage of total biomass of individual prey groups. Percentages of total biomass caught in canopy pan traps and from sweep netting combined.

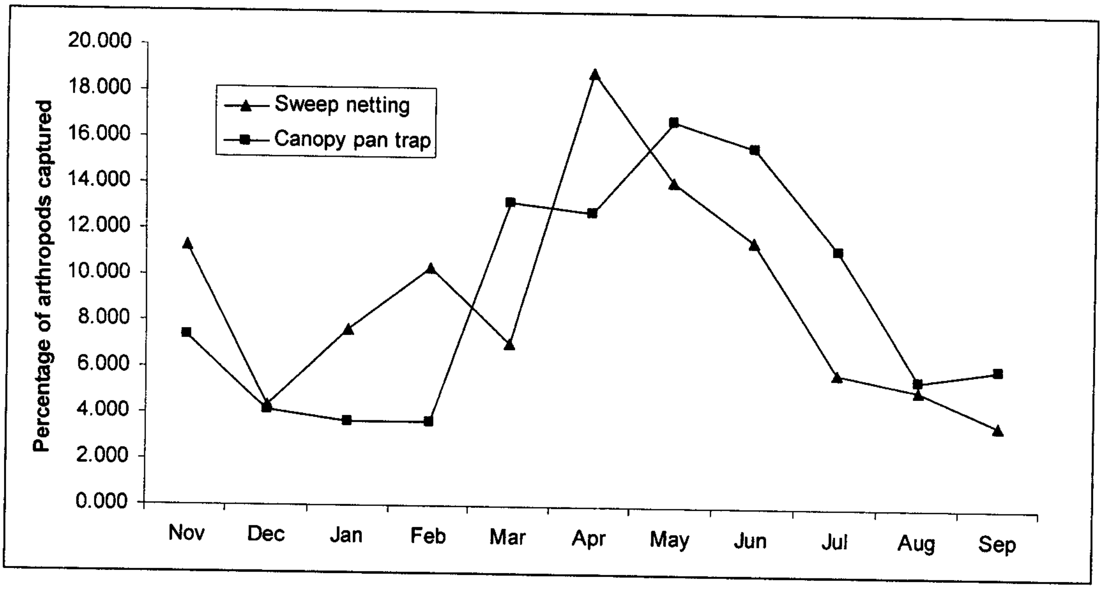


Figure 5.5. Proportional changes in total biomass captured by each sampling technique, displayed as a percentage of the total biomass captured over the 11 months by that sampling method.

5.2.4. Biomass indices

Poulin and Lefebvre (1997) suggested that prey groups represented by five or fewer captures should be excluded from index calculation due to the large effect they have on the final index values. The Hemiptera family, Cicididae, represented in the samples by only 3 pan trap and 1 sweep net captures was therefore excluded from the biomass index.

The resulting arthropod biomass varied in similar ways for both trapping techniques. Sweep netting biomass peaked in April and pan traps one month later in May (Figure 5.5) When both trapping techniques' percentage biomass were combined arthropod biomass peaked in April; declined, but remained high, in May and June (Figure 5.6 a). The biomass index (Figure 5.6 b) shifted the peak to June. Similarly once weighted to OBT and RHT diets both peaks occurred in June with decreased values in the preceding months (Figure 5.6 c and d).

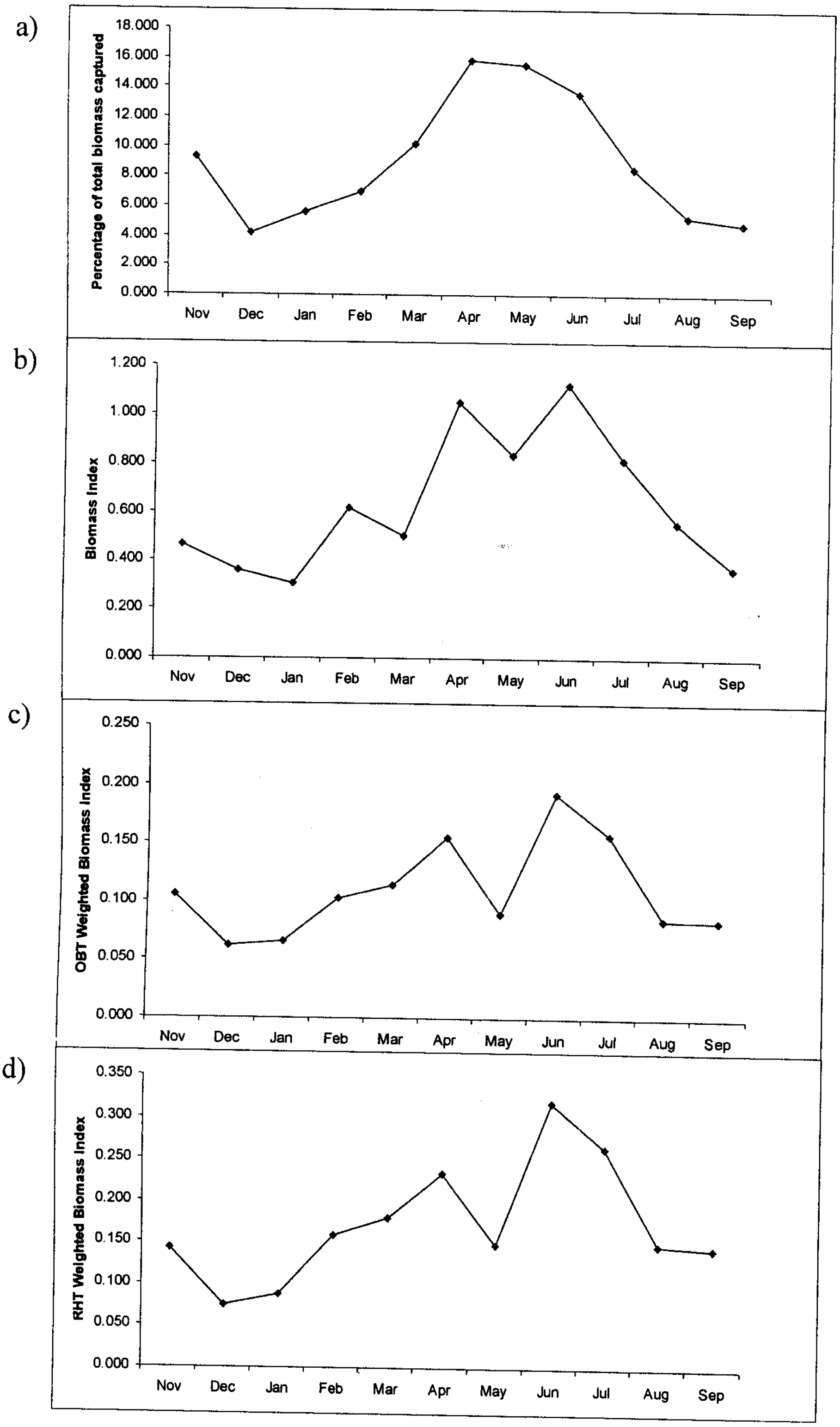


Figure 5.6. Combined (sweep-netting and pan traps) trapping techniques monthly variation in (a) percentage of arthropods captured, (b) indices of arthropod biomass, (c) OBT-weighted arthropod biomass index (food availability), (d) RHT-weighted arthropod biomass index.

5.3. Cross-correlation

Cross-correlation analysis of monthly reproductive effort (number of eggs laid) and food availability (weighted biomass index) (Figure 5.7) showed firstly a sinusoidal pattern for both species, indicating that food supply was strongly seasonal and that breeding was tied to food. RHT showed the clearer sinusoidal relation, indicating that breeding and food were more closely coupled than in OBT. Secondly RHT showed strongest positive and a significant correlation at -1 lag months and OBT the strongest positive correlation at -5 lag months (Figure 5.8). The correlation in OBT was not significant (although in this study we are interested more in the when the strongest positive correlation occurs, rather than in its strength or significance. The strength of the relationship between the timing of breeding and food availability is examined by observing the sinusoidal pattern.)

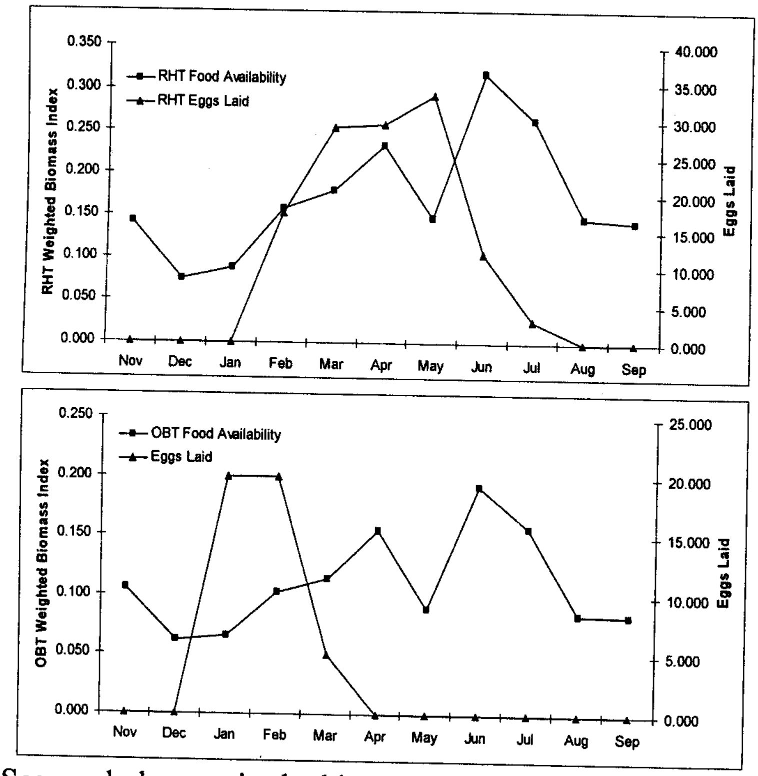


Figure 5.7. Seasonal changes in the biomass of arthropods preyed upon by RHT and OBT and RHT and OBT reproductive effort (eggs laid).

The cross-correlation analysis indicates that RHT breeding was timed one month in advance of food peaks which, according to the food hypothesis, suggests that feeding of nestlings coincided with the highest food availability. OBT breeding was timed five months in advance of food peaks. In this species the highest food availability therefore coincided with the period of late post-reproductive events (Figure 5.8).

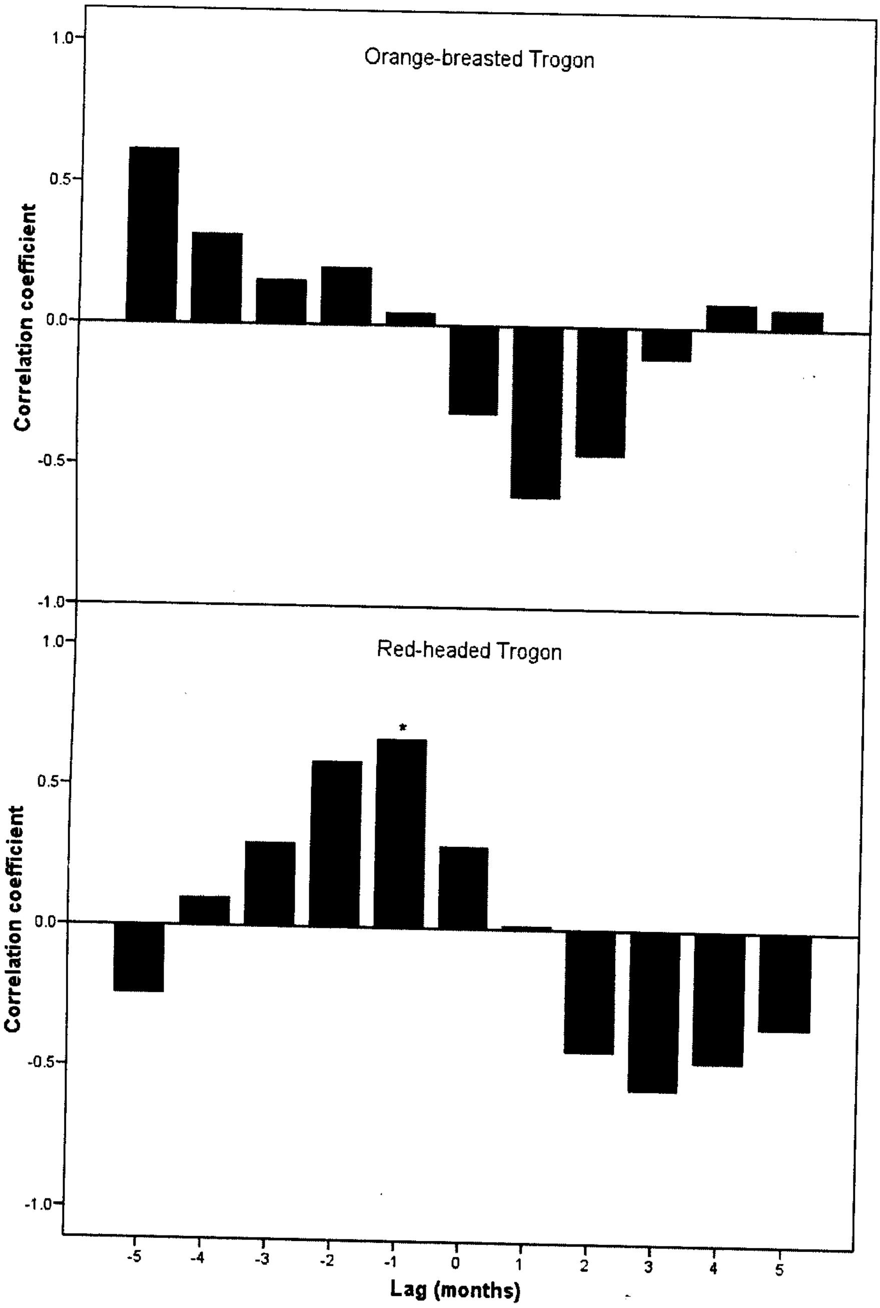


Figure 5.8. Cross-correlation analysis of the weighted biomass index and reproductive effort in Figure 5.7. (*P < 0.05)

CHAPTER VI
DISCUSSION

6.1. Composition of arthropods in the diets of the Red-headed Trogon and Orange-breasted Trogon.

Both RHT and OBT diets were similar both in the arthropod groups preyed upon, and in the proportionate contributions of each group in the diets. Orthoptera, Lepidoptera larvae and Phasmatodea together contributed 87 and 81 percent of RHT and OBT prey items respectively. This result is not surprising considering that both species forage in a structurally similar and largely over lapping microhabitat and unlike many other species of forest birds (that have multiple foraging techniques) both trogon species relied almost exclusively on the "sally-stall" foraging manoeuvre described by Remsen and Robinson (1990). The sally-stall manoeuvre describes the classic trogon behaviour of flying from a perch in pursuit of the food item, stalling in front of the target briefly with a fluttering motion in order to seize it and then returning to a perch (normally a different one).

6.2 Seasonal changes in arthropod food availability.

As both trogons prey on similar arthropod groups, with the same three groups making up the majority of their diet (Figure 5.2), both species are exposed to similar seasonal changes in food availability. In this study food availability increased with rainfall; was high from April to July; peaked in June, one month after peak rainfall, and was at its lowest in December and January (Figure 6.1 a). A three to fourfold difference separated minimum and maximum availability of insect prey. It has been found in other studies that insect numbers are related to rainfall, with a general pattern of highest abundance and biomass occurring in the wet season and lowest abundance and biomass in the dry season. (Fogden, 1972, Janzen, 1973, Kwok and Corlett, 2002). This is thought to be due to the relationship between rainfall and leaf production (Fogden, 1972, Wolda, 1978). Arthropods in MST started increasing after the onset of rainfall in February and decreased well before the last rains, a trend also observed in other tropical habitats that experience a severe dry season (Wolda, 1977, Poulin et al., 1992). The two leanest months in this study, December and January, were the two driest with a lack of, or only a few mm of, rainfall. Temperature was also at its coolest during these two months. The seasonality of rainfall is generally considered a more important influence than temperature upon the number of arthropod in tropical habitats (Wolda, 1988, Kwok and Corlett, 2002). Essentially, as stated by Kwok and Corlett (2002), separating the influence of temperature, rainfall and plant phenology is difficult because the three are themselves linked and show similar seasonal patterns. Because the MST rainfall and temperature pattern is regular from year to year (Figure 2.1 and 6.1. b) both the period of high arthropod availability and the lean period are likely regular and seasonally reoccurring periods of low and high food availability for both trogon species (and by implication for other insectivores)

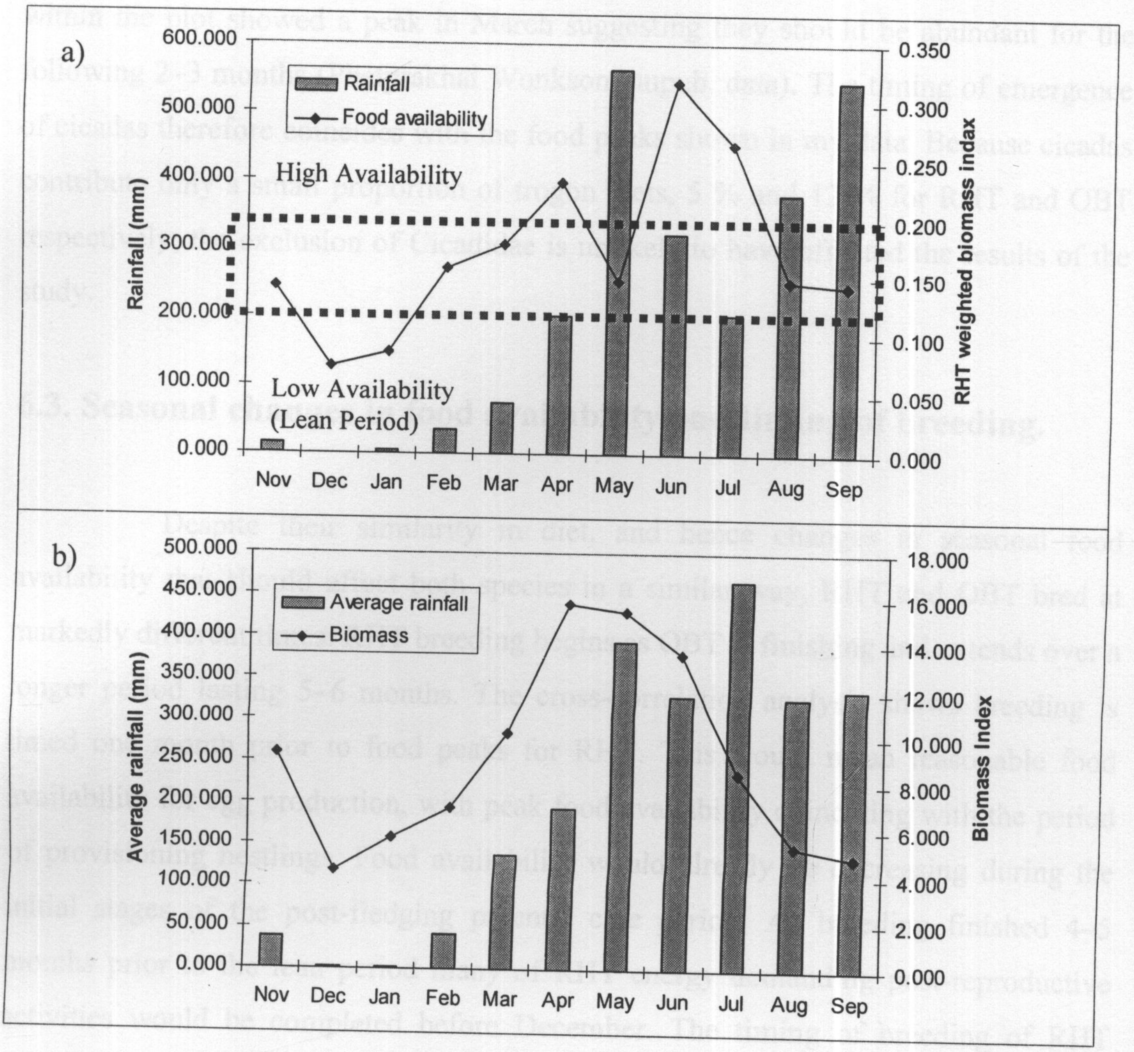


Figure 6.1. a) 2007–8 monthly rainfall and changes in food availability. Food availability points above the dotted box were considered months of high food availability and the two months below of low availability or the lean period. b) Biomass index (2007–8) and average monthly rainfall on the MST from March 2006–September 2009.

The decrease in food availability detected during May may have been due to a methodological problem rather than any real drop in prey availability. Thus, the heavy rainfall during the sampling period which made sampling by sweep-netting difficult due to the extremely wet conditions may have resulted in fewer arthropods being captured.

The only prey group excluded from both prey biomass indices were cicadas because of the low number captured. A 2009 study of cicada exuvia numbers within the plot showed a peak in March suggesting they should be abundant for the following 2–3 months (Phetprakhai Wonkson, unpub. data). The timing of emergence of cicadas therefore coincides with the food peaks shown in my data. Because cicadas contribute only a small proportion of trogon diets, 5 % and 12 % for RHT and OBT respectively, the exclusion of Cicadidae is unlikely to have affected the results of the study.

6.3. Seasonal changes in food availability and timing of breeding.

Despite their similarity in diet, and hence changes in seasonal food availability that should affect both species in a similar way, RHT and OBT bred at markedly different times. RHT breeding begins as OBT is finishing and extends over a longer period lasting 5–6 months. The cross-correlation analysis shows breeding is timed one month prior to food peaks for RHT. This would mean reasonable food availability for egg production, with peak food availability coinciding with the period of provisioning nestlings. Food availability would already be decreasing during the initial stages of the post-fledging parental care period. As breeding finished 4–5 months prior to the lean period many of RHT energy demanding post-reproductive activities would be completed before December. The timing of breeding of RHT therefore closely resembles that of Fogden's (1972) results from his community-wide study in Sarawak where he concludes that breeding is timed to avoid any activities with a major energy demand during the two month lean season (Figure 6.2.).

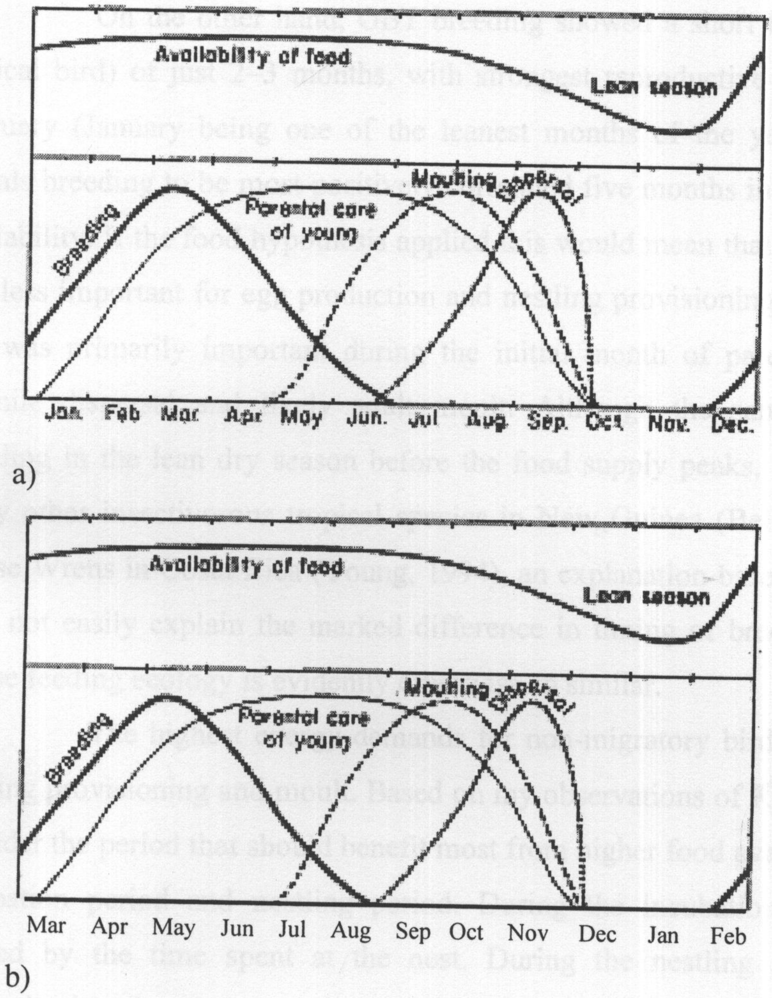


Figure 6.2. Modified from Fogden (1972): a) summary of seasonality in forest birds in Sarawak, b) summary of seasonality in Red-headed Trogon in Khao Yai National Park (note the 2 month movement of x-axis)

Little information is available on the post-reproductive activities (parental care of young, moulting and dispersal) listed by Fogden (1972), for either trogon, but time spans presented in figure 6.2 seem likely for RHT. The prolonged periods of parental care found for insectivorous forest birds at Semmengo, Sarawak is likely to be true for the trogons. (The one trogon species mentioned in the study, a Scarlet-rumped Trogon, *H. duvaucelii*, pair were still providing 56% of a juvenile food 17 weeks after fledging (Fogden, 1972). A Red-headed Trogon juvenile on MST was still being fed by both parents 46 days after fledging (personal observation, this study).

On the other hand, OBT breeding showed a short breeding season (for a tropical bird) of just 2–3 months, with strongest reproductive effort in January and February (January being one of the leanest months of the year). Cross-correlation reveals breeding to be most positively correlated five months in advance of peak food availability. If the food hypothesis applied this would mean that high food availability was less important for egg production and nestling provisioning in OBT than in RHT and was primarily important during the initial month of parental care and during juvenile dispersal and likely adult moult. Although the same relationship, early breeding in the lean dry season before the food supply peaks, has been reported for many other insectivorous tropical species in New Guinea (Bell, 1982) and Tropical House Wrens in Costa Rica (Young, 1994), an explanation based on food availability does not easily explain the marked difference in timing of breeding for two species whose feeding ecology is evidently otherwise so similar.

The highest energy demands for non-migratory birds are egg production, nestling provisioning and moult. Based on my observations of RHT and OBT I would consider the period that should benefit most from higher food availability would be the incubation period and nestling period. During the incubation period, foraging is limited by the time spent at the nest. During the nestling period the birds are constrained in foraging time, both through the demands of brooding and provisioning up to three chicks, and also through the need to feed themselves. High food availability would be of the greatest advantage at that time, and the observed timing of breeding in RHT (one month in advance of the food peak) fits well with this supposition. However, the timing of breeding in OBT (five months in advance of the food peak, with maximum food availability during post reproductive activities) does not fit this hypothesis and seems paradoxical.

6.4. Differences in feeding ecology between the two species.

The similar diets and foraging technique used by both species, and the overlap in foraging range, implies that some competition over food resources would be expected. Direct competition over food may be reduced by the difference in feeding strata between the two species. Although, as mentioned above, there are many similarities in the two trogon species' feeding ecology, observations show a clear difference in mean foraging height. This suggests spatial partitioning of the prey resource with OBT predominantly using a higher vegetation stratum than RHT.

6.5. Difference in timing of breeding between the two species.

Given their similar ecology and dietary preferences why do RHT and OBT breed at such different times? The optimal breeding period should be similar for both species. One possible explanation is the predation hypothesis (Morton, 1971). The similarity in nest site selection and the similar Mayfield (1961) estimates of nest success (0.07 for both species, unpub. data) yields no evidence that there is any differential predation pressure between the two species that can account for the different timing of breeding.

The most likely explanation is that it is the similarity in nest-sites, and hence nest-site competition, that drives the two species to breed during different, periods, with RHT excluding OBT from using nest-stumps at the optimal time. This conclusion is based on several pieces of evidence. (1) Detailed examination of individual years' data corroborates that there is very little overlap between timing of breeding in the two species. Once the first RHT nest was found, on only two occasions were further OBT nest found in the same season (one additional nest per season). (2) On three different occasions RHT were recorded nesting in cavities excavated and used by OBT earlier in the same season. (3) The only aggressive interaction between the two species was observed around a potential nest-stump, that an OBT had begun to excavate. An excavating OBT was aggressively chased off the potential nest stump by a RHT. Even though both species were frequently observed feeding, relatively close together and even perched in the same tree, no agonistic behaviour was ever observed between feeding birds. (4) Suitable, well-rotted nest-stumps used by trogons are a limited and highly fragile transient resource, with very few available on MST at any one time. Direct competition for this scarce resource would therefore be expected. (5) RHT should be the more dominant species due to its greater size. (6) RHT is estimated to be present in the study area at a greater density than OBT which would be expected if RHT is the more successful competitor. (7) The weaker sinusoidal pattern of the

OBT cross-correlation analysis indicates that OBT breeding is less closely coupled to food availability than for RHT.

Based on ecological niche theory, two species cannot coexist over time, exploiting limited resources in an identical way, as one will eventually replace the other (Hutchinson, 1959, Schoener, 1974). To avoid direct competition a resource can be partitioned. In this case it appears that the limiting resource (nest sites) is partitioned temporally, with the smaller OBT breeding earlier, during a less favourable period of lower food availability, so as to avoid competition with the larger RHT. This leads to OBT population being restricted by a short breeding season, possibly contributing to its lower density in the study area. As RHT breeding lasts 5–6 months this leaves at least six months when nest sites are available. OBT's short breeding season in only 2–3 of these months likely represents a compromise between breeding when stumps are available (before occupancy by RHT) yet with adequate food resources to enable completion of all high energy-demanding reproductive and post-reproductive activities before the onset of the lean season.

6.6. How does seasonality vary year-to-year?

All insect sampling was carried out during a single season during November 2007–September 2008. The resulting measures of seasonal changes in relative food availability for both species were assumed to be typical. Breeding data, on the other hand was necessarily pooled over 6–7 years (in order to obtain a reasonably large sample of nests), and assumed to be representative of reproductive effort for the 2008 breeding season. To investigate the legitimacy of these two assumptions other data were analysed.

Firstly I analysed data from 20 canopy malaise traps, set as part of a separate study carried out on the MST during January–September the following year (Phetprakhai Wonkson, unpub. data). Data were available from the study as abundance (number of individuals per month, no data on biomass was available) at the order level with some life-stage split into adults and juvenile life stages when ecologically distinct (e.g. Lepidoptera adults and Lepidoptera larvae). Arthropods < 10 mm were excluded and the same mathematical technique (as described in equations 4.5 and 4.6) was used to calculate a measure of arthropod availability. The formulae were applied to abundance (as done originally by Poulin and Lefebvre 1997) rather than biomass. As before arthropod groups represented by five or fewer individuals captured were excluded from the analysis (Appendix E).

Cross-correlation of the converted malaise data with January–September reproductive effort leads to the same conclusions. Red-headed Trogon again showed the greatest positive correlation one month prior to maximum food availability (Figure 6.3 a). Although Orange-breasted Trogon showed the greatest positive correlation at -3 (rather that -5 months) the same conclusion was reached: namely that maximum food availability coincided with post-reproduction activities (post fledging parental care, juvenile dispersal and moult) (Figure 6.3 b).

For comparison my 2008 arthropod data from both sweep-netting and canopy pan traps were also analysed as weighted abundance index (as opposed to biomass) (Figure 6.3 c and d). OBT showed the same -5 lag month, but RHT showed greatest positive correlation one month earlier (-2 months rather than -1 months) than the same data analysed as biomass. One reason for this could be that earlier in the breeding season there are a greater abundance of arthropods but of a smaller size and biomass. Seasonal variation in size was found in Hong Kong with a higher proportion of larger arthropods in May-August than winter (November-February) (Kwok and Corlett, 2002).

Secondly, a direct cross-correlation analysis of 2008 RHT reproductive effort (Appendix A) and 2008 RHT food availability was used to investigate the validity of clumping multiple years' breeding data (Figure 6.4). Analysis of RHT using 2008 breeding data produced a similar result to that found using the 2004-2008 breeding data.

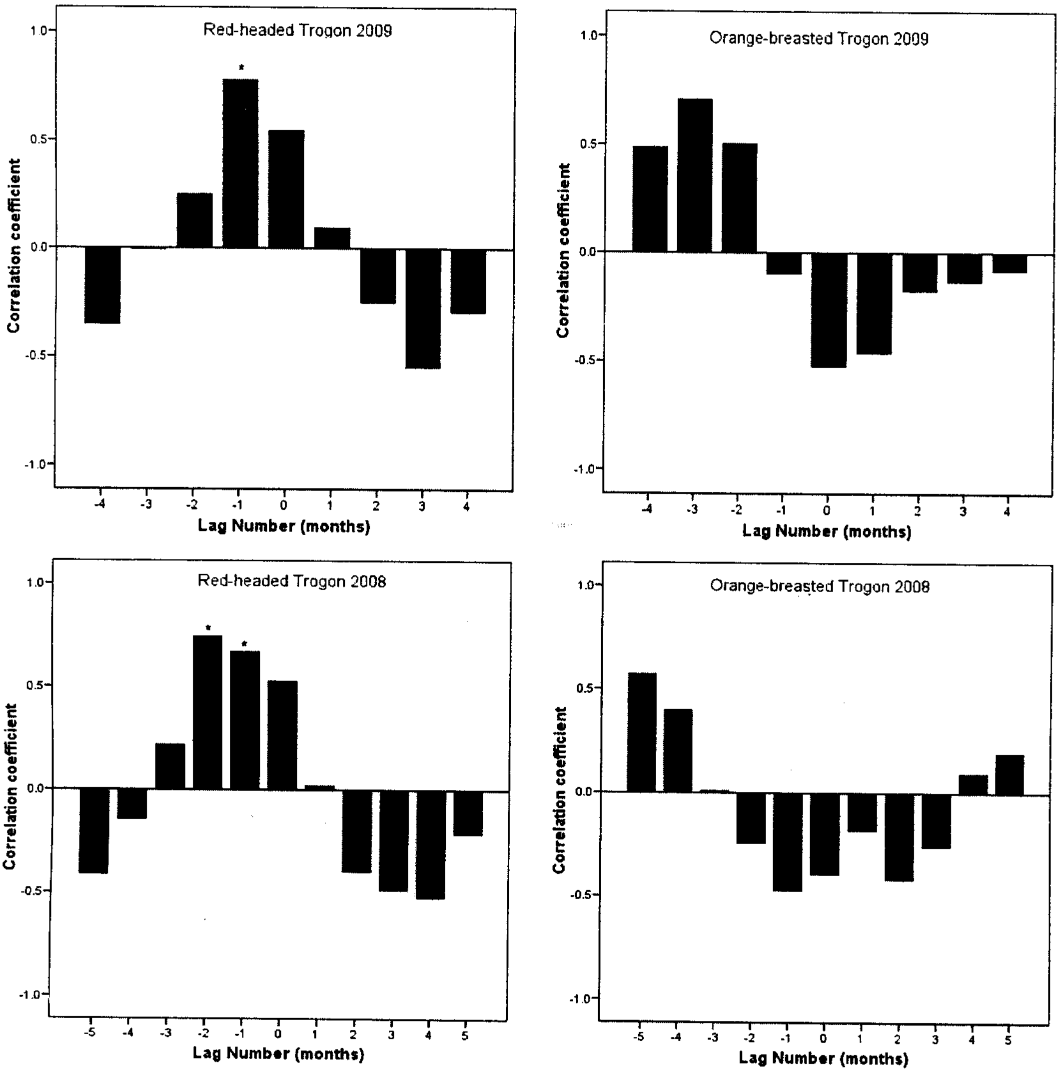


Figure 6.3. Cross-correlation analysis of a) RHT weighted abundance index from Jan-Sept 2009 malaise traps and RHT Jan-Sept reproductive effort, b) OBT weighted abundance index from Jan-Sept 2009 malaise traps and OBT Jan-Sept reproductive effort, c) RHT weighted abundance index from combined sweep netting and canopy pan traps 2008 and RHT reproductive effort, d) OBT weighted abundance index from combined sweep netting and canopy pan traps 2008 traps and OBT reproductive effort.

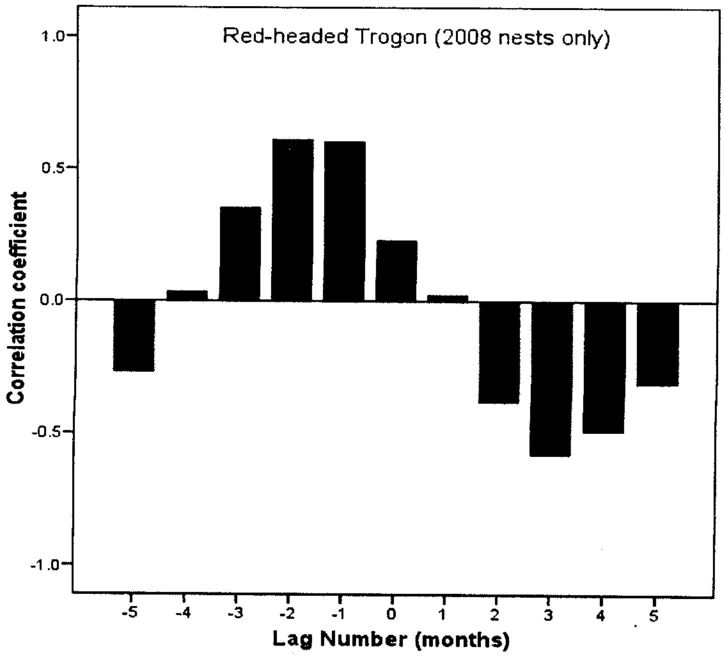


Figure 6.4. RHT weighted biomass index from combined sweep netting and canopy pan traps 2008 and 2008 RHT reproductive effort (number of eggs laid per month).

CHAPTER VII
CONCLUSIONS

7.1. Why do Orange-breasted Trogon and Red-headed Trogon breed when they do?

The reproductive asynchrony between the two species cannot be explained by differing food availability, since foraging technique, type of prey and composition in diet were all found to be similar in both. The only difference identified was the greater average foraging height of OBT compared with RHT. There is no reason to believe this difference has any affect on the seasonal changes in food availability to which each species is exposed.

The most likely reason that would explain the difference in breeding is nest site competition, with the timing of OBT breeding representing a compromise between nest site competition and avoidance of post-reproduction energy-demanding activities with the lean season (December and January). This limits OBT to a short 2–3 month breeding period, before the onset of nesting in RHT, in which nest sites are free from competition, and when all other high energy-demanding activities (provisioning of nestlings, parental care, adult and juvenile moult) can be completed prior to the lean period.

7.2. Suggestions and recommendations for future studies

1. The arthropods that featured in diets and food availability estimates were only examined around the order level. An analysis at a lower taxonomic level may reveal greater differences in feeding ecology between the two species.

2. Testing the nest-site competition hypothesis as an explanation could be problematical. Possible means of investigation could include determining whether the

artificial provision of additional nest sites, or the removal of the competing species, RHT, might allow OBT to extend its breeding season. However, the removal of RHT from study site would be ethically questionable. Additionally, if the difference in the timing of breeding is an evolutionary rather than a behavioural response OBT would be unlikely to respond. Another approach would be to re-examine the seasonality of nesting in relation to food supply in a site where OBT is the only trogon species present.

3. Although from personal observations and time spent searching for potential nest sites I considered suitable nesting stumps to be a limited resource, no attempt was made in this study to try and estimate potential nest site availability. To do this firstly more detailed information would need to be collected on both species nest site selection.

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APPENDICES

APPENDIX A

Number of Red-headed Trogon nest found and number of eggs they contained 2004 – 2009. As all nests found contained 2 or 3 eggs nest of unknown number of nests were given the mean value of 2.6 eggs.

RHT	2004		2005		2006		2007		2008		2009		Total		Total -09	
	Nests	Eggs	Nests	Eggs	Nests	Eggs	Nests	Eggs	Nests	Eggs	Nests	Eggs	Nests	Eggs	Nests	Eggs
Jan																
Feb					5	14.6			1	3			6	17.6	6	17.6
Mar	1	3	4	10	1	3	2	6	3	7	1	3	12	32	11	29
Apr			3	5.6	2	6	4	10	3	8	3	9	15	38.6	12	29.6
May	1	2	2	5.6	4	10	1	8	3	8			11	33.6	11	33.6
Jun	1	2	1	2			3	6	1	2			6	12	6	12
Jul			1	3									1	3	1	3
Aug																
Sep																
Oct																
Nov																
Dec																
Total	3	7	11	26	12	33.6	10	30	11	28	4	12	51	136.6	47	124.6

APPENDIX B

Number of Orange-breasted Trogon nest found and number of eggs they contained 2003 – 2009. As all nests found contained 2 or 3 eggs nest of unknown number of nests were given a value of (2.4) eggs.

OBT	2003		2004		2005		2006		2007		2008		2009		Total	
	Nests	Eggs	Nests	Eggs	Nests	Eggs	Nests	Eggs	Nests	Eggs	Nests	Eggs	Nests	Eggs	Nests	Eggs
Jan	1	2.4	1	2			3	7	3	6.4			1	2	9	19.8
Feb					3	7	1	3			1	2	3	8	8	20
Mar							1	3					1	2	2	5
Apr															0	0
May															0	0
Jun															0	0
Jul															0	0
Aug															0	0
Sep															0	0
Oct															0	0
Nov															0	0
Dec															0	0
Total	1	2.4	1	2	3	7	5	13	3	6.4	1	2	5	12	19	45

APPENDIX C

Regression data set collected at Khao Yai National Park

Araneae		Cicadidae		Coleoptera		Lepidoptera adult		Lepidoptera larvae		Mantodea		Orthoptera		Phasmatodea	
Length (cm)	Weight (g)	Length (cm)	Weight (g)	Length (cm)	Weight (g)	Length (cm)	Weight (g)	Length (cm)	Weight (g)	Length (cm)	Weight (g)	Length (cm)	Weight (g)	Length (cm)	Weight (g)
0.560	0.002	2.960	0.376	2.100	0.192	1.700	0.035	0.920	0.001	6.950	0.226	2.000	0.193	7.850	0.087
0.900	0.015	2.600	0.195	1.650	0.115	2.250	0.080	2.500	0.054	6.420	0.146	1.500	0.037	6.940	0.058
0.850	0.008	1.830	0.165	1.000	0.046	1.500	0.017	2.450	0.015	2.300	0.030	1.200	0.035	4.900	0.027
0.720	0.008	2.800	0.262	2.900	0.357	1.950	0.119	0.950	0.002	2.800	0.098	0.800	0.006	5.700	0.043
0.520	0.003	3.890	0.429	1.700	0.117	1.200	0.005	1.900	0.022	3.700	0.102	2.700	0.334	2.600	0.004
0.520	0.003	2.970	0.383	1.500	0.042	1.800	0.051	2.500	0.178	2.500	0.035	0.730	0.009	6.930	0.053
0.730	0.010	2.840	0.210	1.150	0.043	1.250	0.015	1.800	0.040	2.400	0.034	2.150	0.157	5.300	0.080
0.600	0.006	2.390	0.145	2.000	0.066	2.500	0.235	2.050	0.005	1.870	0.032	0.800	0.025	6.000	0.027
0.410	0.002	4.700	0.865	1.450	0.085	1.650	0.049	2.300	0.009	3.360	0.109	1.180	0.023	7.000	0.058
0.920	0.012	2.800	0.188	1.600	0.135	3.200	0.273	1.950	0.009	6.680	0.228	0.720	0.013	6.100	0.033
0.560	0.005	3.600	0.228	1.500	0.080	2.200	0.068	5.000	0.177	3.660	0.114	1.400	0.030	2.750	0.043
0.560	0.009	2.880	0.427	2.250	0.295	1.200	0.011	2.490	0.060	1.670	0.010	2.000	0.185	4.470	0.026
0.360	0.002	3.100	0.323	1.050	0.060	1.300	0.035	2.720	0.039	1.100	0.009	2.800	0.478	7.700	0.120
0.650	0.005	3.200	0.330	0.950	0.016	1.500	0.028	1.980	0.019			0.800	0.007	2.490	0.006
0.410	0.002	2.390	0.152	2.050	0.331	1.950	0.050	2.940	0.020			1.100	0.045	1.050	0.001
0.890	0.012	4.000	0.279	3.300	0.243			1.450	0.005			1.100	0.060	5.640	0.064
1.500	1.116	3.070	0.319									2.200	0.218	4.160	0.025
0.650	0.010	3.950	0.472									1.100	0.025	1.650	0.003
0.900	0.013	4.450	0.692									1.200	0.024	3.700	0.015
2.300	0.613	2.750	0.187									2.900	0.287	7.350	0.160
0.900	0.012	4.200	0.445									1.800	0.162	1.500	0.001

Regression data set (continued)

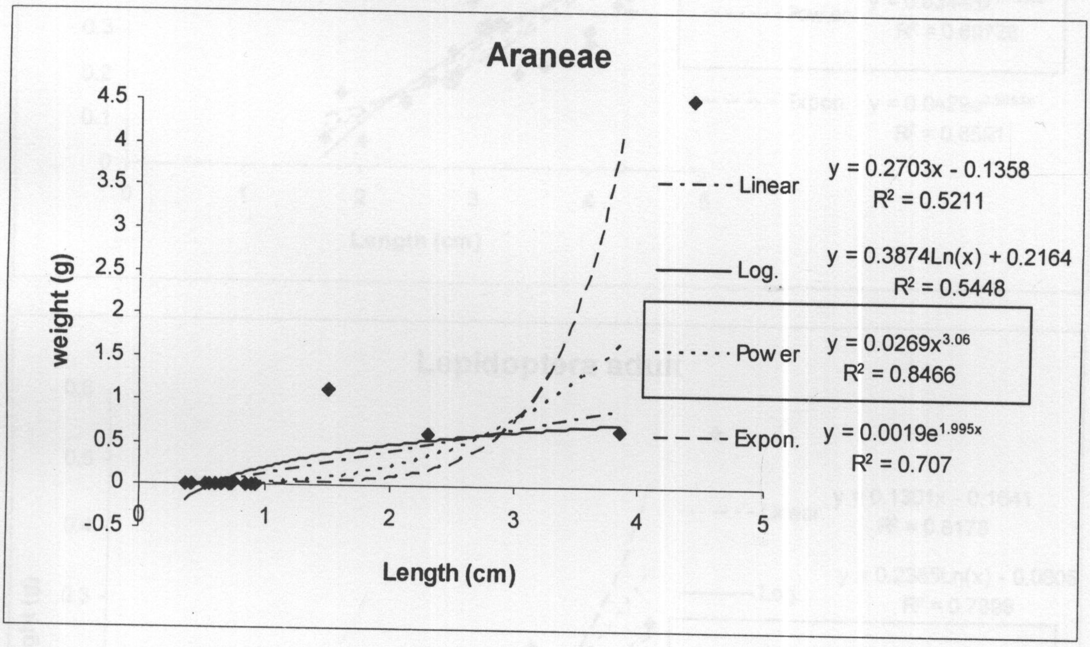
Araneae		Cicadidae		Coleoptera		Lepidoptera adult		Lepidoptera larvae		Mantodea		Orthoptera		Phasmatodea	
Length (cm)	Weight (g)	Length (cm)	Weight (g)	Length (cm)	Weight (g)	Length (cm)	Weight (g)	Length (cm)	Weight (g)	Length (cm)	Weight (g)	Length (cm)	Weight (g)	Length (cm)	Weight (g)
0.750	0.020	4.350	0.354									1.250	0.031	6.300	0.061
3.850	0.668	4.000	0.312									1.330	0.040	4.800	0.027
		4.350	0.430									1.400	0.026	4.440	0.029
		4.220	0.368									1.050	0.027	8.980	0.099
		3.38	0.21									1.00	0.03	1.94	0.01
		3.98	0.30									1.20	0.05	6.03	0.07
		2.02	0.06									0.77	0.01	6.02	0.04
		2.02	0.0581									0.77	0.005	6.02	0.0375
		3.040	0.310									2.250	0.199	12.050	0.523
		4.320	0.393									3.300	0.680	8.570	0.321
		2.810	0.207									1.300	0.032		
		3.130	0.320									1.700	0.074		
		3.940	0.423									1.350	0.025		
		1.690	0.064									2.400	0.157		
												1.150	0.026		
												2.7	0.505		
												1.7	0.108		
												2	0.09		
												0.45	0.002		
												2.35	0.298		
												1.15	0.018		
												1.45	0.06		
												1.2	0.037		
												0.9	0.01		
												0.5	0.001		
												3.25	0.455		
												1.35	0.036		
												1.9	0.087		

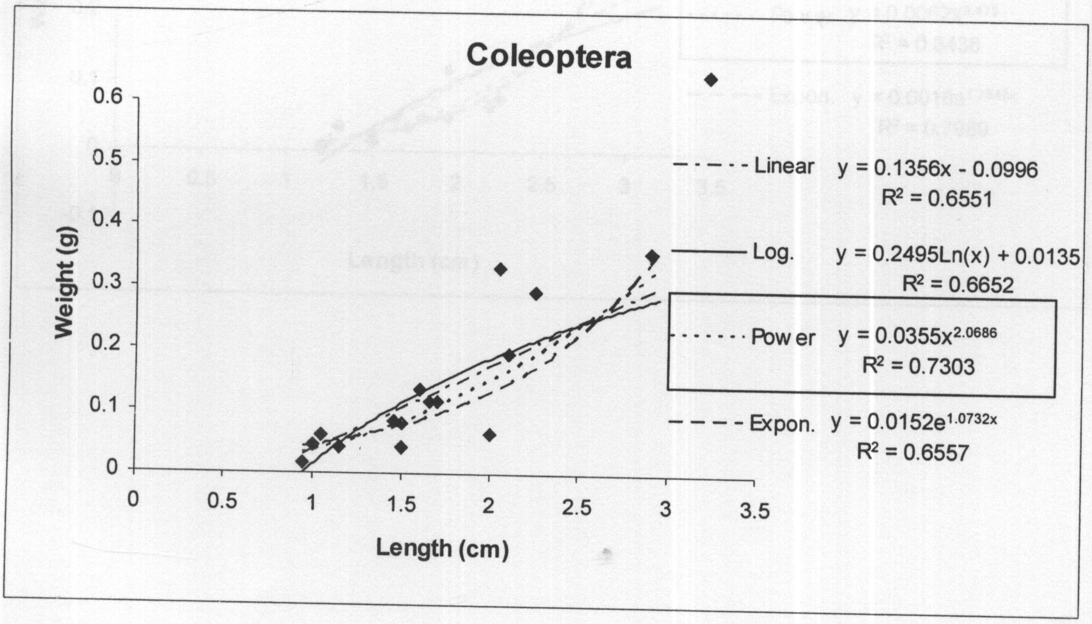
Regression data set (continued)

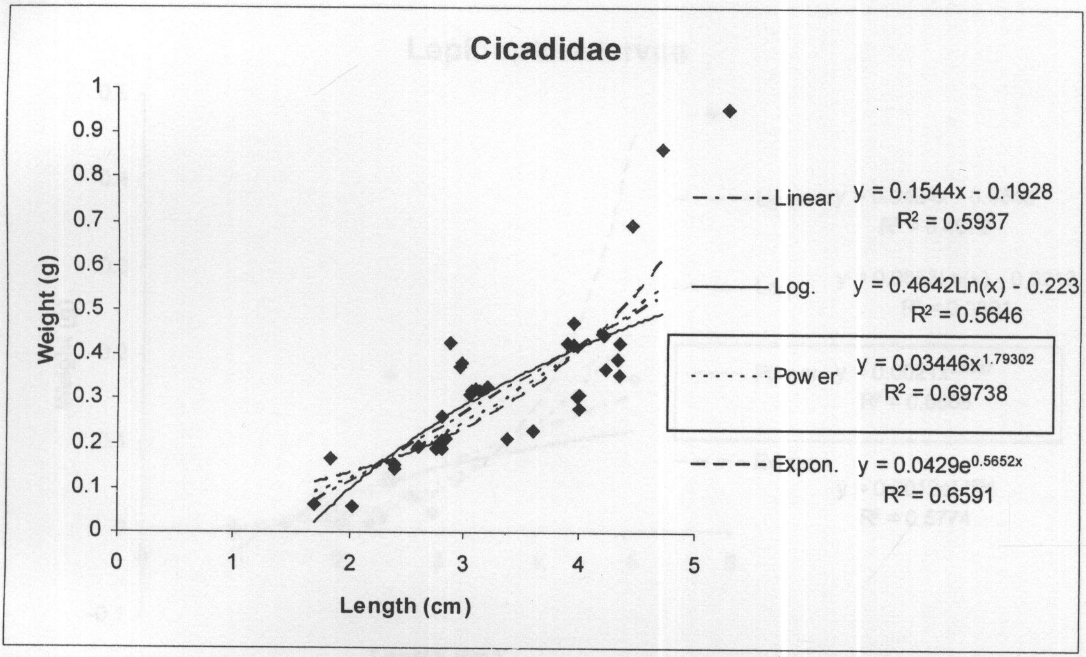
Araneae		Cicadidae		Coleoptera		Lepidoptera adult		Lepidoptera larvae		Mantodea		Orthoptera		Phasmatodea	
Length (cm)	Weight (g)	Length (cm)	Weight (g)	Length (cm)	Weight (g)	Length (cm)	Weight (g)	Length (cm)	Weight (g)	Length (cm)	Weight (g)	Length (cm)	Weight (g)	Length (cm)	Weight (g)
												1.6	0.07		
												2.85	0.183		
												2.49	0.234		
												2.85	0.6761		
												3.39	0.5473		
												3	1.1341		
												2.98	0.6239		

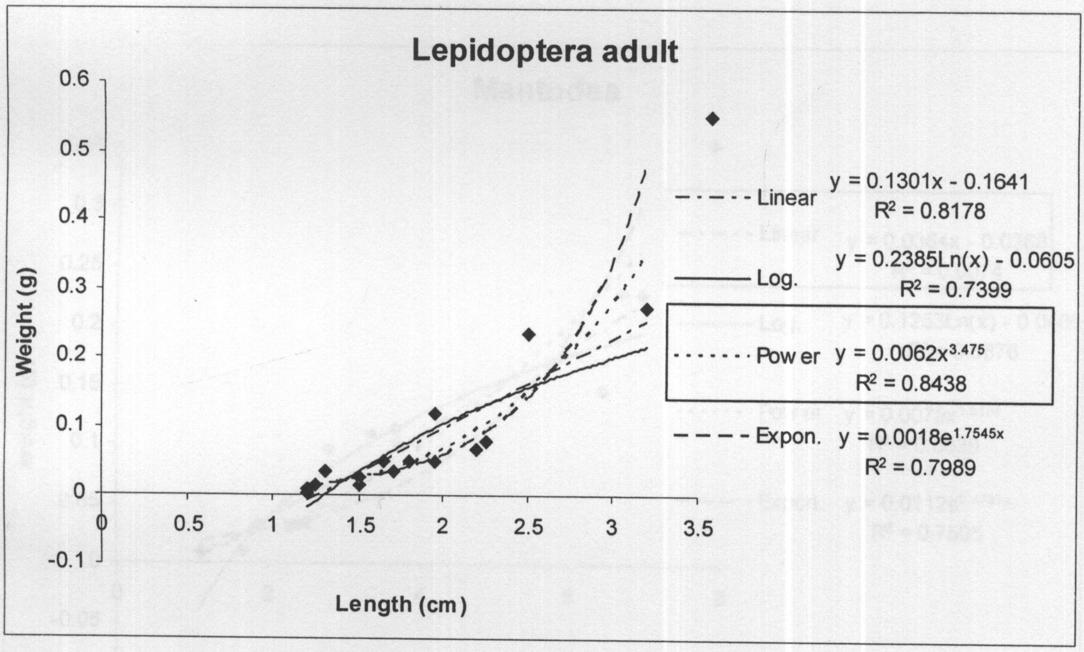
APPENDIX D

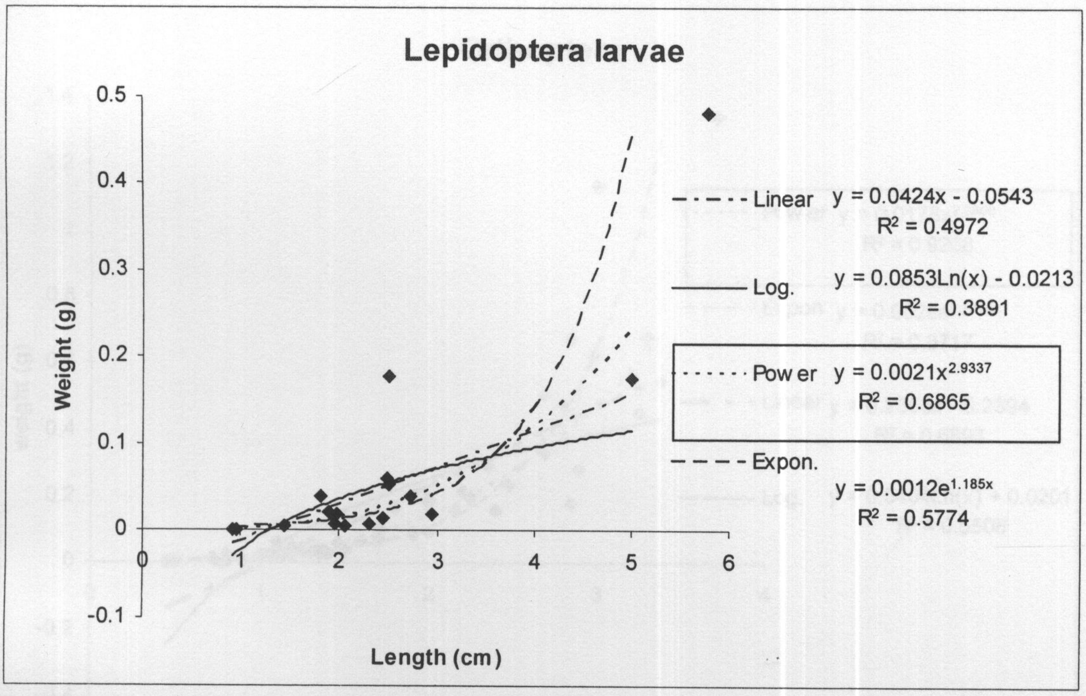
Results of the regression analysis. The model with the highest R^2 value (highlighted) was used to convert arthropod lengths to mass

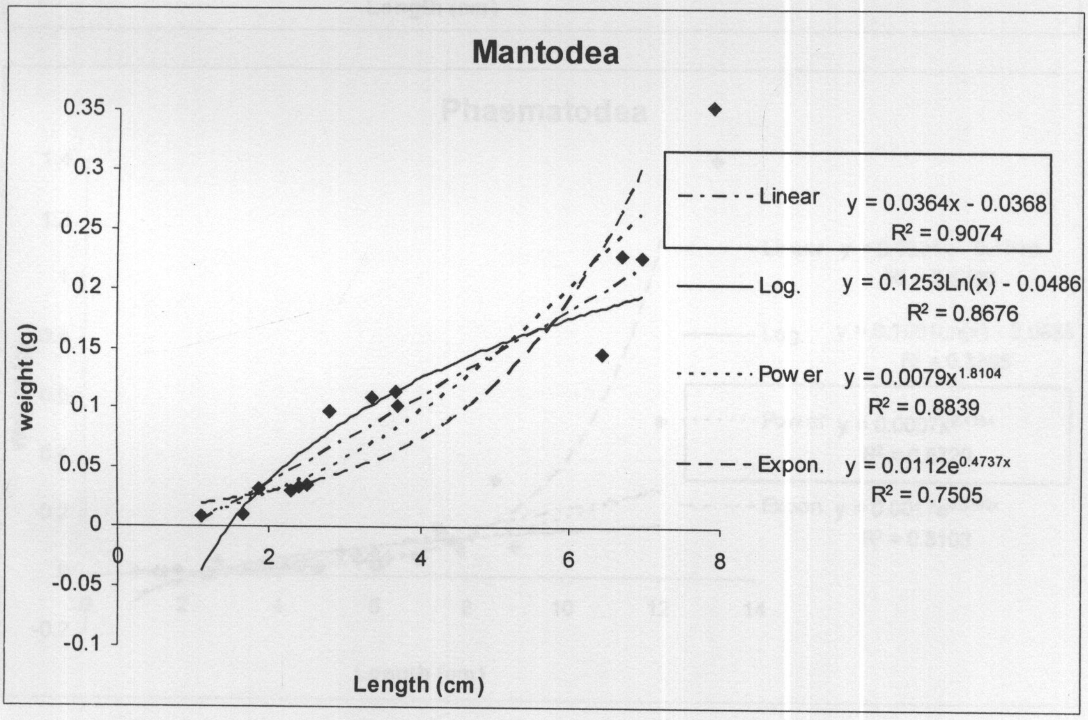


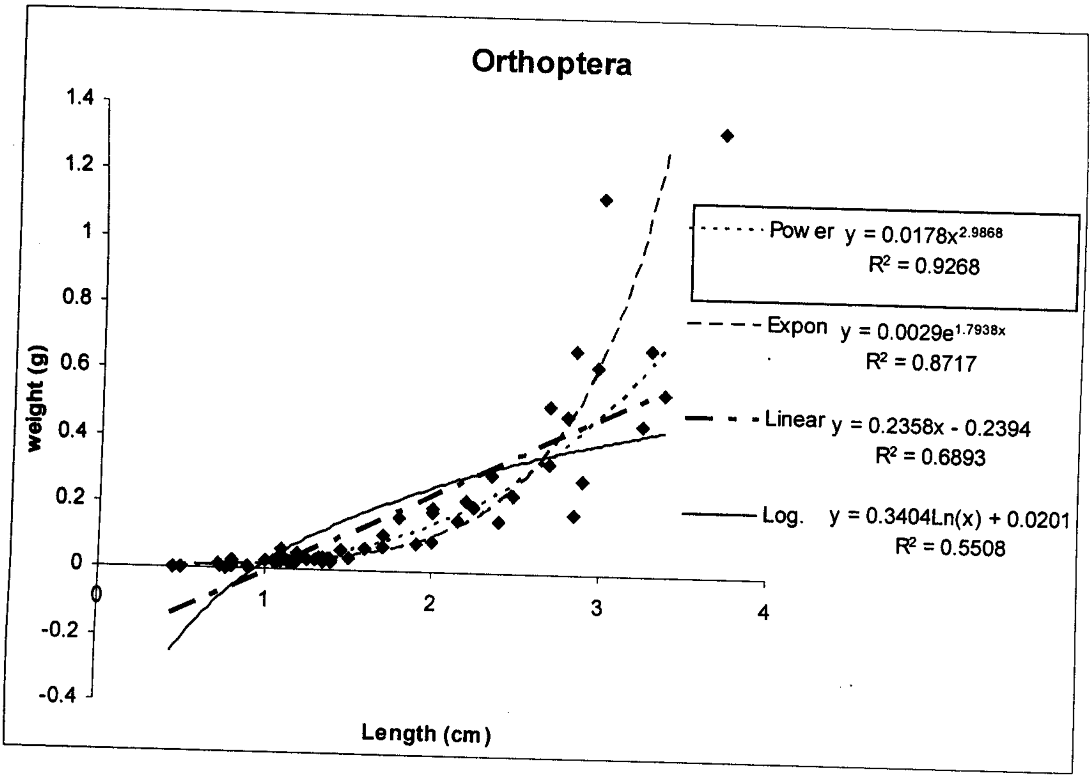


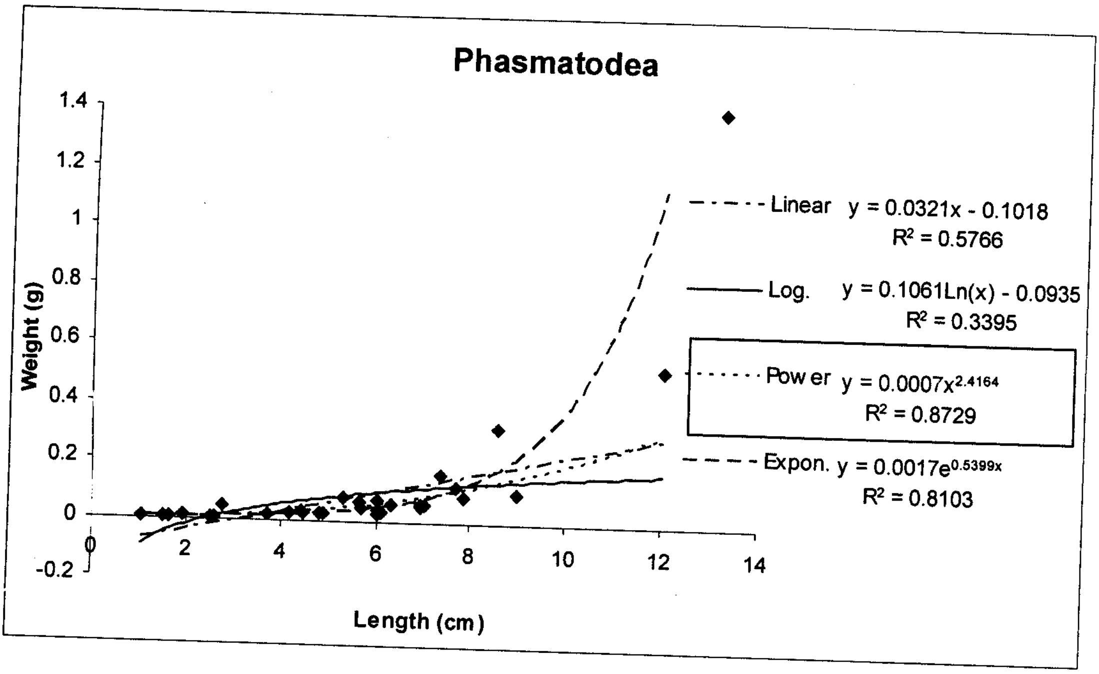

Cicadidae
Weight (g)
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
0
1
2
3
4
5
Length (cm)
Linear $y = 0.1544x - 0.1928$ $R^2 = 0.5937$
Log. $y = 0.4642\text{Ln}(x) - 0.223$ $R^2 = 0.5646$
Power $y = 0.03446x^{1.79302}$ $R^2 = 0.69738$
Expon. $y = 0.0429e^{0.5652x}$ $R^2 = 0.6591$


Lepidoptera adult
Weight (g)
0.6
0.5
0.4
0.3
0.2
0.1
0
-0.1
0
0.5
1
1.5
2
2.5
3
3.5
Length (cm)
Linear $y = 0.1301x - 0.1641$ $R^2 = 0.8178$
Log. $y = 0.2385\text{Ln}(x) - 0.0605$ $R^2 = 0.7399$
Power $y = 0.0062x^{3.475}$ $R^2 = 0.8438$
Expon. $y = 0.0018e^{1.7545x}$ $R^2 = 0.7989$


Lepidoptera larvae
Weight (g)
0.5
0.4
0.3
0.2
0.1
0
-0.1
0
1
2
3
4
5
6
Length (cm)
Linear y = 0.0424x - 0.0543
R2 = 0.4972
Log. y = 0.0853Ln(x) - 0.0213
R2 = 0.3891
Power y = 0.0021x2.9337
R2 = 0.6865
Expon. y = 0.0012e1.185x
R2 = 0.5774


Mantodea
weight (g)
0.35
0.3
0.25
0.2
0.15
0.1
0.05
0
-0.05
-0.1
0
2
4
6
8
Length (cm)
Linear y = 0.0364x - 0.0368
R2 = 0.9074
Log. y = 0.1253Ln(x) - 0.0486
R2 = 0.8676
Power y = 0.0079x1.8104
R2 = 0.8839
Expon. y = 0.0112e0.4737x
R2 = 0.7505


Orthoptera
1.4
1.2
1
0.8
0.6
0.4
0.2
0
-0.2
-0.4
weight (g)
0
1
2
3
4
Length (cm)
Power y = 0.0178x^2.9868
R² = 0.9268
Expon y = 0.0029e^1.7938x
R² = 0.8717
Linear y = 0.2358x - 0.2394
R² = 0.6893
Log. y = 0.3404Ln(x) + 0.0201
R² = 0.5508


Phasmatodea
1.4
1.2
1
0.8
0.6
0.4
0.2
0
-0.2
Weight (g)
0
2
4
6
8
10
12
14
Length (cm)
Linear y = 0.0321x - 0.1018
R² = 0.5766
Log. y = 0.1061Ln(x) - 0.0935
R² = 0.3395
Power y = 0.0007x^2.4164
R² = 0.8729
Expon. y = 0.0017e^0.5399x
R² = 0.8103

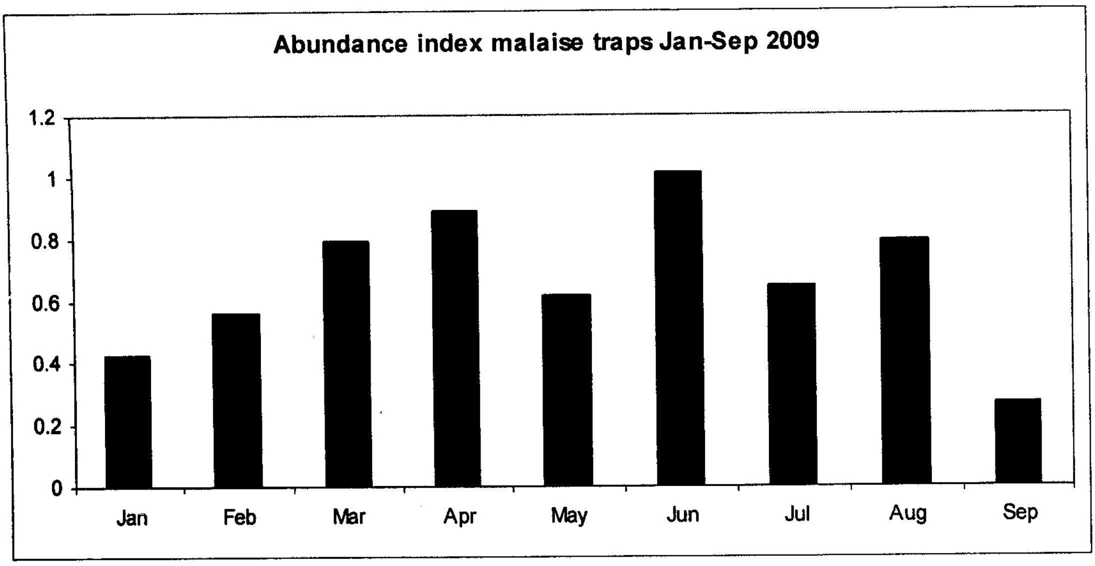
APPENDIX E

Canopy Malaise Traps (Phetprakhai Wonkson, unpub data)

a) No of individual > 10 mm in length caught in 20 canopy malaise traps data on the MST from Jan 2009 – Sep 2009. Prey groups represented my less than 5 catches (shaded) were excluded from the abundance index calculation.

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Total
Araneae			1	1			2	2		6
Cicadidae										0
Coleoptera	3	7	21	19	20	18	10	6	4	108
Lepidoptera adult	6	9	1	2	2	7	1	4	3	35
Lepidoptera larvae	1	1	2		1	2	1	3		15
Mantodea	1	1	1		1					4
Orthoptera	1	2	12	23	32	5	13	9	7	104
Phasmatodea	2	2	2			6			1	13

b) Monthly changes in abundance index from malaise traps set during January–September 2009 on the MST.



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