

Reproductive ecology of Tibetan Eared Pheasant *Crossoptilon harmani* in scrub environment, with special reference to the effect of food

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We studied the nesting ecology of two groups of the endangered Tibetan Eared Pheasants *Crossoptilon harmani* in scrub environments near Lhasa, Tibet, during 1996 and 1999–2001. One group received artificial food from a nunnery prior to incubation whereas the other fed on natural food. This difference in the birds' nutritional history allowed us to assess the effects of food on reproduction. Laying occurred between mid-April and early June, with a peak at the end of April or early May. Eggs were laid around noon. Adult females produced one clutch per year. Clutch size averaged 7.4 eggs (4–11). Incubation lasted 24–25 days. We observed a higher nesting success (67.7%) than reported for other eared pheasants. Provisioning had no significant effect on the timing of clutch initiation or nesting success, and a weak effect on egg size and clutch size (explaining 8.2% and 9.1% of the observed variation, respectively). These results were attributed to the observation that the unprovisioned birds had not experienced local food shortage before laying, despite spending more time feeding and less time resting than the provisioned birds. Nest-site selection by the pheasants was non-random with respect to environmental variables. Rock-cavities with an entrance averaging 0.32 m² in size and not deeper than 1.5 m were greatly preferred as nest-sites. The birds were also more likely to place their nests in denser high-scrub and closer to streams. In the study area, the low availability of both cliff habitats and high-scrub patches suggested a limitation of sites suitable for nesting, which could be reflected in the between-year re-use of nest-sites (8.9%) and intraspecific nest parasitism (3.8%). Despite the apparent preference for certain nest-site variables, we found no effect of these on clutch fate, suggesting that the risk of nest predation was random.

The Tibetan Eared Pheasant *Crossoptilon harmani* is endemic to the Tibetan plateau, and was recently reclassified as a full species (Sibley & Monroe 1990, Cheng 1994) from its previous status as a subspecies of the White Eared Pheasant *C. crossoptilon* (Delacour 1977). Little has been known about the general breeding biology of this species, either in the field or in captivity.

Eared pheasants typically rely on forest habitats (Johnsgard 1999). However, the Tibetan Eared Pheasant occurs in primary forest in eastern Tibet, and in the alpine scrub vegetation typical of mountains around the middle Brahmaputra River (Lu

& Zheng 2002). The vegetation is a product of degraded forest: since the mid-Pliocene the Himalayas have blocked the warm moist currents of the Indian Ocean from reaching the inner plateau, resulting in cold dry weather unsuitable for tree growth (Li 1988). The Tibetan Eared Pheasant is the only species of pheasant that has survived this dramatic change of environments. Compared with forest habitats, the scrub vegetation found on the plateau offers poor nesting conditions for conspicuous ground-nesters. Studies of nesting ecology are crucial to understand the species' life history, and can provide a foundation for the conservation of these endangered birds.

Food is one of the principal factors affecting reproduction of birds (Lack 1968, Perrins 1970). Food

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supplementation experiments on a variety of bird species in the wild have investigated the effects of food on several key reproductive parameters, including egg-laying date, egg size, clutch size and nest success (e.g. Davies & Lundberg 1985, Schoech 1996, Hoodless *et al.* 1999), but the results have varied. In the present study, some pheasants took food provided by a Tibetan nunnery from autumn until pre-incubation. This created a unique opportunity to examine the effects of supplementary feeding on the basic breeding ecology of the birds.

Our objectives were: (1) to provide basic information on breeding biology of this poorly known species, (2) to estimate the effects of food on major reproductive parameters, (3) to describe the habitat characteristics at nest-sites and clarify the nesting requirements of the birds, and (4) to determine which nest-site characteristics were related to nesting success of the birds.

METHODS

Study area

Fieldwork was carried out in the Xiongse valley (29°27'N, 91°40'E, elevation ranging from 4000 to 4500 m, total area about 400 ha) near Lhasa, Tibet, during 1996 and 1999–2001. With an annual average temperature of 4.5 °C and annual precipitation of 543.6 mm (> 90% occurring during June to September), the study area is characterized by alpine scrub and meadow. The dominant plant communities include Rose *Rosa sericea* plus Barberry *Berberis hemleyana* (4000–4500 m), and Wilson Juniper *Sabina pingii* (4500–4900 m) on the south-facing slopes, Spiraea *Spiraea alpina* (4000–4200 m), and Rhododendron *Rhododendron* spp. plus Willow *Salix sclerophylla* (4200–4900 m) on the north-facing slopes. Lu and Zheng (2002) gave a detailed description of the habitat.

Supplementary feeding

The Tibetan Eared Pheasant is the only pheasant species in the area. It lives in family flocks outside the breeding season and each flock uses a year-round roost site. In our study area, two flocks (some 30–80 birds) came to a Buddhist nunnery (at 4200 m and about 1 ha) every day and searched for food (mainly highland barley) provided by the nuns during late autumn until the females began incubating, whereas others (some 50–100 birds) fed exclusively on plants (mainly their roots) in the wild. We categorized them

as provisioned and non-provisioned birds, respectively. Through receiving high-nutrition food, during the non-breeding season the provisioned birds were able to spend a significantly smaller proportion of their day feeding (34.3%) and more time resting (39.3%) than did the non-provisioned birds (63.5 and 17.1%, respectively) (Lu 1997). No hunting activity or agricultural practice took place in the study area.

Data collection

Field data were collected during 1996 and 1999–2001. Each spring we marked the provisioned birds with coloured leg-rings. Used to the presence of people, these birds allowed us to approach to 1–5 m for extended periods. We set a string noose on the ground, put some food in it and then called the birds to feed. Once a bird entered we pulled the noose around its leg to catch it. Trapping and processing took less than 5 min, without adverse effects on reproductive behaviour. We marked a total of 102 birds during the four breeding seasons. In addition, we identified some individuals either in provisioned or in non-provisioned flocks by unique plumage characters. Marked birds helped us to determine the affiliation (provisioned or without) of a breeding pair.

During each breeding season, we systematically searched for the pheasant nests throughout the valley. Once a clutch was located, we monitored it closely to obtain data on laying, incubation and hatching. We also marked the eggs, measured their length and maximum breadth to 0.1 mm with vernier calipers and weighed them using a spring balance to 0.1 g during regular nest-site visits. An egg volume index (= length × breadth²) was calculated as a measure of egg size. The incubation period was determined from successful clutches located during the laying period. For some clutches found during incubation, and for broods less than 10 days old (chicks could be caught easily), we determined their earliest possible egg-laying date by back-dating from subsequent events, such as egg-laying interval, incubation time, mean water loss of incubated eggs (obtained from the successful clutches) and age of the chick.

We also revisited nest-sites used previously by the pheasants. The old nests were easy to identify by their location, shape, materials and fragments of eggshell left after hatching. For each of both active and old nest-sites, we estimated the location (altitude, slope direction, slope degree), presence or absence of Willow within 10 m, distance to water (streams)

and background habitat (presence or absence of cliffs). Nest-sites were always within the flock's home ranges, but there were differences among the home ranges in geography and vegetation type (Lu & Zheng 2002). Because the birds' habitat selection depends mainly on the overall configuration of vegetation structure (James 1971), we took those features of vegetation common to the different nest-sites to be nest-site habitat variables. We centred a 10×10 -m quadrat sampling plot on each nest-site. This was subdivided into four 5×5 -m quadrats by marking bushes. Vertical layers of vegetation were classified as high- (> 1.5 m) or low- (< 1.5 m) scrub. In each subplot, we estimated the proportion of vertical projection of canopy of each vegetation layer by drawing a chart on gridded paper. The mean of the four subplots was treated as the cover value of the sampling plot. We determined canopy height as the mean of the heights of five randomly chosen bushes in each sampling plot. Microenvironmental features of the nest-site itself, including type of background, position (under rock or in bushes), and size and depth of rock-cavity, were also measured. All the nest-site measurements were taken after hatching. To estimate the availability of nesting habitats, we randomly chose samples over the study area and made the same measurements as those at nest-sites. Climate data obtained from a meteorological station (3650 m) 15 km from the study site were used to estimate values for the site according to established regression equations between temperature, precipitation and altitude (Gao 1984).

In order to increase sample size for the analysis of nesting success, we used data from previous nest-sites. The presence of large eggshell fragments in a nest was taken to indicate a successful hatch; bird-remains or large numbers of feathers at the nest-site were taken to indicate that the incubating hen had been killed or injured by predators.

Over the four breeding seasons, we recorded 89 (active 62 and old 27) nesting attempts at 82 separate (independent) nest-sites.

Statistics

We compared the differences in laying date between provisioned and non-provisioned birds by means of a two-way analyses of variance (two-way ANOVA) with year as a random factor. In order properly to assess the effects of food on egg size and clutch size of the pheasants, we used analyses of covariance (ANCOVA) with clutch size and egg laying date as

covariates of the two corresponding reproductive parameters. The non-parametric Mann–Whitney U -test was used for comparisons of habitat variables between nest-sites and random-sites, and the χ^2 test for comparisons of the frequency distribution of nest-sites or their types among different environments. The relationship between two variables was examined using Spearman's rank correlation coefficient (r_s). With several major nesting and environmental parameters as independent variables, we ran stepwise multiple linear regression analyses to determine whether the food supply contributed directly to variations in reproductive outputs. Through these analyses, we tried to identify which habitat variables affected nest-site selection and clutch fate significantly. Prior to analysis, the data for vegetation cover (%) were arcsine transformed and others, except for the binary data, natural-logarithmically transformed. All the statistical tests are two-tailed and values given are mean \pm se.

RESULTS

Nest morphology

The Tibetan Eared Pheasant nests consisted of a simple hollow in the ground, averaging 30.9 cm (se = ± 0.8 , range 27.2–39.4, $n = 25$) in outside diameter, 25.0 cm (se = ± 0.7 , range 20.2–30.5) in inner diameter, and 6.8 cm (se = ± 0.5 , range 3.2–10.6) in depth. Materials used for constructing the nests included sticks of bushes and grasses gathered nearby. More than 95% of the sticks were thin (< 1 mm in diameter) and short (< 100 mm in length), but a few were thick (1–6 mm) and long (100–410 mm). Female feathers often appeared in the nests: the number per nest ranged from 15 to 141 ($n = 12$, counted after hatching). The total weight of the materials varied considerably among nests, from 5 to 167 g ($n = 12$). Pheasants nesting in the Rhododendron–Willow community on the north-facing slopes did not collect material, but simply used soft twigs and leaves that had fallen directly on the nest-sites ($n = 14$).

Egg laying

Females typically laid one egg every 2 days until completing the clutch, but a few laying events happened irregularly: three eggs from normal-sized clutches were laid on successive days, one in a 3-day and one in a 4-day interval. Oviposition time (defined as the time when the laying hen left the nest)

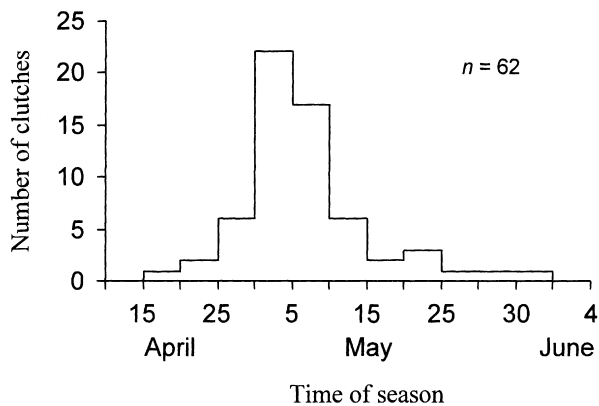


Figure 1. Distribution of the Tibetan Eared Pheasant clutches according to first egg laid date in a 5-day interval. Pooled data of the four breeding seasons.

Table 1. A comparison of the first egg laid date between provisioned and non-provisioned Tibetan Eared Pheasants. 1 = April 16.

Year	Provisioned				Non-provisioned			
	<i>n</i>	Mean	se	Range	<i>n</i>	Mean	se	Range
1996	6	16.7	2.6	5–24	9	20.6	2.0	16–35
1999	8	19.3	4.5	1–46	11	23.6	4.3	6–54
2000	8	22.6	1.4	18–29	8	24.4	2.1	18–35
2001	5	19.4	1.8	14–25	7	20.1	3.5	10–38
Total	27	19.7	1.5	1–46	35	22.3	1.7	6–54

occurred during the period 10:55–18:18 h ($n = 12$ eggs), most (80.0%) around noon (12:30–16:40 h). Five of another 11 eggs were laid before 17:30 h, and the remaining six after 12:10 h. The laying bouts (the time between the hen entering and leaving the nest) ranged from 57 to 125 min ($n = 5$ eggs). In several cases we found that hens covered the eggs with a little nest-material after laying.

Within the population, the earliest laying-date was 16 April and the latest was 9 June during the four breeding seasons, with over 80% of clutches

having their first eggs laid between late April and mid-May (Fig. 1). On average, provisioned hens laid about 2 days earlier than the non-provisioned hens, but the difference was not statistically significant (two-way ANOVA, with year as a random factor, food: $F_{1,43} = 8.54$, $P = 0.04$; year: $F_{3,43} = 2.10$, $P = 0.28$; Table 1). Our regression model of first-egg lay-date included food level, year, clutch size, mean April temperature, total April precipitation, altitude and slope direction of nest-site, but only clutch size was significant and explained 30.2% of the variation ($F_{1,49} = 16.90$, $P < 0.001$).

Egg morphology, egg size and clutch size

Egg colour varied both between and within clutches, and included white, light brown or light green, with or without small spots. Provisioned hens produced slightly heavier and larger eggs than non-provisioned hens (ANCOVA with clutch size as a covariate, fresh weight: $F_{1,64} = 0.90$, $P = 0.35$; clutch size: $F_{1,64} = 0.24$, $P = 0.63$; egg volume: $F_{1,166} = 1.50$, $P = 0.22$; clutch size: $F_{1,166} = 4.72$, $P = 0.03$; Table 2). In the egg size model consisting of clutch size, food provisioning, and first egg lay-date, the two former contributed 23.4% ($F_{1,49} = 10.57$, $P < 0.001$) and 8.2% ($F_{2,48} = 7.65$, $P < 0.001$), respectively, of interclutch variation in the mean egg volume index.

The average within-clutch difference in volume index was 12.11 (se = ± 1.30 ; range 4.62–28.05, $n = 51$). Larger clutches had larger average egg sizes ($r_s = 0.66$, $n = 51$, $P < 0.001$) and the difference was mainly caused by egg width ($r_s = 0.62$, $P < 0.001$) rather than length ($r_s = 0.28$, $P = 0.21$).

The mean clutch size was 7.4 (se = ± 0.2 , $n = 51$, pooled data from birds with and without provision), ranging from four to 11 eggs (excluding two clutches involved in intraspecific nest parasitism, see below), and most (76.5%) fell within the range 6–9 eggs. Clutch size declined significantly with laying date ($r_s = -0.49$, $n = 42$, $P < 0.001$). Provisioned females

Table 2. A comparison of egg size between provisioned and non-provisioned Tibetan Eared Pheasants.

Year	Provisioned				Non-provisioned			
	<i>n</i>	Mean	se	Range	<i>n</i>	Mean	se	Range
Fresh weight (g)	55	54.81	0.45	49.7–61.2	32	53.23	0.61	7–59.5
Length (cm)	116	5.82	0.01	5.35–6.18	86	5.75	0.02	5.32–6.15
Breadth (cm)	116	4.17	0.01	3.84–4.39	86	4.15	0.01	3.81–4.34
Egg volume index	116	101.01	0.57	83.4–115.4	86	99.14	0.73	83.5–111.8

Table 3. A comparison of clutch size between provisioned and non-provisioned Tibetan Eared Pheasants.

Year	Provisioned				Non-provisioned			
	<i>n</i>	Mean	se	Range	<i>n</i>	Mean	se	Range
1996	6	7.33	0.42	6–9	7	7.72	0.90	5–11
1999	7	7.86	0.63	6–11	9	7.11	0.72	5–11
2000	7	8.29	0.42	7–10	6	7.00	0.58	5–9
2001	3	7.00	0.58	6–8	6	6.50	0.76	4–9
Total	23	7.74	0.27	6–11	28	7.04	0.37	4–11

produced relatively larger clutches (ANCOVA, with egg laying date as a covariate, food: $F_{1,48} = 2.46$, $P = 0.12$; egg laying date: $F_{1,48} = 12.42$, $P = 0.001$; Table 3). Among first-egg lay-date, food supply, year, altitude and slope direction, the first two variables were responsible for 29.4% ($F_{1,49} = 16.49$, $P < 0.001$) and 9.1% ($F_{2,48} = 10.32$, $P < 0.001$) of the variation in clutch size, respectively.

We had circumstantial evidence for intraspecific nest parasitism in two clutches, in which one received 19 eggs in 21 days and another 12 eggs in 14 days. The total rate of parasitism was 3.8% (two of 53 full-egg clutches).

Incubation and hatching

The female began incubation with the last egg laid. For the first 2 days she stayed on the nest all day ($n = 3$). After this, she spent less than 2 h daily feeding around her nest (within 100 m), usually between 10:50 and 16:20 h ($n = 5$).

Sitting hens tolerated a very close approach (< 1.0 m). In most cases (36 out of 43) when we had to force the hens off the nests to check incubation progress, they left and stayed silently 0.2–20 m away, feeding and even watching their eggs being measured. In a few cases (seven of 43) they ran in panic, giving alarm

calls nearby. Once eggs chipped, the hens became nervous in response to disturbance (eight of 12 observations), even attempting to attack investigators.

Eggs became lighter as the incubation progressed. Daily water loss per egg averaged 0.47 g (se = ± 0.01 , range 0.30–0.58, $n = 56$) or 0.87% per day. Incubation period (from laying to hatching of the last egg) lasted 24–25 days ($n = 8$).

Each egg took 5–8 h from pipping to hatching for one clutch, and 18–25 h for four others. The hatching spans of the clutches of more than six eggs extended 23–30 h. Hatching weights before leaving the nests averaged 34.6 g (se = ± 0.7 , range 28.0–40.0, $n = 21$), or 63.8% of fresh egg weights.

Reproductive success

Of 144 eggs produced by provisioned birds and 127 by non-provisioned birds, 138 (95.8%) and 124 (97.6%), respectively, were fertilized, and out of these fertilized eggs, 129 (93.5%) and 120 (96.8%) hatched successfully (Table 4). We found no differences in the proportions of fertilized eggs (Mann–Whitney U -test over the four breeding seasons, $z = -0.82$, $n_1 = 20$, $n_2 = 19$, $P = 0.41$) or of eggs hatched successfully ($z = -1.15$, $n_1 = 20$, $n_2 = 19$, $P = 0.25$), between birds with different nutritional histories. Egg loss occurred during either the laying or incubation periods. Of 62 nesting attempts, 42 (67.7%) led to hatched young. Most nest failures resulted from predation. Black-billed Magpies *Pica pica*, despite their low density (only four or five breeding pairs in the valley), probably accounted for most eggs lost (X. Lu pers. obs.). Siberian Weasel *Mustela sibirica* was the only species of carnivore in the study area; it killed or injured incubating hens, causing a clutch loss of 11.3%. Two pheasant nests next to those of Red-billed Chough *Pyrrhonorax pyrrhonorax* (fewer than eight breeding pairs in the valley) survived until hatching, although the pheasants never attacked the

Table 4. Causes of nesting failure of the Tibetan Eared Pheasants.

Year	Provisioned							Non-provisioned						
	<i>n</i>	Deserted	Failed before incubation	Failed during incubation	Failed nests	% failed	<i>n</i>	Deserted	Failed before incubation	Failed during incubation	Failed nests	% failed		
1996	6	0	0	0	0	0.0	9	1	2	0	3	33.3		
1999	8	0	1	1	2	25.0	11	1	2	2	5	45.5		
2000	8	0	1	2	3	37.5	8	1	1	1	3	37.5		
2001	5	1	1	0	2	40.0	7	1	0	1	2	28.6		
Total	27	1	3	3	7	25.9	35	4	5	4	13	37.1		

Table 5. Measurements of several habitat parameters at the Tibetan Eared Pheasant's nest-sites ($n = 82$) and at random-sites ($n = 82$).

Habitat variable	Nest-site			Random-site			Mann–Whitney U -test
	Mean	se	Range	Mean	se	Range	
Slope angle	37.4	1.2	10–60	38.5	0.6	25–55	$z = -0.36, P = 0.72$
High-scrub cover	43.2	2.3	8–85	33.5	1.5	0–60	$z = -3.63, P < 0.001$
Low-scrub cover	37.1	2.8	10–90	34.8	2.9	12–90	$z = -0.85, P = 0.40$
High-scrub height	182.3	2.2	150–225	177.1	3.8	150–225	$z = -1.28, P = 0.20$
Low-scrub height	73.9	1.1	50–95	72.3	1.1	55–90	$z = -1.09, P = 0.28$
Distance to water	50.0	6.8	2–300	76.6	9.4	5–400	$z = -2.93, P < 0.001$

choughs. We had no evidence that Golden Eagle *Aquila chrysaetos* (encounter rate during the breeding season = 0.06 bird/h) or Eagle Owl *Bubo bubo* (one or two breeding pairs) preyed on sitting hens, and there were no snakes or lizards in the study area.

Neither food supply, year, clutch initiation date nor clutch size was able to predict reproductive success (logistic regression, Wald $\leq 1.16, P \geq 0.28$).

Nest-site habitat

Logistic regression detected three variables that contributed to habitat differences between nests and random sites (Table 5). Sixty-six of 82 (80.5%) nest-site samples were correctly classified. Rock-dependent habitat showed the heaviest weighting (54 out of all 82 nest-sites, 65.9%, Wald = 26.40, $P < 0.001$). Nest-sites were more likely to be sheltered with higher bushes (Wald = 10.29, $P = 0.001$) and to be close to water (Wald = 4.99, $P = 0.03$) than would be expected from the random sites. Also, the birds placed their clutches in three of the five main scrub communities over the study area, with a trend towards selecting the Rose plus Barberry community (53 of 82). Nest-sites were evenly distributed with regard to altitude (32, 27 and 23 at 4020–4200 m, 4200–4400 m and 4400–4650 m, respectively, $\chi^2_2 = 1.49, P = 0.48$).

Nest-sites always had a background object for the nest, such as rocky walls, tree trunks or dense bushes. Among types of objects, the rocky walls were most preferred. Of 54 'rock-dependent' nest-sites, 44 (80.0%) were in rock-cavities (Fig. 2) and ten (20.0%) under projecting rocks. The cavity-entrance size averaged 0.32 m² (se = ± 0.05 , range 0.14–0.98, $n = 31$) and depth 0.70 m (se = ± 0.09 , range 0.23–1.45, $n = 31$). Outside the cavities, clumps of bushes often camouflaged the nests. The distance from the centre of a nest hollow to the edge of the nest-cavity averaged 5.6 cm (se = ± 0.9 , range 0–18, $n = 31$), significantly



Figure 2. A Tibetan Eared Pheasant hen incubating her nest within a rock cavity.

smaller than the distance (35.0 cm, se = ± 4.5 , range 11.5–72.5) from the midpoint of a rock-cavity to its edge (Mann–Whitney U -test, $z = -6.6, P < 0.001$). Those cavities with larger openings or being too deep were never used as nest-sites.

Of the 68 nest-sites, five (7.4%) were used twice and one (1.5%) three times. Two of 22 nest-sites located in 1996, two of 27 in 1999 and one of 19 in 2000 were re-used in 1999, 2000 and 2001, respectively. Only one remained active from 1999 through 2001.

We found that none of 12 nest-site parameters was a significant predictor of nesting success (logistic regression, Wald $\leq 1.92, P \geq 0.17$), suggesting that nest predation of the pheasants occurred randomly.

DISCUSSION

Nesting biology

Several characteristics of the eggs and clutches of the Tibetan Eared Pheasants were similar to those of other eared pheasants (Table 6). Tibetan Eared

Table 6. A comparison of reproductive parameters among four species of eared pheasant.

Species	Egg volume index	Clutch size ^a	Incubation period	% predation rate	Source
White Eared Pheasant	106.59	7.59 (5–12)	24–25	63.2	Lu (1986), Jiangchu <i>et al.</i> (1995), Wu & Peng (1996)
Tibetan Eared Pheasant	99.09	7.35 (4–11)	24–25	24.2 ^b	this study
Blue Eared Pheasant	85.87	6–13	26–28	–	Zheng & Liao (1983), Liao (1984)
Brown Eared Pheasant	114.91	7.79 (4–12)	26–27	44.2 ^c	Liu <i>et al.</i> (1991)

^aNot including the occasional large supernormal clutches.

^bNot including the abandoned clutches.

^cOnly involving those predated by crows.

Pheasants in this study laid about 7 h after sunrise, compared with 4.5–6.8 h in Brown Eared Pheasants *C. mantchuricum* in northern China (Liu *et al.* 1991). The incubation period of the Tibetan Eared Pheasant was the same as that of the White Eared Pheasant, but 2–3 days shorter than those of Blue and Brown Eared Pheasants.

Extremely large clutches have also, occasionally, been reported in other eared pheasants. Jiangchu *et al.* (1995) reported 21 eggs in a White Eared Pheasant clutch. Of 27 Blue Eared Pheasant *C. auritum* clutches recorded by several investigators (Zheng & Liao 1983, Liao 1984, X. Lu pers. obs.), one had 21 eggs. Among 43 Brown Eared Pheasant nests located by Liu *et al.* (1991), 42 had clutch sizes ranging from four to 12; only one contained 17 eggs. The large supernormal clutches probably indicate intraspecific nest parasitism. Therefore, the normal clutch sizes of four species of eared pheasant vary within a similar range.

The habitat complex is probably responsible for interspecific differences in the probability of nest failure. Our study area had a low diversity and density of predator species compared with forest areas that can support abundant predator faunas (for example, it was estimated that more than 10 species were potential predators of Brown Eared Pheasant eggs or adults, Table 6). Predation pressure was therefore less in our study than in other studies of breeding eared pheasants. Egg predation seems to be more serious for forest-dwellers. Egg predators destroyed 36.8% of the clutches of White Eared Pheasants in western Sichuan, whereas carnivores caused 26.3% clutch loss by killing incubating hens (for references see Table 6). Thick-billed Crows *Corvus macrorhynchos*, as a main egg predator of Brown Eared Pheasants, cause 44.2% clutch failure. However, in the scrub environments in our study area, the carnivorous mammals may pose a more serious threat.

Food provisioning

Perrins (1970) suggested that the food supply available for the breeding female was an important determinant of clutch initiation time. This has been supported by several field feeding experiments (Ewald & Rohwer 1982, Davies & Lundberg 1985, Schoech 1996, Soler & Soler 1996), but rejected by others (Arnold 1994, Wiebe & Bortolotti 1995, Hoodless *et al.* 1999). Similarly, associations between supplemented food and egg size (Wiebe & Bortolotti 1995, Soler & Soler 1996; but see Arnold 1994, Hoodless *et al.* 1999, Jager *et al.* 2000), clutch size (Nilsson 1991, Soler & Soler 1996, Clifford & Anderson 2001; but see Arnold 1994, Hoodless *et al.* 1999) and reproductive success (Soler & Soler 1996; but see Nager *et al.* 1997) remain controversial. The present study found little evidence that provisioning altered reproductive parameters or improved the productivity of Tibetan Eared Pheasants.

On the basis of both literature and their own work, Svensson and Nilsson (1995) and Nager *et al.* (1997) concluded that reproductive traits of birds respond to supplemental feeding only in poor environments. Birds must build up body reserves for reproduction (Brittas 1988, Robb *et al.* 1992) and this is particularly true for precocial species that lay yolk-rich eggs, as this imposes a strain on the female for egg production (Sotherland & Rahn 1987, Zheng 1995). On the basis of a dynamic programming model, McNamara *et al.* (1994) predicted that when food availability is higher, birds should show a lower overall level of foraging and a burst of foraging at the start of the day and in the afternoon, whereas when food is scarce they should forage intensively throughout the day. In our study area, plant roots (the main food of the non-provisioned pheasants prior to reproduction) were abundant and evenly distributed. Although the non-provisioned birds spent a significantly larger

Table 7. A comparison of nest-site features among four species of eared pheasant. Percentage is given in parentheses.

Species	<i>n</i>	Under rock wall	Under bush roof	With tree trunk leaning	Under fallen tree	In bush	Source
White Eared Pheasant	20	3 (15.0)	0 (0.0)	9 (45.0)	3 (15.0)	5 (25.0)	Lu (1986), Jiangchu <i>et al.</i> (1995), Wu & Peng (1996)
Tibetan Eared Pheasant	82	54 (65.9)	0 (0.0)	8 (9.8)	0 (0.0)	20 (24.4)	this study
Blue Eared Pheasant	5	0 (0.0)	0 (0.0)	2 (40.0)	1 (20.0)	2 (40.0)	Zheng & Liao (1983), X. Lu (pers. obs.)
Brown Eared Pheasant	35	1 (2.9)	25 (71.4)	1 (2.9)	4 (11.4)	4 (11.4)	Liu <i>et al.</i> (1991)

proportion of the day feeding than the provisioned birds prior to reproduction (Lu 1997), the fact that they can take some time to rest even on cold short midwinter days (9.5% of daytime) suggested that they faced no heavy energetic constraint. The non-provisioned birds may therefore be able to obtain the amount of food needed to breed, which is beyond that required for daily self-maintenance, as suggested by Davies and Lundberg (1985). In particular, the willow buds appearing before and during the laying period could allow the non-provisioned birds to put on body reserves to the same level as provisioned birds and therefore to lay at the same time as them. One should expect a significant influence of food supply on reproductive output in the non-provisioned birds only to occur when they suffer such a severe food shortage that they cannot meet their basic nutrient requirements.

Nest-site selection and nesting success

Several studies have shown that predation is the principal source of nesting mortality in Galliform species (Tapper *et al.* 1996, Jimenez & Conover 2001). Amongst other factors, nest survival can depend on nest-site complexity and concealment. Therefore, physical characteristics of nest-sites, particularly those that are hidden from predators, often represent key cues for nesting selection by ground-nesters (Ricklefs 1969, Hanson 1970). For eared pheasants, the extended nesting period (egg laying and incubation nearly 40 days on average) might pose a great risk to eggs and hens owing to their longer exposure to predators. Thus, a site should be selected that can provide adequate camouflage from potential predators. A background object may function as a shelter for nests and thus is a common feature of eared pheasant nest-sites (Table 7). Forest species often use living or fallen tree trunks as a background. By contrast, eared pheasants under scrub

conditions had to take rock-walls for the nest's background. Moreover, a roof over a nest should effectively reduce predator detectability. As an extreme example, Brown Eared Pheasants (25 of 43 nests) typically nest under a roof constructed of dead sticks of trees and bushes (Liu *et al.* 1991). For Tibetan Eared Pheasants in our study area, no objects can serve as better shelters than can rock-cavities. However, when choosing a rock-cavity as a nest-site, the birds must resolve the following problems. (1) If a hen sits in a deeper nest-cavity, her ability to detect an approaching predator must be reduced. To resolve the conflict between concealment from and detectability of predators, the pheasants did not place their clutches in the deepest parts of the cavities. (2) Cavities that were too shallow or had a larger opening would be more exposed to predators. As we observed, these kinds of cavity were avoided. (3) The birds never used the deep cavities where the weasels appeared more often. Indeed, we frequently found the remains of pheasants and other animals such as Tibetan Partridge *Perdix hodgsoniae* and Woolly Hares *Lepus oisstolus*, probably killed by weasels.

Dense bushes could provide better shelter for a nest and thus were selected. Food resources seemed less important for incubating hens. During incubation, the hens that nested far from streams never travelled far for water, suggesting that drinking was unnecessary for them. We therefore assumed that the pheasants' preference for sites closer to streams might reflect their preference for the denser high bushes there. Microclimates at nest-sites are often responsible for reproductive success and thus may influence the nesting decisions of birds (Wiebe & Martin 1998, Hooge *et al.* 1999, Wagner & Seymour 2001). In our study area, with poor cover, insolation and wind were strong and snow occurred frequently during the peak nesting period. The rock-cavities could create a microclimate that favoured the thermoregulation of incubating hens and development of the eggs.

In contrast to forest complexes, the limited availability of cliff habitats and dense high-scrub patches suggested a potential shortage of suitable nest-sites for the pheasants. This view is partly supported by the re-use of nest-sites and intraspecific nest parasitism. The preservation and management of the two critical habitats are important for long-term survival of the birds.

Despite the apparent strong selection by the pheasants of several habitat features, nesting success showed no significant association with any of them. The independence of nest predation with regard to preferred nest-site features has been observed in other studies. This is attributed to non-specialist nest predation (Howlett & Stutchbury 1996) or low predation pressure (Rowe & Jones 2000). In a case similar to that observed in the Namaqua Sandgrouse *Pterocles namaqua* reported by Lloyd *et al.* (2000), the lack of a significant relationship between preferred nest-site parameters and nest survival of the Tibetan Eared Pheasant could be because the weasels detected the bird's nests only when they were very near these nests, so the physical structure surrounding nest-sites played little role in obstructing the vision of the predators. By contrast, several hens sitting in dense bushes were killed, suggesting that the bushes might hinder the hens' escape from predators. It appears that Tibetan Eared Pheasants cannot deal with the conflict between enhancing concealment and effectively fleeing from predators.

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