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ORIGINAL ARTICLE

Elevational range and timing of breeding in the birds of Ladakh: the effects of body mass, status and diet

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Abstract We studied the effects of body mass, status (resident or migratory) and diet on the breeding elevation range and timing of reproduction of the birds in the Trans-Himalayan region of Ladakh, northwestern India. Most of breeding birds of Ladakh are Palearctic or breed at high elevations in the mountains. There is a small proportion of Oriental species, and no bird is endemic to this region. We found that heavier birds tended to start their egg-laying earlier than lighter ones. Since body mass is related to the length of incubation and nesting periods, it would appear that one result of this phenomenon is that the time of peak demand for food for most birds coincides with peak food abundance in summer. Status affected the elevation of the breeding range, with resident birds tending to breed at higher elevations than summer visitors. Residents and summer breeders also differed significantly in their diet composition, with the former feeding mainly on plants and seeds, and the latter feeding on molluscs, insects and worms.

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Introduction

Avifaunas in alpine regions are subjected to adverse climatic conditions at their high-altitude habitats. As a result, they have adapted their breeding schedules to maximize their reproductive success in the energetically demanding and harsh environmental conditions of these regions. Food availability is a critical factor that affects the breeding success of birds, which need to time reproduction so that chick-rearing coincides with peak food availability (Lack 1978). Food availability is often essential for the breeding female to attain reproductive state and also important after the chicks leave the nest, as fledglings need adequate food to maintain themselves, in part because their thermoregulatory costs increase outside the nest (Perrins and Birkhead 1983). Ambient temperature is another factor known to affect breeding success in birds, especially in the alpine regions where birds start laying eggs early when the temperature is favorable but delay it when under colder conditions. Therefore, birds may adjust their breeding schedules depending on food availability and weather conditions.

The Ladakh region in northern India is a high-altitude cold desert with harsh climatic conditions and low primary productivity; as such the conditions resemble those found in the arctic. This alpine region represents a fragile and impoverished ecosystem, but surprisingly it harbors a diverse array of avifauna comprising more than 300 species, most of which are migratory; of these, about 100 species are known to breed there. The breeding species are mainly Palearctic (with a large proportion of high mountain

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birds) and Oriental species. The marshes around the high-altitude lakes serve as critical habitats, providing abundant food to the large number of migratory birds that visit this alpine region for a few months in the summer to breed. Due to its remoteness and limited accessibility, this avifauna has barely been studied, and only a few ornithologists have worked there (but see Osmaston 1925; Koelz 1940; Holmes 1983; Mallon 1987; Gole 1992; Pfister 2001 and Namgail 2005). For many years, Ali and Ripley's (1978) handbook served as the sole source on the biology and distribution of the birds of Ladakh, but Pfister's (2004) more recent book is now the most comprehensive and updated work.

The breeding birds of Ladakh range in body mass from 7 g (Mountain Chiffchaff *Phylloscopus sindianus*) to 9 kg (Himalayan griffon *Gyps himalayensis*). The summer breeders arrive in the region in the spring to lay their eggs, and they leave in autumn after completing their breeding cycle (Pfister 2004). The resident species also start laying their eggs early in spring so that they can have chicks in their nests during the peak food growth season (July–August). The parents must struggle to create conditions suitable for the successful development of the embryos in the stochastic environment of Ladakh (Pfister 2004). Although the birds feed on a variety of food (e.g. insects, plants, seeds, fish, etc.), the breeding season in the region is relatively short (2–3 months). Not only is the timing of the breeding season critical for development of young, but there must also be enough food available to allow both fledgling and adult migrants to store enough fat reserves for their long journey back to the wintering grounds.

The aim of this study was to explore the relationships between body mass, status (resident or summer breeder) and diet at the start and end of the breeding season and the elevation of the breeding range of the birds. We hypothesized that: (1) large birds in Ladakh should start breeding earlier than small ones, and (2) residents will have their range at higher elevations than summer breeders.

Materials and methods

Study area

Ladakh (32–36°N and 75–80°E) is the northernmost province of India and is a high (2,800–7,650 m a.s.l.), cool region in the westernmost part of the Tibetan plateau that encompasses an area of approximately 80,000 km^2 (Fig. 1). Its location in the Trans-Himalaya places it in the rain shadow of the annual Indian monsoon, resulting in an annual rainfall between 500 and 1000 mm near the Himalayas, decreasing in the eastern and northeastern parts to about 100 mm (Hartmann 1983). Winter temperatures may fall to −30°C, while in summer the weather is generally clement, although temperatures may rise as high as 35°C. The region is characterized by high, steep and rugged mountains separated by deep valleys into which the

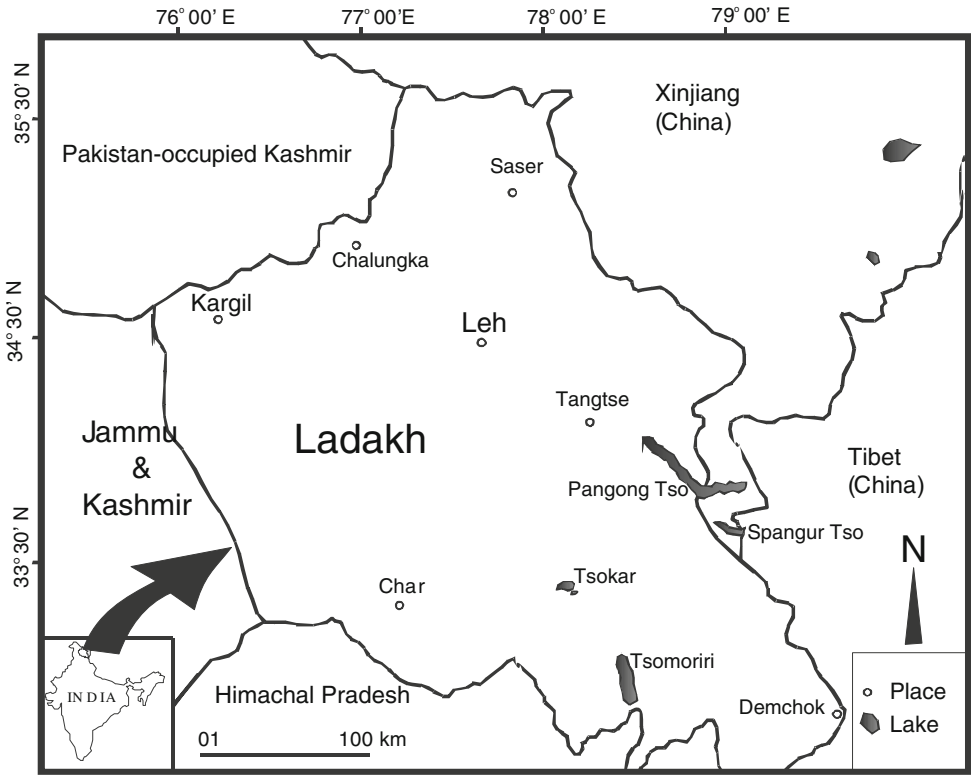

Fig. 1 The study area in northmost Indian state of Jammu and Kashmir

Indus and Zanskar rivers and their tributaries flow. The soils of Ladakh are sandy or sandy-loam and are generally characterized by being poor in organic matter and nitrogen content (Murti 2001). However, there are some plant nutrients in the soil, largely due to low precipitation and hence less weathering of the rocks. Nevertheless, there is no forest cover in Ladakh due to a severe shortage of water, and the vegetation is desert-like, consisting of low shrubs and herbs (Rawat and Adhikari 2005). Annual and perennial herbs and shrubs are relatively abundant between 3,000 and 4,800 m a.s.l., where summer temperatures are generally moderate. The vegetation in the valleys is richer than that found on the mountain slopes, and several high-altitude mountain lakes are surrounded by marshes. Nevertheless, Ladakh is considered to be a high-altitude desert region, as is indicated by the scarcity of water and shore birds: no Ciconiformes or Ralli breed in the region, and there are only two Anseriformes and three Charadriformes (Pfister 2004). Ladakh is sparsely populated, with a human population of less than 300,000.

Data collection and analyses

Data on mean body mass (grams), mean start and end of the breeding season (month), altitudinal range at which nesting occurs (meters), and status in Ladakh (resident or migrant) and their Palearctic (Palearctic, Oriental, or other) were gathered from the literature. Most data were from Pfister (2004), complemented from other sources (Ali and Ripley 1978; Roberts 1991). Body mass data (adult male and female) were augmented by data from Dunning and Odum (1993). For those species whose lower altitudinal breeding range was not provided by Pfister (2004), we used our field sightings (TN, personal observations).

We examined the effects of body mass, status (resident or migrant), taxa (order, family and genus) and diet on various breeding parameters by nested analysis of variances (ANOVAs) using the JMP software program, ver. 5.1 (SAS Institute, Cary, NC). We used a contingency table to check for significant differences between residents and summer breeders in terms of diet (herbivorous or carnivorous).

The use of multiple species within a taxon for comparative analyses has been criticized (Harvey and Mace 1982). Ideally, the most satisfactory analysis should be based on a comparison of phylogenies. However, no accurate genetic data are available for many of the species in our sample. Instead, we analyzed our data using the nested ANOVA test (Sokal and Rohlf 2001). Nested ANOVA was used to account for the variation at various taxonomic levels and to examine the effects of body mass, status (resident or summer breeder) and diet (herbivore or carnivore). The effect of body mass was studied by allocating all birds to one of three categories (small <100 g, medium 101–1,000 g and large >1,000 g).

Results

Of the 101 species of birds known to breed in Ladakh, some are rare or occasional breeders. Of these 101 species, 41 are residents (40%) and 60 are migrants. The proportion of resident species is similar between the passerines (42%) and non-passerines (38%). Most species (61) breed in the Palearctic region or in the Palearctic and Africa, an additional 26 species breed mainly in high mountains in the Palearctic, seven species have Oriental distribution and the rest are Holartic or cosmopolitan in distribution. None of the species is endemic to this region.

Results of nested ANOVA revealed that body mass affected the start of the breeding season ($P = 0.0051$), but not its end ($P = 0.2397$). There was also no effect of this factor on the altitudinal range of breeding (Table 1). Phylogeny (order, family and genus) affected both the start and end of the breeding season but not low and high breeding elevation (Table 1). One-way ANOVA showed that the differences between body mass classes were significantly different from each other with respect to the timing of breeding ($R^2 = 0.3423$, $F_{2,97} = 25.2383$, $P < 0.0001$). On average, small birds (body mass < 100 g) started to breed in mid-May (average month 5.5, $n = 63$), medium-sized ones (101–1,000 g) in mid-April (average month 4.65, $n = 23$) and large birds (>1,000 g) towards the end of March (average month 3.71, $n = 14$).

Table 1 Results of the nested ANOVA carried out on four breeding parameters of Ladakh birds (start and end of the breeding season, low and high breeding elevation range)

Breeding parameters assessed	*df*	*F*	*P* overall	*P* order	*P* family	*P* genus	*P* mass class
Season (start)	70, 29	5.9939	<0.0001	0.0006	<0.0001	0.0286	0.0051
Season (end)	68, 29	3.9915	<0.0001	0.0006	<0.0001	0.0425	0.2397
Height (low)	70, 29	1.3393	0.1929	0.2255	0.0603	0.4713	0.1257
Height (high)	70, 29	0.7913	0.7881	0.2681	0.4514	0.9748	0.0972

Significant results (also see text) are underlined

Independent factors include order, family, genus and body mass class (small <100 g, medium 101–1,000 g and large <1,000 g)

Table 2 Results of the nested ANOVA carried out on four breeding parameters of Ladakh birds (start and end of the breeding season, low and high breeding elevation range), all corrected for body mass

Breeding parameters assessed	*df*	*F*	*P* overall	*P* order	*P* family	*P* genus	*P* status
Season (start)	73, 27	4.0352	<0.0001	0.0064	<0.0001	0.1931	0.9764
Season (end)	71, 27	3.3951	0.0004	0.0018	0.0002	0.1023	0.9833
Height (low)	73, 27	1.9034	0.0318	0.0958	0.0105	0.2536	0.0095
Height (high)	73, 27	0.6669	0.9116	0.3414	0.6056	0.9868	0.6549

Significant results (also see text) are underlined

Independent factors include order, family, genus and status (resident and summer breeders)

Table 3 Results of the nested ANOVA carried out on four breeding parameters of Ladakh birds (start and end of the breeding season, low, and high breeding elevation range), all corrected for body mass

Breeding parameters assessed	*df*	*F*	*P* overall	*P* order	*P* family	*P* diet
Season (start)	33, 67	6.0317	<0.0001	0.0081	<0.0001	1.0000
Season (end)	32, 66	4.3353	<0.0001	0.0022	<0.0001	0.5444
Height (low)	33, 67	1.7780	0.0234	0.3153	0.0072	0.2469
Height (high)	33, 67	1.3268	0.1628	0.1050	0.2160	0.6575

Significant results are underlined

Independent factors include order, family, and diet (herbivores or carnivores)

Status affected only the low breeding elevation range ($P = 0.0095$; Table 2), i.e. the lower breeding elevation range of residents is significantly higher than that of summer breeders (on average 3,627 and 3,314 m a.s.l., respectively). Order significantly affected the start and end of the breeding season ($P < 0.001$), family affected the start and end of the breeding season ($P < 0.001$) and low elevation range ($P = 0.0105$), while genus had no significant effect on any of the breeding parameters examined (Table 3).

In order to test the effect of diet we carried out an additional nested ANOVA using the above three taxonomic levels, but since there was not enough power to carry out this test with all the above taxon levels, we omitted genus from the analysis and carried it with order, family and diet (herbivore or carnivore). The results indicated that the phylogenetic effects as well as that of status were retained (Table 3), while diet did not have a significant effect on any of the breeding parameters.

Using a contingency table we found that resident and summer breeders significantly differed in the composition of their diets (permutation test; $\chi^2 = 19.43$, $P = 0.0006$). The correspondence analysis showed that residents tend to feed on seeds and plants, while summer breeders tend to feed on animals, either vertebrates or insects (Figs. 2, 3).

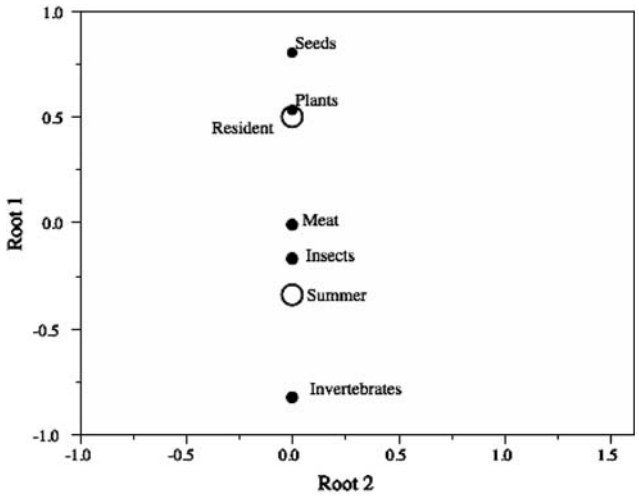

Fig. 2 Correspondence analysis of the diet in relation to status (resident and summer breeders) among the birds of Ladakh

Discussion

Ladakh borders the Oriental region, and one would expect that a large proportion of its breeding birds would have an Oriental distribution. However, of the 101 bird species breeding in Ladakh the majority are of Palearctic origin (61) or breed in the high mountains (26), while only seven are Oriental. This finding is in agreement with Janzen's (1967) prediction that due to their physiological tolerances, tropical lowland organisms are less likely than temperate ones to overcome high mountain passes and thus will have a smaller distribution (reviewed by Ghalambor et al. 2006). Furthermore, a large proportion of Ladakh birds are restricted to the high mountains, but none are endemic to Ladakh. The climate of the Ladakh region is strongly seasonal. Consequently, this observation is in accordance

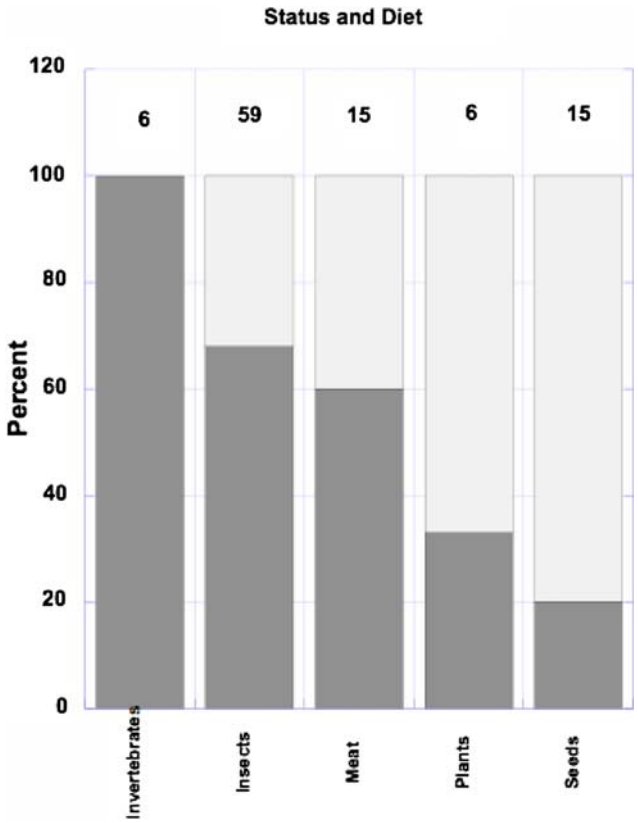

Fig. 3 The percentage and number of resident (*empty bars*) and summer breeders (*filled bars*) feeding on various diets. The number of species in each foraging category is marked *above its column*

with Jetz et al. (2004), who found that in sub-Saharan Africa low seasonality and high endemism are strongly associated.

Our results support our initial hypothesis, as we found that large birds start breeding earlier than smaller ones, which is in agreement with the findings of Pramod and Yom-Tov (2000) who studied the breeding season of passerines throughout the Indian subcontinent. This is likely attributable to the birds' reproductive strategy of timing chick-rearing with peak food availability (Lack 1978). Because the lengths of the incubation and nestling periods are significantly related to body size (Rahn and Ar 1974; Yom-Tov and Ar 1993), large birds have longer developmental periods and thus need to start breeding earlier to assure that their chicks' peak dietary requirements coincides with the peak food abundance. Although large birds of different orders consume more than one food type, in a highly seasonal region such as Ladakh it is reasonable to assume that all food types peak during the relatively short period summer. Our finding that the end of the breeding season is not significantly affected by body mass further supports the assumption that all birds aim at coinciding the peak food demand with peak food availability in early summer.

It is interesting to note that the lower breeding elevation range of residents is significantly higher than that of summer breeders (Table 2). This is probably due to several factors, among them that the former are more adapted to a cold climate, a fact that enables them to settle at a higher elevation at the start of the breeding season. A closer look reveals that this phenomenon is also related to diet. Since the summer breeders include a high proportion of insects and invertebrates in their diet, they tend to be at lower altitudes where they can find a high abundance of these animals during the few summer months. The lower breeding elevation of the herbivorous species is significantly higher (by an average of 305 m) than that of carnivorous ones (on average 3,585 and 3,280 m, respectively; t test on low breeding elevation corrected for body mass: $n = 101$, $t = 2.6179$, $P = 0.0140$) and is particularly pronounced (average of 529 m) among passerines (3,727 and 3,198 m, respectively, for granivorous and insectivorous birds; t test on low breeding elevation corrected for body mass: $n = 64$, $t = 3.6628$, $P = 0.0024$).

The difference in diet between resident and summer breeders may be explained by food availability. Insects and other invertebrates, including aquatic ones, are scarce in the extremely cold winter, and most species that rely on these prey types migrate to warmer climates (68 and 100%, respectively). The 19 insectivorous species that reside in Ladakh during the winter include six species of corvids and the house sparrow, all of which are at least partially commensal with man and thus partially independent of natural food resources. Similarly, among carnivorous birds, only the larger ones that feed at least partially on carrion (the lammergeier *Gypaetus barbatus*, the golden eagle *Aquila chrysaetos* and the Himalayan griffon *G. himalayensis*), the two nocturnal birds of prey (the eagle owl *Bubo bubo* and the little owl *Athene noctua*) that feed mainly on rodents as well as the merganser *Mergus merganser* that feed on fish remain in Ladakh during the winter. The smaller raptors that feed on insects or small birds and mammals (the common kestrel *Falco tinnunculus*, the hobby *Falco subbuteo*, the sparrowhawk *Accipiter nisus*, the black kite *Milvus migrans*, the long-legged buzzard *Buteo rufinus* and the upland buzzard *Buteo hemilasius*) are all summer breeders and leave Ladakh before winter—apparently due to a shortage of food. In contrast, of the 15 granivorous species (including eight species of finches, three species of doves and a sandgrouse), 80% are residents and only three are summer breeders. Similarly, of the six species that feed on other parts of plants, including seeds, all four Galliformes are residents, while the two plankton feeder ducks are summer breeders.

Zusammenfassung

Höhenverbreitung und Brutzeitpunkt bei Vögeln in Ladakh: Effekte von Körpermasse, Status und Nahrung

Wir haben die Effekte von Körpermasse, Status (Stand- oder Zugvogel) und Nahrung auf die Höhenstufe und den Zeitpunkt des Brütens der Vögel in der Trans-Himalaya-Region des Ladakh in Nordwestindien untersucht. Die meisten Brutvögel in Ladakh sind paläarktisch oder brüten hoch im Gebirge, einen geringen Anteil machen orientalische Arten aus, und keine Art ist endemisch in dieser Region. Wir fanden, dass schwerere Vögel dazu neigten, früher mit der Eiablage zu beginnen als leichtere. Da die Körpermasse mit der Bebrütungs-und Nistdauer zusammenhängt, scheint ein Ergebnis dieses Phänomens zu sein, dass der Zeitpunkt des höchsten Nahrungsbedarfs für die meisten Vögel mit der höchsten Nahrungsverfügbarkeit im Sommer zusammenfällt. Der Status beeinflusste die Höhenstufe des Brutgebiets; Standvögel neigten dazu, auf größerer Höhe zu brüten als Sommergäste. Standvögel und Sommergäste unterschieden sich außerdem signifikant in der Zusammensetzung ihrer Nahrung—erstere fraßen hauptsächlich Pflanzen und Samen, letztere Mollusken, Insekten und Würmer.

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