Estimation of abundance and fawn survival in chital (*Axis axis*) populations using photographic capture-recapture sampling

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Declaration

I declare that the thesis entitled "Estimation of abundance and fawn survival in chital (*Axis axis*) populations using photographic capture-recapture sampling" comprises research work done by me under the guidance of Dr. K. Ullas Karanth and co-guidance of Mr. N. Samba Kumar and Mr. Devcharan Jathanna. The work is original and has not been done earlier by anyone else. Part of this work, which is related to or similar to work done by other researchers, has been referred to in this thesis at appropriate places. The results presented in this thesis have not been submitted previously to this or any other University for an M.Sc. or any other degree.

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Certificate

I declare that this thesis entitled "Estimation of abundance and fawn survival in chital (*Axis axis*) populations using photographic capture-recapture sampling" comprises research work carried out by Milind Panchakshari Pariwakam at the Centre for Wildlife Studies under my guidance and the co-guidance of Mr. N. Samba Kumar and Mr. Devcharan Jathanna during the period 2005-2006 for the Degree of Master of Science in Wildlife Biology & Conservation of the Manipal Academy of Higher Education (MAHE). The results presented in this thesis have not been submitted previously to this or any other University for M.Sc. or any other degree.

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EXECUTIVE SUMMARY

Population studies are important for management, conservation and science. Regular monitoring of animal populations helps in setting objectives and monitoring the progress of conservation programmes. Chital (*Axis axis*), an important prey species for the tiger (*Panthera tigris*), leopard (*Panthera pardus*) and dhole (*Cuon alpinus*), are uniquely marked and can be individually identified using spot patterns.

State variables such as abundance and density, as well as vital rates such as survival, reproduction and movement are important for understanding population dynamics, and for management and conservation. Conventional distance sampling methods cannot be applied in certain locations due to logistical constraints. To overcome such constraints I developed a protocol for identifying chital using photographic captures in Bandipur Tiger Reserve, India, and to use the resulting histories of captures to estimate population parameters.

The goals of this study were to estimate:

1) Abundance and density of chital using closed model photographic capture-recapture sampling; and
2) Estimate weekly survival rate of chital fawns using open model photographic capture-recapture surveys

Chital photographs collected in part of Bandipur Tiger Reserve, using capture-recapture sampling, were used to identify individual chital and build capture histories. These capture histories were used under closed and open capture-recapture models to

estimate abundance of chital stags, and survival of fawns, respectively. Density was estimated after estimating the area effectively sampled.

I obtained a 365 usable photo-captures of chital stag left flanks over 4 sampling occasions, from which I was able to identify 174 individuals, while 189 individual fawns were identified from 349 usable photo-captures of right flanks.

Model selection tests and the discriminant function score indicated heterogeneity in capture probabilities between individual stags, and estimation was therefore based on the jackknife estimator under model M_h (Ref). The model estimated an average $\hat{p}$ of 0.18. Program CAPTURE estimated stag abundance within the study area as $\hat{N}$ = 337 and $S\hat{E}(\hat{N})$ = 21.21. Total chital abundance was estimated at 1248 animals in the sampled area of 36.3 km^2, and estimated density $\hat{D}$ was 34.38 km^2 and $S\hat{E}(\hat{D})$ 2.066

Using information theoretic approaches to model selection, I compared four different models to estimate fawn capture probability $\hat{p}$ and weekly survival $\hat{\phi}$: the fully time varying Cormack-Jolly-Seber model, and reduced parameter models where either capture probability $\hat{p}$ or weekly survival rate $\hat{\phi}$, or both were held constant. Akaike's Information Criterion (AIC) supported the use of the simplest model with both $\hat{p}$ and $\hat{\phi}$ held constant over sampling occasions. Based on this model, capture probability $\hat{p}$ for chital fawns was estimated to be 0.18 with $S\hat{E}$ ($\hat{p}$) 0.08, and their weekly survival rate $\hat{\phi}$ was estimated at 0.805 with $S\hat{E}$ ($\hat{\phi}$) 0.17.

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I would like to end my acknowledgements with a few lines from my favorite poem, "The road not taken", by Robert Frost, which kept me going….

Two roads diverged in a wood, and I-
I took the one less travelled by,
And that has made all the difference.

CONTENTS

GENERAL INTRODUCTION

Previous scientific studies have found a strong relationship between prey abundance and densities of large carnivores such as the tiger, and their ungulate prey (Karanth and Nichols 1998, Karanth and Stith 1999, Karanth et al., 2004). Therefore, large carnivore conservation initiatives often focus on securing and maintaining a healthy prey base. To be able to assess the effectiveness of managerial interventions, set future conservation targets and to develop better scientific understanding of prey species' ecology, we must be able model and assess population dynamics of important prey species. In addition to monitoring population state variables, such as abundance (or density) and tracking their changes over time, it is important to estimate vital rates such as survival recruitment to understand the processes that drive population changes (Williams et al., 2002).

Chital (*Axis axis*) are a numerically dominant, widespread ungulate prey species of large carnivores including tigers (*Panthera tigris*), dholes (*Cuon alpinus*) and leopards (*Panthera pardus*) (Sunquist 1981, Johnsingh 1983, 1992, Karanth and Sunquist 1995, 2000, Karanth et al., 2004). Consequently, obtaining reliable estimates of chital population parameters has a direct bearing on the conservation of these carnivores also.

Typically, chital densities are estimated using distance sampling methods such as line transect surveys. However, under some field conditions, factors like rough terrain or logistical problems may render line transect surveys difficult or even impossible to implement.

Biologists have also used an alternative method with sound theoretical and practical foundations, known as capture-recapture sampling to estimate abundance and other population parameters for many animal species. Although traditional capture-recapture studies have depended on physical capture of animals and artificial marking (e.g. tagging) for identifying individual animals, over the last ten years, biologists have started using non-invasive animal 'capture' methods like photo-captures using automated camera traps (Karanth 1995, Karanth and Nichols 1998) in the case of naturally marked species such as tigers, jaguars and leopards. However, given appropriate survey protocols similar approaches can be developed for photographic captures using conventional photography, at least for diurnal animal species.

This study employed capture-recapture sampling to estimate abundance (and subsequently, density) of chital stags using individual identifications based on natural markings in the form of spot patterns on flanks. Thereafter, abundances of all age-sex classes of chital were estimated using the estimates of stag abundance in combination with age-sex ratios in chital population determined from field surveys. Since survival rates of chital fawns are important for shaping the population dynamics of chital populations (Schaller, 1967), I also used capture-recapture sampling to rigorously estimate weekly survival rates of chital fawns.

Although the research work had two major objectives, data for both aspects of the study were collected using the same field survey protocols and sampling design. Abundance of chital stags was estimated using closed capture-recapture models in program CAPTURE (Otis et al., 1978). Survival rate estimation of fawns was done using open capture-recapture models in program MARK (White and Burnham, 1999).

The findings from these two aspects of the study are presented in the form of form of manuscripts as required for submission in peer reviewed journals.

Chapter-2, titled "Estimation of Chital (*Axis axis*) abundance using photographic capture-recapture sampling" covers details of the procedure used to estimate chital abundance and densities. This chapter is formatted for submission to the Journal of Mammalogy.

Chapter-3 titled "Use of photographic capture-recapture sampling to estimate weekly survival of chital (*Axis axis*) fawns" covers details of the procedure used to estimate weekly survival rate of chital fawns. This chapter is formatted for submission to the Journal of Zoology.

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SUGGESTED RUNNING HEAD: Chital abundance estimation from photographic sampling.

ESTIMATION OF CHITAL (AXIS AXIS) ABUNDANCE USING PHOTOGRAPHIC CAPTURE-RECAPTURE SAMPLING

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ABSTRACT

Population studies are important for management, conservation and science. Regular monitoring of animal populations helps in setting objectives and monitoring the progress of conservation programmes. Chital (*Axis axis*), an important prey species for the tiger (*Panthera tigris*), leopard (*Panthera pardus*) and dhole (*Cuon alpinus*), are uniquely marked and were individually identified using spot patterns. Conventional distance sampling methods cannot be applied in certain locations due to logistical constraints. To overcome such constraints I developed a protocol for identifying chital using photographic captures in Bandipur Tiger Reserve, India. I estimated abundance of stags using closed model photographic capture-recapture (CR) sampling. Total chital abundance was derived using observed age-sex compositions. The abundance estimates derived using CR methodology will provide useful inputs for setting management objectives and monitoring the successes of conservation programmes that benefit major predator and prey species. Abundance for stags was estimated at 337, and total chital density calculated as 34.38 per km^2. I suggest that this protocol be used to estimate chital abundance where conventional methods are not applicable.

Key words: *Axis axis*, abundance, photographic capture-recapture, population estimation, uniquely marked

INTRODUCTION

Large carnivore research worldwide has focused on the factors driving patterns of carnivore distribution and abundance. Studies have found a strong relationship between prey abundance and predator population densities and distribution, as in the case between populations of the tiger and ungulate prey in the Indian sub-continent (Karanth and Nichols 1998; Karanth and Stith 1999; Karanth et al. 2004). Chital (*Axis axis*) are a medium sized deer endemic to the Indian subcontinent. They inhabit mainly dry and moist deciduous forests, occasionally being found even in evergreen and thorn forests.

They are an important constituent of ungulate prey assemblages in southern Asia for the highly endangered large carnivores such as the tiger (*Panthera tigris*), dhole (*Cuon alpinus*) and the leopard (*Panthera pardus*) (Sunquist 1981; Johnsingh 1983, 1992; Karanth and Sunquist 1995, 2000; Karanth et al. 2004). Consequently, obtaining reliable estimates of chital abundance is important for both management and conservation, to understand how their population dynamics respond to biological processes as well as anthropogenic interventions. (Williams et al. 2002).

Monitoring of chital populations meets several objectives: to generate data to set specific conservation goals; to evaluate successes or failures of earlier interventions; and to adaptively solve problems that may arise. Thus such studies help reduce management uncertainty and ensure sustainability of populations over the long term (Nichols et al. 1995; Williams et al. 2002). They also improve understanding of prey-predator ecology and may lead to a body of scientific knowledge with predictive capacity to deal with new situations (Karanth and Nichols 2002).

Estimating abundance involves counting study animals within the area of interest. However, the important problems of partial detectability (the inability to count all animals within surveyed areas) and of incomplete spatial sampling (inability to survey the entire area) necessitates that such field counts be corrected using the concepts underlying the 'canonical estimator' (Lancia et al. 1994; Williams et al. 2002; Nichols and Karanth 2002). This approach to estimation of detection probabilities and effectively sampled area from field counts is specifically implemented in modern statistical models of animal abundance estimation such as distance sampling (Buckland et al. 2001; 2004) and closed model capture-recapture sampling (Otis et al. 1978).

However, earlier workers (De and Spillett 1966; Schaller 1967; Johnsingh 1983; Sharatchandra and Gadgil 1975) used ad hoc methods that do not statistically deal with the issue of incomplete detectability to derive chital abundance. However, more recent studies of chital abundance (Karanth and Sunquist 1992; Khan et al. 1995; Biswas and Sankar 2002; Jathanna et al. 2003; Karanth et al. 2004; Bagchi et al. 2004) have successfully used formal distance sampling methods employing line transect surveys to generate chital abundance and density estimates in a variety of forested settings. However, under some field conditions in which chital occur, inappropriate terrain or other logistical difficulties may render line transect surveys difficult to or even impossible to implement (e.g. steep terrain, tall grasslands, mangrove swamps). I note that under such conditions workers (Karanth and Nichols 1998; O'Brien et al. 2003; Karanth et al. 2004; Kawanishi and Sunquist 2004) have successfully used 'photographic capture recapture sampling' to estimate abundances of tigers and other elusive species. Capture-recapture sampling (Otis et al. 1978;

Williams et al. 2002) is an alternative approach widely employed for estimating abundance of animals, which cannot be easily surveyed using distance sampling methods. In this study, taking advantage of the fact that chital are also naturally marked with unique spot patterns, I explore the application of photographic capture-recapture sampling for estimating their abundance.

The overall goal of this study was to develop field and analytic protocols to estimate chital abundance and density in the study area using photographic capture-recapture sampling. My specific objectives were:

1. To develop a field protocols for photographing chital herds in the study area in a manner amenable for subsequent capture-recapture analysis.
2. Deploy appropriate software for identifying individual chital based on spot patterns from photographs and build their photographic capture-histories.
3. To estimate chital abundance using closed model capture-recapture sampling to estimate abundance and densities.

The study was carried out in the 880 km^2 Bandipur Tiger Reserve, Karnataka, India. Altitude within the reserve ranges from 780 m to 1454 m with mean annual rainfall recorded in different areas of the park ranging from 914-1270 mm. The chital habitat comprises of tropical dry deciduous and tropical moist deciduous forests.

My study area of 17.6 km^2 was located in the eastern part of the reserve (Figure 1) where chital herds are large, frequent open short grass areas and tolerate approach in cars facilitating easier photo-captures. The area has a good road network (road density of 3.57 km/km^2) that ensured no 'holes' occurred within the study area where individuals had virtually no chance of being photo-captured (Nichols and Karanth 2002).

Figure 1.- Map showing location of study area in Bandipur Tiger Reserve and location of Bandipur in India (inset)

MATERIALS AND METHODS

Field Methods

Photographic Captures.-

The total closed model capture-recapture survey period was 38 days and assumed to be sufficiently short to ensure demographic closure of the sampled population. Sampling was carried from 13 February to 22 March 2006. Photo-captures of 3 consecutive days were pooled to increase sample sizes, resulting in 6 sampling occasions.

Photographic sampling was carried out from a vehicle while slowly driving along a preselected network of roads of 62.8 km length ensuring uniform temporal and spatial coverage of the sampled area (Figure 2). Sampling was carried out between 0630 hours to 1030 hours and 1430 to 1800 hours, when chital were most active. Photographs permitting unambiguous identification could be obtained from about 2-80 m distance using a digital still camera (Sony DSC-H1) that provided sufficient resolution (5 mega-pixels) and magnification (12x). I focused particularly on the spot patterns on the flank of each animal that I photographed.

For each detection and photographic event, I recorded the sampling occasion number, encounter time and location, number of photographs taken, and GPS coordinates of the encounter where possible. Any additional natural marks such as an injuries or antler shape were also recorded. The digital photos were transferred and stored in a computerized database for easy retrieval.

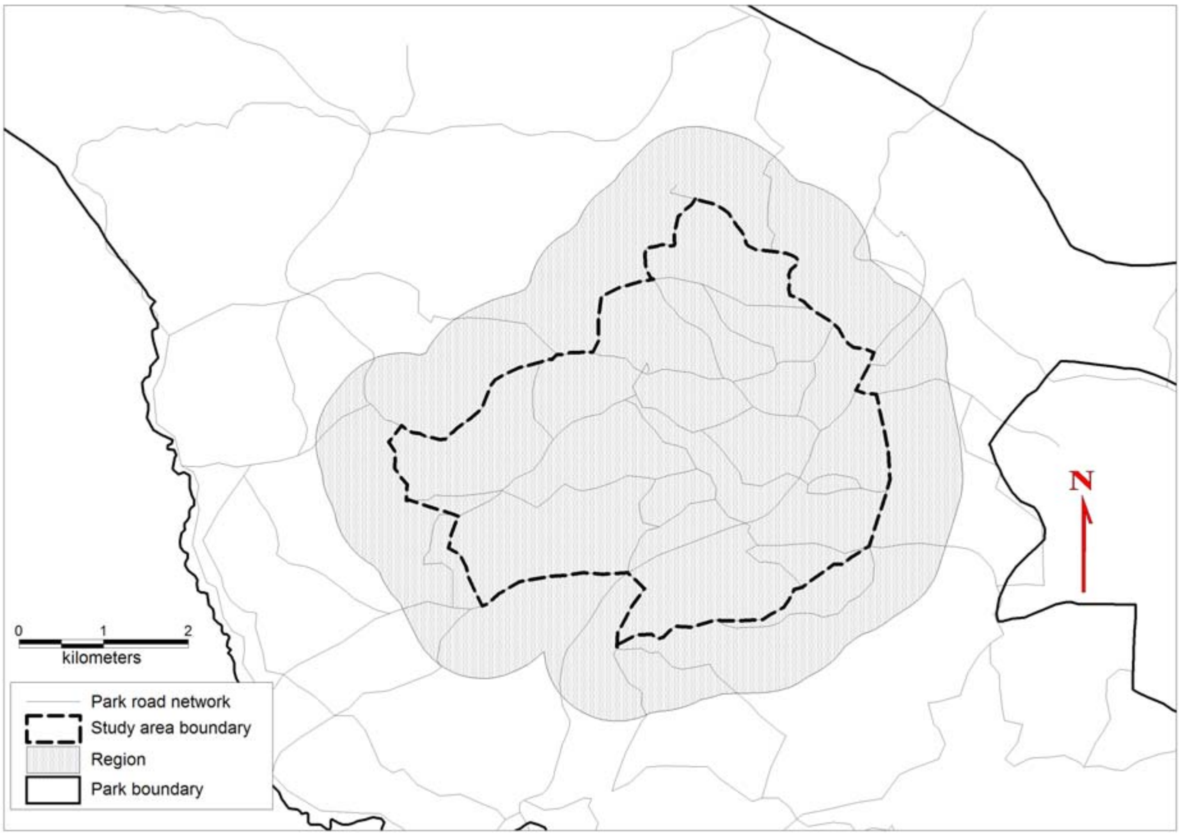

Figure 2.- Map showing study area and effectively sampled area with intensive road network

Population Structure Data.-

Age-sex composition of chital population was estimated from direct visual counts carried out during the photographic surveys. These counts were conducted over 30 days between February 13-May 3, 2006. Age-sex category of chital in the herds was observed using binoculars. All counted chital were classified as stags (adult and yearling males), does (adult and yearling females) and current year fawns. With large herds, where movement and mixing made rapid classification difficult, only animals on one side of the road were classified.

Analytic Methods

Protocol for selection of photographs.-

Only clear photographs that permitted unambiguous individual identifications either manually or using the 3-D pattern matching program CHITAL (Kelly 2001) specially developed for this study by Lex Hiby were used for the analysis. The following criteria were applied to select or reject photographs: (1) Photographs where the flank of a clearly visible individual chital is perpendicular (90°) to the photographic plane were considered ideal (2) Photographs where animals were at 60^o and 120^o angle to photographic plane were also used; (3) Photographs where the spot patterns were unclear were rejected; (4) The pattern recognition algorithm implemented in Program CHITAL uses the flank portion between the shoulder and the hip for pattern comparisons. I used only those undistorted photographs where a major portion (>75%) of this area was clearly visible.

Protocol for analyzing photographs and assigning Tag IDs.-

Selected photographs were entered into an MS-ACCESS® database. A unique code number was generated for each individual animal within each group photograph. These individuals were assigned a temporary Tag ID by the program CHITAL.

The spot patterns on the central area of the flank, and if further necessary, shank (hind foot near the femur area) and on the neck were used to distinguish individuals by visually comparing the photographs for similarities. Because the number of photographs was high I used program CHITAL for quick and automated preliminary comparisons (Kelly 2001). program CHITAL extracts a standardized flattened spot pattern from the flank after correcting for varying posture and photographic angle based on the 3 dimensional model of chital body shape. It then uses the extracted spot patterns for comparison among individuals.

For pattern extraction, standard points on the body of the animal were marked. The standard points were the mid-back, near shoulder and hip and the dorsal and ventral outline of the animal. A 3-D model of a chital, constructed using a pair of photographs, one with a flank view and the other a top-down view of chital, was fitted on the photograph and the far shoulder and hip were marked, if necessary, to improve the model fit. Before extraction the program aligned the photograph with the 3-D model of the flank, as patterns tend to look different with varying camera angles (Kelly 2001). Pattern extracts, corrected for camera angles were saved before running the batch comparison process.

The program computed similarity coefficients for each pair of photographs comprising of a new photograph and a photograph with a previously assigned Tag ID in the database and ranked each pair in decreasing order of the similarity coefficients. Pairs of photos with the highest similarity value had the highest probability of being the same individual. Unambiguous final identification and assignment of unique Tag IDs (in ascending order after first capture) was done through visual inspection of the top fifteen ranked pairs by the first author. Thus while the automated process in program CHITAL helped speed up the identification process, the final identification of photographically captured chital were based on careful visual inspections.

Because this was envisaged as a pilot study of the capture-recapture analysis of chital based on individual identifications and due to constraints of time and resources, for the purpose of this analysis I will be reporting only capture-data analysis for chital stags (adult males).

Construction of Capture Histories for chital stags.-

Standard capture history matrices consisting of row vectors of 1s (indicating capture) and 0s (no capture) were constructed (Otis et al. 1978) separately for the left and right flank captures. For the capture-recapture analysis, the data from left flanks which had larger sample sizes (by sheer chance 174 versus 160) were used.

A preliminary analysis of the capture history data showed that, probably due to movement of animals in and out of the sampled area and other unidentified reasons the assumption of demographic closure was met only during the first four sampling occasions covering survey period of 24 days between 13 February and 8 March 2006. Therefore, the closed model capture-recapture estimation and analyses are reported only for this period.

Estimation of abundance of chital stags.-

The capture history data for chital stags were analyzed using program CAPTURE (Otis et al. 1978; Rexstad and Burnham 1991). This analysis included the following stages:

1. A statistical test of the assumption of population closure.

2. Testing the fit of different capture-recapture models that deal with three possible sources of variation in capture probabilities. These sources of variation are incorporated by different models that incorporated time-related variation (M_t), behavioural response to trapping (M_b) and heterogeneity of capture probability among individuals (M_h) (Otis et al. 1978). On the other hand, the null model M_0 assumes that every individual has the same capture probability across all sampling occasions (Otis et al., 1978; Karanth and Nichols, 2002). In addition to these there are also models that combine the sources of variation (e.g. M_{tb}, M_{th}, M_{bh}). The model selection protocols implemented in Program CAPTURE test fit of various models against the observed data and finally ranks the models using an overall discriminant function score.

3. After selecting the appropriate capture-recapture model and estimator for the data on hand, program CAPTURE can be used to compute estimates of capture probability and abundance of animals in the sampled population (Rexstad and Burnham, 1991).

Estimation of age-sex ratios and computation of total chital population size.-

Ratio of chital stags to total number of chital present was computed using the chital herd composition data recorded separately from photographic capture surveys. This ratio was used to estimate the total number of chital present in the area from the estimate of abundance of stags computed using capture-recapture analysis.

Estimation of effective area sampled and chital density.-

The effectively sampled area consists of the area covered by the photographic sampling routes and an additional buffer area around it from which individual chital could potentially be captured during the surveys (Figure 2). To estimate such an area addition of a boundary strip of width ($\hat{W}$) to the study area was required. This boundary strip can be potentially calculated using the method of "mean maximum distance moved" MMDM (Wilson and Anderson 1985; Karanth and Nichols 1998; Nichols and Karanth 2002) for individual captured twice or more during the survey.

Because of logistical constraints, however, I could not use the classical Wilson and Anderson (1985) method described above. For estimating MMDM I used an approximation based on estimated distances between 3 or more observations of individually identified chital stags observed during the age-sex ratio surveys. Subsequent analytic procedures for estimating the buffer width and sampled area followed the Wilson and Anderson (1985) approach. Using these location data on chital stags, the maximum distance moved between captures ($\hat{d}_i$) was calculated for each stag observed 3 times or more. The boundary strip width ($\hat{W}$) and effectively sampled area $\hat{A}(W)$, and variances of $\hat{\bar{d}}$, $\hat{W}$ and $\hat{A}(W)$ were computed as described in Nichols and Karanth (2002).

Abundance estimates of chital stags ($\hat{N}$) derived from closed model capture-recapture sampling were divided by the area effectively sampled ($A(\hat{W})$) to arrive at the estimate of density of stags ($\hat{D}$) for the study area.

RESULTS

Capture Frequencies.-

Photographic sampling was more successful than I had anticipated resulting in 1222 photographic captures. I obtained 365 usable left flank photographs of individuals and 361 usable right flank photographs. 174 individual chital stags were identified from left flanks and 160 stags from right flank photos, respectively. Because sample size of number of captured individuals based on left flank photos was larger, I used these capture histories for further analyses. The photographic capture histories of individual stags are reported in X matrix format in Appendix and summarized capture statistics in standard program CAPTURE format are reported in Table-1 below:

Sampling Occasion (j)	1	2	3	4	m(t+1)
Animals caught n(j)	52	65	70	59	
Total caught M(j)	0	52	101	143	174
Newly caught u(j)	52	49	42	31	
Frequencies f(j)	122	34	16	2	

Table 1. Summary of captures from program CAPTURE. Notations follow Otis et al. (1978).

Results of tests for population closure and model selection.-

The closure test (Otis et al. 1978) indicated that the assumption of population closure could not be rejected during the survey period covering sampling occssion 1-4 ($z = -1.611$, $P = 0.05361$) (See methods).

The χ^2 tests comparing the null model M_o against models M_b ($\chi^2 = 1.851$,; d.f = 1; $P = 0.17368$), and, M_t ($\chi^2 = 3.192$,; d.f = 3; $P = .27112$) failed to reject the null model. However, The χ^2 test of fit of the null model against the alternative of model M_h supported the latter ($\chi^2 = 11.014$,; d.f = 1; $P = 0.0091$). A goodness of test of model M_h showed a reasonable fit ($\chi^2 = 3.949$,; d.f = 3; $P = 0.26702$) to the observed data providing additional evidence in support of model M_h.

The objective discriminant function test based model selection procedure scored the various possible models as: Model $M_h = 1.0$, $Mo = 0.69$, $M_{tbh} = 0.65$, $M_{bh} = 0.61$, $M_{th} = 0.37$, $M_b = 0.30$, $M_{tb} = 0.26$, $M_t = 0$. Based on the between model comparisons, discriminant function test score results I selected model M_h as the most appropriate model explaining capture-recapture process that generated the capture histories I observed in this study.

Estimates of capture probabilities and Abundance of Chital stags.-

The capture probabilities were estimated under model M_h using the jackknife estimator (Burnham and Overton 1978) that is known to be robust to violation of assumptions and performed well in earlier simulation studies (Otis et al. 1978; Williams et al. 2002; Nichols and Karanth 2002). The estimated average (across individuals) capture probability per sampling occasion ($\hat{p}_i$) was estimated at 0.18 leading to an estimate of abundance ($\hat{N}$ =337) and $S\hat{E}(\hat{N})$= 21.21. Based on the estimated abundance and the number of individuals captured, I estimated the overall average probability of capture during the entire survey was ($\hat{p}$) = $\frac{M_{t+1}}{\hat{N}}$ = 0.51, where $M_{t+1} = 174$ and $\hat{N} = 337$.

Estimates of overall chital abundance based on population structure data.-

The proportion of chital in different age sex classes in the population based on surveys carried out independently (Table-2) was: stags 27%, does 57% and fawns 16%. The capture-recapture based abundance estimate for chital stags ($\hat{N}$ =337) was used in conjunction with above age-sex proportion to compute the abundances of chital in other age-sex classes at: does= 711 and fawns= 200, adding up to a total chital population size estimate of 1248 animals in the sampled area.

Age-sex composition				
	Stags	Does	Fawns	Total
Sample size (N_c)	2839	5900	1760	10499
Proportion	27	57	16	100

Table 2. Age sex composition of chital population. Sample sizes (N_c) are number of count of animals classified over 30 days. Descriptions of age-sex categories are in text.

Estimates of effectively sampled area chital density.-

-Using methods described earlier mean maximum distance moved (MMDM) for chital stags ($\hat{\bar{d}}(S\hat{E}(\hat{\bar{d}}))$ was estimated at 1.73 km (0.126 km) and the width of the additional boundary strip was estimated at $\hat{W}(S\hat{E}(\hat{W}))$ = 0.86 (0.063) km, yielding an estimate of the effectively sampled area $\hat{A}(W)(SE(\hat{A}(W)) = 36.3$ (1.358) km^2. Based on this area, the estimated density of all chital $\hat{D}\,(\,S\hat{E}(\hat{D})$ was computed as 34.38 (2.066) chital/ km^2.

DISCUSSION

Individual chital could be successfully identified using the spot patterns on their body, enabling the application of capture-recapture using photographs. Capture rates of chital were relatively high, as can be seen from the sample size of individuals (M_{t+1}= 174) caught during a 4 sampling occasion study. Probabilities of capture for an individual per sampling occasion, $\hat{p}_i$= 0.18 was reasonable enabling comparison of several plausible models and for estimation of parameters (Otis et al. 1978). Overall, my sample survey was able to capture 51% of all individual chital stags during the survey period.

However, it is likely that during my surveys the proportion of chital fawns, which sometimes remain obscured by vegetation cover or adult animals may have been underestimated. The density of chital derived from capture-recapture and age-sex ratios is $\hat{D}(S\hat{E}(\hat{D})$=34.38 (2.066). Density estimates derived from line transect surveys ($\hat{D}(S\hat{E}(\hat{D})$=20.1(6.75) are for a larger area of 284.1 km^2 (Karanth and Nichols 2000). I expected the density to be higher in the study area, due to intensive management activities like creation of water holes, controlled burning and regular maintenance of road-side clearings leading to increased forage availability and favourable habitat conditions, which was different from the area covered by the line transect surveys.

This study shows that photographic capture recapture sampling is a reasonable approach for estimating the abundance of chital in areas where line transect surveys cannot be easily carried out. For areas with relatively high chital densities and a good road network such as Bandipur, there is no need to set up camera traps as in the case of elusive species (Karanth et al. 2004). Photographs easily obtained from cars can be used to generate capture-recapture data. For areas where chital live at low densities, are wary or lack road access, camera trap based capture-recapture sampling can be employed.

My preliminary analysis of the capture data on stags shows that subsequent to sampling occasion 1-4 there may have been a violation of the population closure assumption. This could be due to either animals from neighbouring areas moving in due to changes in forage availability or even because of shifts of herds within the sampled area in which some animal might have initially had very low capture probabilities. I plan to explore this issue in the future through analyses using open capture-recapture models employing the robust design (Pollock et al. 1990; Kendall et al. 1997; Kendall 1999; Williams et al. 2002).

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USE OF PHOTOGRAPHIC CAPTURE-RECAPTURE SAMPLING TO ESTIMATE SURVIVAL OF CHITAL (*Axis axis*) FAWNS.

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SHORT TITLE – FAWN SURVIVAL USING CAPTURE-RECAPTURE

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Abstract

Robust estimates of animal vital rates such as survival are important in understanding the biological processes underlying changes in populations. Chital deer (*Axis axis*), are an important ungulate in south Asian forests, being a principal prey species for endangered large carnivores such as the tiger (*Panthera tigris*). Because of the heavy mortalities fawns suffer in early weeks, their survival rate is a key determinant of annual growth in chital populations. However, fawn survival is a difficult demographic parameter to estimate. In this study I estimated weekly fawn survival rates in Bandipur Tiger Reserve using photographic capture-recapture sampling using open population models of the Cormack-Jolly-Seber type. Based on photographic capture and identification of 189 individual fawns in a 6 week sample survey, I estimated a constant weekly survival rate of 0.805.

KEYWORDS: *Axis axis*, fawn survival, capture-recapture, open models

Introduction

Change in populations over time—whether ultimately driven by biological, physical or anthropogenic factors—is determined by changes in vital rates such as survival, reproduction or movement rates (Williams, Nichols & Conroy, 2002). Studies that aim to identify and address factors responsible for population declines must necessarily understand how exactly drivers such as vital rates affect population declines. Modelling population change requires modelling and estimation of parameters from empirical survey data. Population parameters may be state variables such as abundance, or vital rates such as survival, or nuisance parameters such as capture probability. For most species, the vital rates that have the greatest influence on population size are age/ sex specific survival rates.

Population studies may be targeted at the conservation of the species itself, or at the role the species plays in a system. For conservation of large carnivores such as tigers, efforts have to be targeted at securing an adequate prey bases (Karanth and Nichols, 1998; Karanth and Stith, 1999; Karanth *et al.*, 2004). Because they are usually an abundant ungulate species in most protected areas of southern Asia, chital deer *Axis axis* Erxleben are an important prey for the tigers and other large carnivores such as —dhole *Cuon alpinus* Pallas and leopard *P. pardus* L. (Johnsingh, 1983, 1992; Karanth and Sunquist, 1995). Endemic to the Indian subcontinent, chital mainly inhabit deciduous forests at altitudes below 3,500 feet. Estimates of ecological densities of chital in India range from a 2.3 individuals/ km^2 in Bhadra Tiger Reserve to 51.3 individuals/ km^2 in Pench Tiger Reserve, Madhya Pradesh (Karanth and Nichols, 2000).

Abundance and vital rates of chital fawns has an important influence on the annual dynamics of chital population as a whole (Schaller, 1967). Fawn survival rate and subsequent recruitment into the yearling age class, particularly, are likely to have an important effect on the trajectory of a chital population.

Because chital fawns are small and vulnerable, possible causes of mortality include predation, disease and forest fires (Schaller, 1967). Tigers, leopards and dhole have been recorded preying on chital fawns (Johnsingh, 1992; Schaller, 1967; Karanth and Sunquist, 1995). Because of this chital fawn mortality rates are expected to be high during the first few weeks. Based on ad hoc assessments from observed changing ratios of does to fawns, mortality for the first year has been estimated to be 48% (Schaller, 1967) and even as high as 92% (Sharatchandra and Gadgil, 1975). Raman (1996) reports a mean monthly mortality rate of 9.7% between March and October in 1991, however in 1992 mortality was negligible. The above results imply fawn survival ranging from 8% to 50 % year. However, these ad hoc estimates are weakened by the fact that they are not based on rigorous sampling protocols that account for detection probability and sampling variances.

All three studies (Schaller, 1967; Sharatchandra and Gadgil, 1975; Raman, 1996) are based on certain assumptions. The resulting estimates are highly sensitive to these assumptions, and may thus not provide reasonable estimates if the assumptions are not met. Therefore I explored alternative approaches based on more current methods.

Survival rates have been rigorously estimated for many animal species using formal capture-recapture sampling methods based on artificial tagging or even using natural markings (Nichols, 1992). Williams *et al*. (2002) outline the conceptual framework and provide details of such capture recapture studies. In these survival rates are typically estimated using open models which allow for losses and gains between sampling occasions. Open models estimate both survival rates and capture probabilities, usually through methods of maximum likelihood estimation. Survival rates have been estimated using such open capture-recapture models (Pollock *et al*., 1990) for a range of species ranging from voles (Johannesen and Andreassen, 1998), toads (Schmidt, Schaub & Anholt, 2002), orthopterans (Leisnham, Cameron & Jameison, 2003) and waders (Sandercock, 2003). Weekly survival rates of wood-thrushes have been estimated by Powell *et al.,*(2000).

Based on the fact that chital fawns are uniquely marked with spots I explored capture-recapture sampling of their populations using photographic capture methods implemented successfully for tigers and leopards in India by Karanth *et al.* (2004). Because early mortality is known to be high among chital fawns I chose to measure survival rate on a weekly basis soon after the peak birth season (December-February).

Study area

The study was carried out in the 880 km^2 Bandipur Tiger Reserve, Karnataka, India (Figure 1). Altitude within the reserve ranges from 780 m to 1454 m above m.s.l., with rainfall ranging from 914 mm to 1270 mm in different parts. The habitat mainly comprises of scrub forest, tropical dry deciduous and tropical moist deciduous forests.

I selected a study area of 17.6 km^2 (Figure 1) where chital herds are large, inhabit open short grass areas and tolerate close approach in cars, thus facilitating easier photo-captures. The high road density (3.57 km/km^2) ensured that the entire chital population could be surveyed without leaving 'holes' in the study area in which some individual chital could have very low chances of being photo-captured (Nichols and Karanth, 2002).

Figure 1. Map showing location of study area in Bandipur Tiger Reserve and location of Bandipur in India (inset).

Field methods

I sampled for chital fawns using non-invasive photographic captures from a vehicle, along the network of roads (Figure 2), driving at speeds of 15-20 km/hour. Sampling was carried out for 36 days between 13th February, 2006 to 3rd May, 2006, with only 3 consecutive sampling days per week.

Captures over each consecutive 3 day period were pooled to increase the capture probabilities per sample ($\hat{p}_i$), thus forming a total of 12 sampling occasions. Sampling was carried out between 0630 hours to 1030 hours and 1500 hours to 1830 hours, as light conditions were suitable between these hours. On encountering individuals, the vehicle was stopped at a distance from which photographs of a quality amenable to unambiguous identification could be taken without disturbing the animals. Photographs of all individuals whose flanks were visible were taken, with a handheld digital still camera (Sony DSC-H1) that provided sufficient resolution (5 mega-pixels) and magnification (12x) for unambiguous individual identification.

Figure 2.- Map showing study area with road network

At each fawn detection and photo-capture, I recorded the sampling occasion number, encounter time and location, number of photographs taken, and frame numbers of photographs. Photographs were transferred daily to a digital database for subsequent analyses.

Analytical methods

I used the pattern of white spots on the rufous brown coat to identify individual chital fawns, since the patterns are unique to each animal. As the number of photographs to be analysed was very high, a 3-D pattern matching program CHITAL was specially developed for this study by L. Hiby for faster comparison (Kelly, 2001) of photographs.

Protocol for selection of photographs

Only clear photographs that permitted unambiguous individual identifications either manually or using the 3-D pattern matching program CHITAL were used for the analysis. The following criteria were applied to select or reject photographs: (1) Photographs where the flank of a clearly visible individual chital is perpendicular (90°) to the photographic plane were considered ideal (2) Photographs where animals were at 60^{o} and 120^{o} angle to photographic plane were also used; (3) Photographs where the spot patterns were unclear were rejected; (4) The pattern recognition algorithm implemented in Program CHITAL uses the flank portion between the shoulder and the hip for pattern comparisons. I used only those undistorted photographs where a major portion (>75%) of this area was clearly visible.

Protocol for analyzing photographs and assigning Tag IDs

Before extracting spot patterns, program CHITAL aligns the photograph with a 3-D model of a chital, as patterns tend to look different with varying camera angles (Kelly, 2001). To fit the 3-D model to the flank photograph, standard points on the mid-back, near shoulder and hip, as well as along the dorsal and ventral outline of the animal were marked. Pattern extracts, corrected for camera angles were saved before running the batch comparison process to calculate similarity coefficients. A temporary Tag ID, based on the individual's position in the photograph and the photograph number, was generated for each individual within a photograph. Similarity coefficients were calculated for each pair of photographs, the pairs comprising of a new photograph, not assigned to any Tag ID and a photograph previously assigned to a Tag ID in the database. The pairs were displayed, in decreasing order of the similarity coefficient, pairs with the highest similarity value having the highest probability of being the same individual. Unambiguous identification and assigning of unique Tag IDs (in order of first capture) was achieved by visually confirming matches that had the top fifteen ranked similarity coefficients. In case of a recapture, the animal was assigned to an existing Tag ID, while in the case of a new capture the temporary Tag ID was confirmed as a new Tag ID.

Capture history matrices consisting of row vectors of 1s (capture) and 0s (no capture) were constructed for the right flank data set for fawns for the first 6 of the 12 sampling occasions as photo-identification was completed only for these occasions.

Estimation of Survival Rates

I used the Cormack-Jolly-Seber (CJS) open models (Williams *et al.,* 2002) to estimate capture probabilities $\hat{p}$ and weekly survival rate $\hat{\phi}$. All analyses were carried out using program MARK (White and Burnham, 1999). I used the single-age CJS model as the data were only for one age class. Capture probabilities and survival rates were either allowed to vary over time $\hat{\phi}(t)$ and $\hat{p}(t)$ or remain constant across sampling occasions $\{\hat{\phi}(.)\ \hat{p}(.)\}$, allowing us to specify four different models: the fully time varying CJS model $\{\hat{\phi}(t), \hat{p}(t)\}$, reduced parameter models $\{\hat{\phi}(t), \hat{p}(.)\}$ and $\{\hat{\phi}(.), \hat{p}(t)\}$, and the fully time-constant model $\{\hat{\phi}(.), \hat{p}(.)\}$

These models were ranked using Akaike's Information Critereon (AIC) modified for overdispersion and small sample size, $QAIC_C$ (Burnham and Anderson, 1998). $QAIC_C$ helps select the simplest model, which adequately fits the data, for small datasets with overdispersion. Considering that chital are a herd living species, I expected a considerable lack of independence in captures, leading to overdispersion in the data. The global model $\{\hat{\phi}(t), \hat{p}(t)\}$ was used to assess fit, and to estimate $\hat{c}$, the variance inflation factor. Since overdispersed data leads to underestimation of variance, $\hat{c}$ was used to inflate the variance estimate. In addition, model selection was based on $QAIC_C$, where the log (likelihood of model | data) is divided by $\hat{c}$. $\Delta QAIC_C$ was computed for each model as $\Delta_i = AIC_i - AIC_{\min imum}$. Akaike weights were then computed as $W_i = \dfrac{e^{(-\frac{1}{2}\Delta_i)}}{\sum \sum_{j=1}^{R} e^{(-\frac{1}{2}\Delta_j)}}$. Akaike weights can be interpreted as the probability that model i is the best model for the observed data, given the candidate set of models (Burnham and Anderson, 1998; Johnson and Omland, 2004).

Results

I obtained 349 usable right flank photographs and captured 189 different individual fawns over the first 6 sampling occasions, out of which 33 fawns were recaptured once or more. Based on the global model, $\{\hat{\phi}(t), \hat{p}(t)\}$ the variance inflation factor was estimated as 4.446. This was used to inflate variances and compute $QAIC_C$. Model selection summaries are presented in Table 1. $\{\hat{\phi}(.), \hat{p}(.)\}$ was ranked the best model with a $QAIC_C$ value of 65.123; $\{\hat{\phi}(t), \hat{p}(.)\}$was next with a value of 71.225; $\{\hat{\phi}(.), \hat{p}(t)\}$with $QAIC_C$ value of 72.259; and the fully time dependant model $\{\hat{\phi}(t), \hat{p}(t)\}$ was ranked last with the highest $QAIC_C$ value of 77.523.

Model	$QAIC_C$	$\Delta QAIC_C$	Model likelihood	Akaike weight
$\{\hat{\phi}(.), \hat{p}(.)\}$	65.123	0.0000	1.000	0.92804
$\{\hat{\phi}(t), \hat{p}(.)\}$	71.225	6.1021	0.0473	0.04390
$\{\hat{\phi}(.), \hat{p}(t)\}$	72.259	7.1367	0.0282	0.02617
$\{\hat{\phi}(t), \hat{p}(t)\}$	77.523	12.400	0.0020	0.00188

Table 1. Summary of model selection statistics for the CJS, and reduced parameter models. Δ $QAIC_C$ for model $i = AIC_i - AIC_{\min imum}$, model likelihood is $e^{(-\frac{1}{2}\Delta_i)}$ and Akaike weight for model i, $W_i = \dfrac{e^{(-\frac{1}{2}\Delta_i)}}{\sum \sum_{j=1}^{R} e^{(-\frac{1}{2}\Delta_j)}}$.

Thus from the QAIC$_C$ rankings model $\{\hat{\phi}(.), \hat{p}(.)\}$, the least parameterised model, with constant survival and capture probabilities best fit the data. The QAIC$_C$ weight for $\{\hat{\phi}(.), \hat{p}(.)\}$ was 0.928 and 0.043 for $\{\hat{\phi}(t), \hat{p}(.)\}$, the next highest ranked model. A ratio of the two model weights indicates that $\{\hat{\phi}(.), \hat{p}(.)\}$ has 21 times more support compared to $\{\hat{\phi}(t), \hat{p}(.)\}$, the next highest ranked model.

Based on $\{\hat{\phi}(.), \hat{p}(.)\}$, capture probability $\hat{p}(S\hat{E}(\hat{p}))$ was estimated as 0.18 (0.08) and weekly survival rate $\hat{\phi}(\mathrm{S\hat{E}}(\hat{\phi})$ was 0.80 (0.17) for the five time intervals separating the six sampling occasions.

Discussion

Weekly survival rate $\hat{\phi}$ compounded over the 6 week study period added up to 66.19% mortality. This estimate differs from results of earlier ad hoc studies, which estimated mortality rates for fawns. Schaller (1967) quotes an annual mortality rate of 48%. This is assuming that the population was stable, and the mortality rate would reflect an average of the mortality rates over smaller time periods. Sharatchandra and Gadgil (1975) also assume a constant mortality rate of 26% per month for the first nine months to arrive at a figure of 91% mortality for the first nine months. Raman (1996) quotes a mean monthly mortality rate of 9.7%.

Capture-recapture methods to estimate survival are currently the most reliable with advances in estimation methods (Lebreton et al, 1992; Pollock *et al.*, 1990; Schmidt *et al.*, 2002). Ad hoc survival estimation using age-structure data is based on assumptions of equal detectability of all age-classes, which may lead to biased estimates. Further assumptions of constant mortality over a time period and constant population size may not be met in field conditions. The three ad hoc studies (Schaller, 1967;Sharatchandra and Gadgil, 1975; Raman, 1996) although valuable as preliminary estimates need to be replaced by more robust estimates. I propose that using open population models under a photographic capture-recapture sampling is an appropriate and robust approach for estimating chital fawn survival.

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This study was conducted with permission from Karnataka Forest Department. I thank the Karnataka Forest Department for permits and cooperation. I am indebted to the Save the Tiger Fund of the National Fish and Wildlife Foundation, and, U.S. Fish and Wildlife Service-Rhinoceros and Tiger Conservation Fund for funding support. I thank Wildlife Conservation Society, New York and Center for Wildlife Studies, Bangalore for various forms of support and assistance. I am grateful to Lex Hiby, Conservation Research Ltd., U.K. for specially developing the program CHITAL and Kaavya Nag for her assistance in photo-cataloguing.

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CONCLUSIONS

Individual chital (both adults as well as fawns) could be successfully identified using the spot patterns on their body, enabling the application of capture-recapture based estimation using photographs.

Capture rates for adult chital stags were very relatively high, as seen from the sample size of individuals (M_{t+1}=174) caught during the 4 sample occasion study. Probabilities of capture for individuals per sampling occasion, $\hat{p}_i$ = 0.18 was high, enabling comparison of several plausible models and parameter estimation. Overall, my sample survey was able to capture 51% of all individual chital stags during the survey period.

Capture probabilities estimated from the capture histories for 189 fawns were also estimated at 0.18, and enabled comparison between the standard Cormack-Jolly-Seber model and the reduced parameter models, as well as maximum likelihood estimation of the model parameters.

Abundance of stags was estimated as 337 and density of chital derived from capture-recapture and age-sex ratios was $\hat{D}\,(\,S\hat{E}(\hat{D})$=34.38 (2.066), which met my expectation given past estimates from a nearby study area, and the fact that chital densities are considerably higher in my study area. Weekly fawn survival $\hat{\phi}(\,\mathrm{S\hat{E}}(\hat{\phi}\,)$ was estimated as 0.80 (0.17), indicating fairly high mortalities during the first few months.

This study shows that photographic capture-recapture sampling is a useful approach for estimating chital abundance in areas where line transect surveys cannot be implemented. Further this study also demonstrates that it is possible to estimate survival rates of chital fawns using capture-recapture sampling.

For areas having high to moderate densities of chital, individuals can be photo-captured from vehicles to generate capture history data. For areas where chital live at low densities, lack a good road network, or animals are wary, camera trap based capture-recapture sampling can be employed for estimation of both abundance as well as survival.

Further work

Further work is needs to be completed, with more data, which is available for both right and left flanks for does and fawns. Estimates derived from both data sets can then be compared.

The preliminary analysis of the capture data on stags shows that subsequent to sampling occasion 1-4 there may have been a violation of the population closure assumption. I plan to explore this issue through analyses using open capture-recapture models employing the robust design, since the field sampling protocol followed was amenable to construct both primary and secondary sampling periods required for such analyses.

A robust design analysis of the fawn data will also help estimate abundance, survival rates, temporary emigration as well as recruitment, which is likely to have been considerable during the study period. The analysis will be carried out for both datasets (right and left flank), and the results will be compared.

APPENDIX

Capture history matrix.- The x-matrix (Rexstad and Burnham, 1991) used for input in program CAPTURE is reproduced below. The first four digits indicate the individual TagID followed by the row vector, consisting of 1s (capture) and 0s (no capture), denoting the capture history.

0100 1110
0102 1000
1038 0100
1039 0100
1071 0101
1077 0110
0108 1000
1081 0101
1088 0110
1099 0100
1109 0110
1128 0100
1140 0100
1141 0100
1146 0110
1147 0101
1158 0100
1185 0010
1205 0010
1209 0011
1211 0001
1216 0011
1239 0010
1247 0010
1248 0010
0125 1000
1296 0010
1298 0011
1302 0010
1320 0010
1370 0010
1373 0010
1379 0010
1396 0010
1402 0010
1404 0010
1407 0010
1414 0010

1425 0010
1427 0010
1430 0010
1441 0010
1541 0010
1598 0010
1631 0011
1634 0010
1635 0010
1636 0010
1637 0010
1648 0010
0171 1110
1730 0010
0174 1000
1745 0010
1769 0010
1803 0011
1805 0010
1807 0010
1810 0011
1814 0010
0184 1101
0185 1101
1854 0010
0186 1000
0189 1100
1902 0001
1954 0001
2014 0001
2034 0001
2035 0001
2040 0001
2041 0001
2045 0001
2046 0001
0205 1000
2069 0001
2070 0001
2074 0001
2110 0001
2112 0001
2115 0001
2173 0001
2180 0001
2198 0001
2200 0001
2209 0001
2213 0001
2279 0001

0287 1010
0288 1011
0289 1011
0290 1011
3156 0001
3157 0001
3158 0001
3160 0001
3162 0001
3163 0001
3167 0001
3169 0001
0327 1000
0330 1000
0331 1000
0333 1101
0334 0100
0335 1000
0345 1000
0346 1001
0348 1000
0349 1100
0371 1010
0396 1100
0401 1001
0406 1000
0414 1010
0415 1000
0418 1100
0419 1000
0420 1000
0423 0010
0436 1110
0447 1100
0449 1000
0450 1000
0452 1000
0457 1000
0459 1000
0531 1000
0548 1111
0549 1110
0551 1110
0552 1110
0576 0100
0601 0111
0604 0111
0609 0100
0649 0100
0065 1000

0650 0101
0662 0100
0671 0100
0690 0100
0695 0110
0696 0100
0697 0011
0699 0110
0070 1011
0700 0100
0702 0100
0071 1000
0712 0100
0713 0100
0714 0100
0717 0100
0724 0100
0856 0100
0862 0100
0087 1111
0872 0100
0889 0100
0089 1000
0890 0101
0897 0100
0898 0111
0901 0101
0902 0100
0905 0110
0908 0100
0091 1001
0914 0110
0934 0110
0961 0110
0097 1000
0986 0100