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Avian Behavior, Ecology, and Evolution

House Sparrows *Passer domesticus* increase in body size and dorsal feather insulation along a Himalayan elevational gradient

Los Gorriones comunes *Passer domesticus* aumentan el tamaño corporal y el aislamiento de las plumas dorsales a lo largo de un gradiente altitudinal del Himalaya

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ABSTRACT. Elevational gradients impact organisms in diverse ways because of lower temperatures and oxygen levels at higher elevations. Birds adapt to these constraints through changes in body size, plumage, metabolism, and behaviors such as elevational migration. But whether species show variation across multiple axes of adaptations along a single elevational gradient is not well demonstrated in the literature. The broad elevational distribution of the House Sparrow *Passer domesticus* in the Himalayas provides a rare insight into whether morphological and plumage modifications can simultaneously arise within a species across its elevational distribution. Drawing insights from eco-physiological patterns, we hypothesized that sparrows at higher elevations would exhibit larger body sizes (Bergmann's rule), shorter extremities (Allen's rule), and a more insulative feather structure. We sampled sparrows at 13 sites (n = 169) from 300 m to 3500 m along an elevational gradient in the western Himalayas and found that sparrows at higher elevations were significantly larger following Bergmann's rule, and had more downy dorsal feathers likely giving higher-elevation sparrows thermal advantages at low temperatures. We show that House Sparrows may show convergent modifications in response to temperature clines whether they are elevational or latitudinal.

RESUMEN. Los gradientes altitudinales afectan a los organismos de diversas maneras debido a las temperaturas y niveles de oxígeno más bajos a mayores altitudes. Las aves se adaptan a estas restricciones por medio de cambios en el tamaño corporal, el plumaje y el metabolismo y comportamientos como la migración altitudinal. No obstante, no está bien demostrado en la bibliografía si las especies muestran variación a través de múltiples ejes de adaptaciones a lo largo de un único gradiente altitudinal. La extensa distribución altitudinal del Gorrión común *Passer domesticus* en los Himalayas brinda una visión poco común sobre si las modificaciones morfológicas y del plumaje pueden surgir simultáneamente dentro de una especie a través de su distribución altitudinal. Teniendo en cuenta patrones ecofisiológicos, hipotetizamos que los gorriones en mayores altitudes exhibirían mayores tamaños corporales (regla de Bergmann), extremidades más cortas (regla de Allen) y una estructura de plumas más aislante. Muestreamos gorriones en 13 sitios (n = 169) desde 300 m a 3500 m a lo largo de un gradiente altitudinal en los Himalayas occidentales y encontramos que los gorriones en mayores altitudes fueron significativamente más grandes, concordando con la regla de Bergmann, y tuvieron más plumones dorsales, lo que probablemente les daría ventajas térmicas a bajas temperaturas. Mostramos que los gorriones comunes pueden exhibir modificaciones convergentes en respuesta a las variaciones de temperatura, ya sean altitudinales o latitudinales.

Key Words: *feather structure; intraspecific variation; mountains; plumage; thermoregulation*

INTRODUCTION

Elevational gradients shape organisms in a variety of ways (Laiolo et al. 2018). Low temperatures and reduced partial pressure of oxygen at high elevations are significant selective forces affecting the ecology and life-histories of montane taxa (Badyaev and Ghalambor 2001). Along elevational gradients, organisms exhibit numerous adaptations to cope with increasingly harsh climates such as an increase in body size (Peterman et al. 2016, Brehm et al. 2019), changes in wing morphology (Ceresa et al. 2022) and physiology (Monge and Leon-Velarde 1991, Storz et al. 2009, Jankowski et al. 2013).

Birds cope with cold temperatures at high elevations chiefly by using one or more strategies such as (1) larger body size at high elevations (both within and among species) thereby reducing the surface to volume ratio and hence rate of heat loss (Blackburn and Ruggiero 2001, Ashton 2002); (2) using their plumage as an insulative layer (Wolf and Walsberg 2000, McCafferty et al. 2017); (3) regulating their metabolic rates to cope with energetic demands of thermoregulation (Londoño et al. 2017, Shankar et al. 2020); (4) caching food to meet energetic needs during resource shortages (Sonnenberg et al. 2019); and (5) showing behavioral adaptations such as elevational migration (Barcante et al. 2017, Menon et al. 2023). However, whether birds show (1) evidence of intraspecific modifications in response to one or more of these strategies along the same elevational gradient, and (2) how these modifications relate to changes documented along latitudinal clines is less well-known.

Despite being a hallmark synapomorphy in birds, the role of feathers in avian thermoregulation, especially at high elevations, is not fully understood (Terrill and Shultz 2023). Contour, or body feathers in birds have a proximal plumulaceous (downy) section and a distal pennaceous section. Birds increase insulation against

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cold by having longer feathers that overlap more to create a deeper plumage (Pap et al. 2017), more dense feathers (Williams et al. 2015, Osváth et al. 2018), or by having greater proportion of the feather having the plumulaceous section, which helps in trapping an insulative pocket of air close to the body (Pap et al. 2020). Montane birds in North America, the Himalayas, and the Neotropics have been shown to have feathers that are longer and/or have a larger proportion of down (de Zwaan et al. 2017, Barve et al. 2021, Barve and Cadena 2022) suggesting that these adaptations have evolved repeatedly in birds. However, many of the studies on feather modifications in response to elevation have been comparative and interspecific. Testing whether species show intraspecific variation in feather structure across a single elevational gradient can help us understand whether it is possible for feather adaptations to arise across small spatial scales despite significant gene flow across the gradient due to physical proximity (Bachmann et al. 2020), as compared to latitudinal gradients that may have populations with more diverse evolutionary histories (Balanyá et al. 2006).

House Sparrows *Passer domesticus* with their wide elevational distribution in the Himalayas provide a strong system to understand whether morphological and plumage modifications can arise simultaneously within species at the spatial scale of a single elevational gradient. Along latitudinal temperature clines, more northern House Sparrows are bigger compared to southern individuals both in Finland and in Israel (Kekkonen et al. 2012, Ben Cohen and Dor 2018). There, body size evolution was inferred as a form of local adaptation to cold temperature despite gene flow.

Here, we studied whether body morphology and feather structure varied with elevation among House Sparrows along a single continuous river valley (300 m–3500 m) in the western Himalayas. Based on eco-physiological predictions such as Bergmann's and Allen's rules, we predicted that birds at high elevations will be larger, have shorter extremities, and have more insulative feather structure (Bergmann 1847, Allen 1876). We thus test whether morphological variation can arise within a species at small spatial scales despite potentially high gene flow.

METHODS

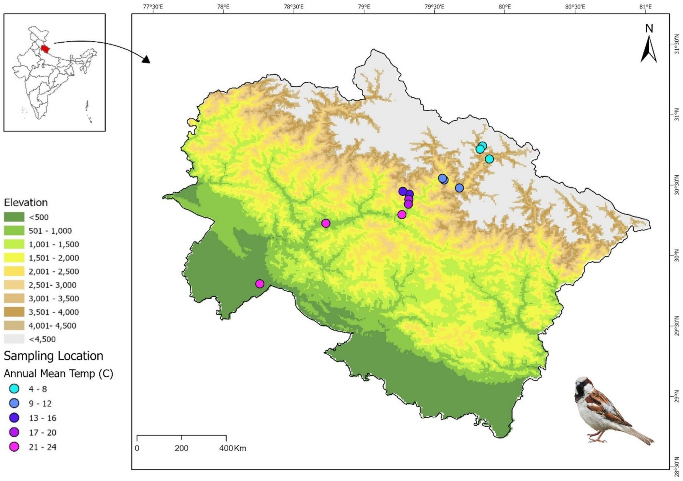
Field site

We carried out fieldwork in the Himalayan state of Uttarakhand in northwest India. Uttarakhand has a large elevational gradient (180 m–7800 m) extending from tropical forests in the lowlands to glaciers at the highest elevations. We sampled House Sparrows along a single elevational transect in the Ganga River watershed from 300 m (lowest elevation site) to 3500 m (highest elevation site), which almost covers the entire elevational distribution of the species in the region (they occur from the lowest elevation in the Gangetic plains to up to 3900 m; Bala et al., *unpublished data*). We sampled birds at 13 sites along the elevational gradient (3500 m; 3360 m; 3040 m; 2620 m; 2460 m; 2200 m; 1700 m; 1500 m; 1200 m; 960 m; 800 m; 570 m; and 300 m; Fig. 1, Appendix 1).

Morphometrics

We captured birds using mist-nets in October 2022 and August 2023 (n = 169 individuals). Upon capture, birds were sexed based on plumage, weighed using a Pesola® balance (0–100 g) to the nearest 0.5 g, and banded with metal rings. For each individual, we also took seven morphometric measurements using Avinet SPI Dial Calipers (0–150 mm) and a wing rule: We measured beak length, beak width, beak height, head length, tarsus length, wing length, and tail length. All morphometric measurements were taken one time and by the same observer. We released the birds as soon as they were sampled.

Fig. 1. Sampling sites along the Alaknanda watershed, an elevational gradient (300–3500 m). Dots show the sampling locations in Uttarakhand, India. Mean annual temperature values in different colors show linear decrease with elevation. Temperature data were downloaded from WorldClim 2.1 (Fick and Hijmans 2017). The map was generated using ArcGIS Pro 3.0.3.



Feather structure

To explore variation in feather structure, we collected two contour feathers each from the same location on the dorsal and ventral sides of the body. We stored feathers in zip-lock plastic bags and stored in a cool, dark place until they were measured. We used a Canon 80D camera and EF50mm lens to photograph feathers with a scale and white reference background for measurements. We then imported the images into ImageJ image analysis software (Schindelin et al. 2015). For each image separately, we converted the distance in pixels into centimeters (calibration) using the reference scale. We measured the length of downy (fluffy, non-interlocking barbs) and pennaceous (rigid, interlocking barbs) region at the rachis, and added them together to obtain the entire feather length. We followed the same procedure for both dorsal and ventral feathers.

Statistical analysis

All the statistical analysis were done using R. 4.3.1 (R Core Team 2023). We tested the relationship between morphometric variables and elevation using linear mixed-models with sex (M/F) as a random effect (Bolker et al. 2009) using the lme4 package in R (Bates et al. 2015). We used elevation as the fixed effect in all the models. We first tested if body mass, tarsus length, wing length, and tail length changed with elevation. We then tested for variation in beak morphology across elevation by taking the ratio of beak length and beak height (depth) as a measure of beak shape (Barve et al. 2017).

Small values of this ratio indicate birds with short and deep beaks while large values indicate thin and long beaks. We tested predictions from Allen's rule to understand whether beak shape is driven by physiological constraints like cold temperature. We used the likelihood ratio test (package lme4) as model diagnostics to compare all models with their respective null models (which includes only the intercept and random variable "Sex"). We also performed a Moran's I (package spdep) test to check for spatial autocorrelation on the residuals of our models (Pebesma and Bivand 2023). For morphometrics that showed significant spatial autocorrelation (see Results), we binned the elevations into four elevational zones (< 1000 m, 1000 m–2000 m, 2000 m–3000 m, and < 3000 m) and used linear mixed-effects models to test whether these elevational zones still showed the same pattern as when we used elevation as a continuous variable.

We first calculated repeatability in our measures of feather structure within the same bird by using the package ICC (Wolak and Wolak 2015). Then, we tested whether proportion of down and relative feather length (total feather length was divided by tarsus length) changed with elevation for both dorsal and ventral feathers using linear mixed-models. All models are described in Tables 1 and 2.

RESULTS

All four morphometric traits increased with elevation indicating that sparrows were in general larger at higher elevations (Table 1, Fig. 2a-d). We also found a significant change in beak shape with elevations with sparrows at higher elevations having longer and shallower beaks than sparrows at low elevations (Fig. 2e). Feather structure variables were repeatable within the same individual (dorsal feather: proportion of down ICC = 0.75; relative feather length ICC = 0.74; ventral feather: proportion of down ICC = 0.70; relative feather length ICC = 0.55). Within feather structure variables, only the downy section of dorsal feathers increased significantly with elevation (Fig. 2f). We found no variation in ventral feathers across the elevations we sampled (Table 2).

The likelihood test results showed that models with the elevation variable provide a significantly better fit to the data compared to the null models (Appendix 2). The residuals of the LMM for body mass, wing length, and tail length did not show spatial autocorrelation while tarsus length, beak shape, and proportion of downy part of dorsal side showed a positive spatial autocorrelation (Appendix 3). However, proportion of downy and beak shape but not tarsus length showed significant differences between the lowest and highest elevations after converting data into elevational zones to control for the spatial autocorrelation confirming our overall pattern (Appendix 4).

DISCUSSION

Animals have evolved a variety of ways to respond to cold. Across a 3200-meter elevational gradient in the Himalayas, we found that House Sparrows show significant intraspecific variation in both morphology and feather structure that indicate adaptations to increasing colder temperatures. House Sparrows were significantly larger at higher elevations and had more downy dorsal feathers likely giving higher-elevation sparrows thermal advantages to cope with low temperatures.

Table 1. Results of linear mixed models testing the role of elevation in explaining variation in morphological characters of House Sparrows (*Passer domesticus*) over an elevational gradient.

	Estimate	Standard error	df	t value	P
Body Weight ~ Elevation + (1 | Sex)					
Intercept	22.48	0.25	167	88.45	< 0.001
Elevation (m)	7.10×10^{-4}	1.24×10^{-4}	167	5.73	< 0.001
Tarsus length ~ Elevation + (1 | Sex)					
Intercept	16.62	0.16	3.6	101.80	< 0.001
Elevation (m)	2.60×10^{-4}	6.44×10^{-5}	166.3	4.04	< 0.001
Wing length ~ Elevation + (1 | Sex)					
Intercept	71.91	1.18	1.2	61.12	0.006
Elevation (m)	1.45×10^{-3}	1.73×10^{-4}	166	8.38	< 0.001
Tail length ~ Elevation + (1 | Sex)					
Intercept	54.17	0.93	1.5	56.29	0.002
Elevation (m)	1.52×10^{-3}	2.28×10^{-4}	166.1	6.65	< 0.001
Beak Shape (BL/BH) ~ Elevation + (1 | Sex)					
Intercept	1.45	2.52×10^{-2}	5.2	58.54	< 0.001
Elevation (m)	5.43×10^{-5}	1.08×10^{-5}	166.4	5.01	< 0.001

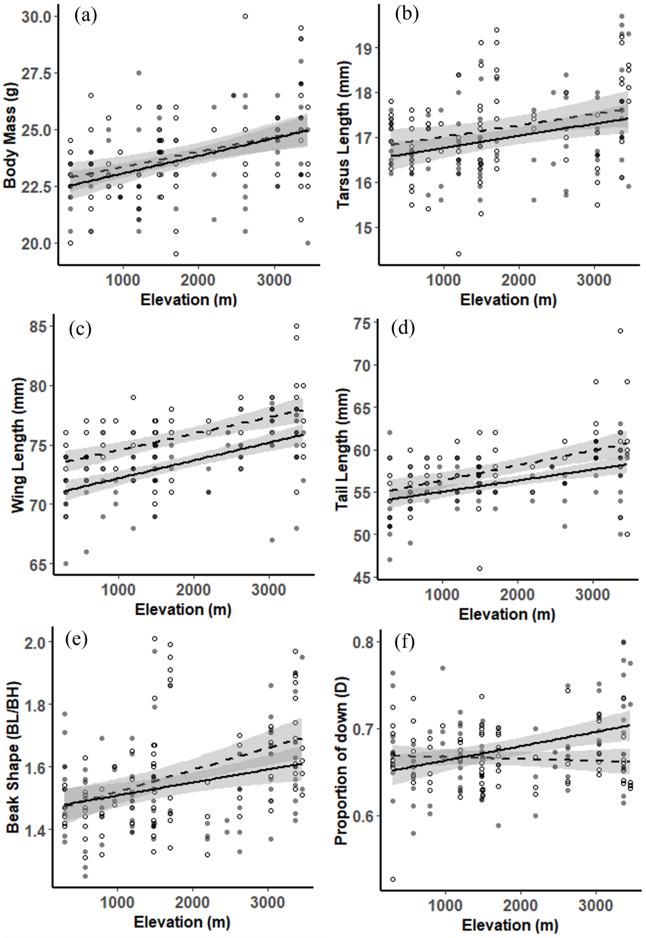
Table 2. Results of linear mixed models testing the role of elevation in explaining the variation in feather structure of House Sparrows (*Passer domesticus*) across the elevational gradient.

	Estimate	Standard error	df	t value	P
Dorsal feathers-					
Proportion of downy section ~ Elevation + (1 | Sex)					
Intercept	0.66	4.11×10^{-3}	331	160.5	<0.001
Elevation (m)	7.02×10^{-6}	1.99×10^{-6}	331	3.5	<0.001
Relative feather length ~ Elevation + (1 | Sex)					
Intercept	0.13	1.55×10^{-3}	331	83.7	<0.001
Elevation (m)	7.20×10^{-8}	7.56×10^{-7}	331	0.1	0.924
Ventral feathers-					
Proportion of downy section ~ Elevation + (1 | Sex)					
Intercept	0.61	6.61×10^{-3}	1.7	92.1	<0.001
Elevation (m)	7.18×10^{-7}	1.81×10^{-6}	330.2	0.4	0.69
Relative feather length ~ Elevation + (1 | Sex)					
Intercept	0.10	1.34×10^{-3}	331	76.8	<0.001
Elevation (m)	2.00×10^{-7}	6.5×10^{-7}	331	0.31	0.76

An increase in body size results in a reduction in the body size to volume ratio thus reducing the rate at which body heat is lost to the environment (Aschoff 1981). Adaptive changes in body size as a response to increasingly cold temperatures are widely seen in birds across latitudes (Ashton 2002). Multiple studies have shown this pattern in House Sparrows (e.g., Kekkonen et al. 2012 in Finland, Ben Cohen and Dor 2018 in Israel). Yet, whether such changes occur across elevation within species in general and House Sparrows in particular is not widely known. We found that House Sparrows do, in fact, exhibit a clinal increase in body size with elevation, suggesting such changes can arise within short spatial scales. Our results thus indicate that House Sparrows show a convergent increase in body size as a response to colder temperatures across both latitude and elevation.

An increasing body of literature has demonstrated that birds can modify the structure of their plumage and feathers to cope with cold temperatures. We also found an increase in the proportion of the downy section of the back (but not breast) feathers in House Sparrows at high elevations, which indicates thermal adaptations. Such an increase in the downy section of feathers has been previously demonstrated in a number of taxa (de Zwaan et al. 2017, Pap et al. 2017, Barve et al. 2021, Barve and Cadena 2022). Previous research has also shown increases in the total length of

Fig. 2. Predicted linear regression lines; shaded areas are standard errors (confidence interval 95%) for male (solid line and open circles) and female (dashed line and solid circles). Morphological variations in House Sparrows (*Passer domesticus*) are consistent with modifications to colder temperatures with increasing elevations. Body weight (a), tarsus length (b), wing length (c), tail length (d), and beak shape (e) were significantly different. Dorsal feathers showed a significant increase in proportion of down with elevation (f).



the feather as a thermal adaptation (Pap et al. 2017) but we did not find such a change in House Sparrows. Back feathers are potentially under greater selection than breast feathers to evolve more insulation because the back is more exposed to the environmental conditions such as cold winds especially in an open-country bird like the House Sparrow. Barve and Cadena (2022) showed that the length of dorsal feathers showed greater change with elevation than ventral feathers. Studies on Horned Larks (*Eremophila alpestris*; Mason et al. 2023) have also shown plumage coloration on the dorsal feathers is linked to balance both crypsis and thermoregulatory costs of their habitats. One might however expect such characteristics in ventral feathers as well, which traditionally protect vital organs. The absence of such a finding highlights the importance of future research to elucidate the underlying mechanisms governing this pattern. In the Himalayas, House Sparrows appear to be responding to cold temperatures at high elevations by both increasing in size and increasing the insulative qualities of their body feathers that are most exposed.

Many questions remain about whether these morphological changes along multiple axes of adaptations result in better thermal adaptations. Although we sampled populations while they were at their breeding elevations, we do not know to what extent House Sparrows may be using other strategies such as elevational migration to escape cold temperatures. Although winter surveys conducted at certain high-elevation sites, where humans seasonally migrated downhill, indicated signs of elevational migration to lower altitudes during severe winter months (Bala et al., *unpublished data*). It is not clear whether all Himalayan sparrow populations show a “sliding migration” downslope or whether the highest populations show a “leapfrog migration” to low elevations while mid-elevation populations do not migrate. A recent study points toward the former (Menon et al. 2023). Radiotracking studies are needed to understand how sparrows may be using elevational movements to survive the cold Himalayan winters.

The positive correlation between wing length and elevation in higher-altitude sparrows also indicates a mechanism for partial elevational migration, with wing length, a crucial aerodynamic trait, potentially influencing winter migrations from higher to lower elevations. Aerodynamic theory predicts that longer, pointed wings enhance flight efficiency (Norberg 1995, Pennycuick 2008). Studies (Pérez-Tris and Tellería 2001, Fiedler 2005) reveal migratory subspecies typically have longer, pointed wings over resident counterparts. If House Sparrows are moving downwards in winters, then the observed increase in wing length is likely linked to dispersal ability (Claramunt et al. 2012, Sheard et al. 2020, Claramunt 2021).

House Sparrows are generalists and human commensals breeding in and near human habitation across a large elevational gradient, presumably with one of the broadest breeding elevational distributions of any Himalayan passerine. Our finding that higher-elevation sparrows have longer, shallower beaks, while being opposite to that predicted by Allen’s rule, suggests that changes in diet occur (Gosler 1987, Grant and Grant 1996, Bardwell et al. 2001) with elevation and may be yet another axis along which sparrows are adapting to their environment in the Himalayas. The presence of longer and shallower beaks at higher elevations may be attributed to a digging and probing feeding behavior, indicative of wild foraging. In contrast, lower elevations, with access to cultivated seeds as a primary food resource, may influence beak morphology differently. However, this hypothesis necessitates thorough investigation to understand the underlying mechanisms and ecological implications. The positive autocorrelation observed in tarsus length, beak shape, and proportion of down on the dorsal side could potentially be attributed to the proximity of sampling sites and greater gene flow between these sites within certain elevational zones. As indicated in the map (Fig. 1), there is a discernible clustering of high and mid-elevation sites that were sampled because of logistical constraints of sparrow distribution and suitable sampling locations. Controlling for the autocorrelation by grouping proximate sampling sites into the same elevational zone revealed that the lowest and highest elevational zones still showed significant differences in beak and feather morphology. This confirms that overall high elevation sparrows show differences over low elevation sparrows consistent with predictions.

This is yet another example of how animals can adjust to changes in temperature or food availability over very small spatial scales along multiple morphological axes simultaneously. Our findings are especially interesting because elevational gradients represent systems of high environmental change over small spatial distances. Thus, House Sparrows in the Himalayas show modifications in the face of potentially extensive gene flow between populations because of the short physical distance between them. How much gene flow actually occurs between populations is yet another unknown, and a topic of future research. Such population level studies have the promise of not only revealing how animals respond to environmental constraints, but also for identifying the genomic basis of these responses. Elevational gradients continue to provide important insights into the evolutionary ecology of birds.

Author Contributions:

R.S.K., S.B., and R.B. conceived the manuscript idea. R.B., S.B., and P.G. carried out the fieldwork and collected the data. R.B. and S.B. analyzed the data and wrote the paper. R.S.K. and D.M. supervised the project. All authors reviewed and approved the final version of the manuscript.

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Data Availability:

The data that support the findings of this study are openly available in Figshare at https://doi.org/10.6084/m9.figshare.26002108. Ethical approval for this research study was granted by Uttarakhand Forest Department Letter no. 591/5-6 Dated 21-08-2021.

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Appendix 1: Overview of sampled sites: Elevation, mean annual temperature, and sample size

Location	Latitude	Longitude	Elevation (m)	Mean Annual Temperature (ºC)	Sample Size
Niti	30.7776	79.84156	3450	4.45	6
Gamshali	30.75551	79.82444	3360	4.97	22
Malari	30.68477	79.88981	3040	7.30	16
Auli	30.53677	79.56769	2620	11.35	10
Subhai	30.47946	79.67710	2460	11.90	2
Sunil	30.54855	79.55648	2240	12.25	6
Gangol	30.43578	79.32012	1700	15.53	12
Mandal	30.45583	79.27509	1500	16.10	27
Pathiyaldhar	30.39853	79.31694	1200	18.76	16
Maithana	30.36431	79.31529	960	19.43	5
Jilasu	30.29111	79.26867	800	20.69	10
Maletha	30.22941	78.72756	570	21.81	17
Gaindikhata	29.79864	78.25943	300	23.77	20
Total					169

Appendix 2: Results of model diagnostics testing the good fit of models

Model	Null Model	Full Model	ΔAIC	Chisq	Pr(>Chisq)
Body Mass ~ Elevation + (1 | Sex)	699.74	670.73	29.01	31.00	<0.001
Tarsus length ~ Elevation + (1 | Sex)	464.92	451.57	13.35	15.35	<0.001
Beak Shape (BL/BH) ~ Elevation + (1 | Sex)	-130.37	-151.61	21.24	23.24	<0.001
Wing length ~ Elevation + (1 | Sex)	846.57	789.91	56.66	58.66	<0.001
Tail length ~ Elevation + (1 | Sex)	918.83	881.72	37.11	39.10	<0.001
PDL ~ Elevation + (1 | Sex)	-1160.9	-1167.8	6.9	8.96	<0.001

Appendix 3: Results of Moran I statistic test for testing spatial autocorrelation. P- value greater than 0.05 indicates no spatial autocorrelation

Model	Moran I statistic standard deviate	p-value	Moran I statistic
Body Mass ~ Elevation + (1 | Sex)	-0.78	0.781	-0.031
Tarsus length ~ Elevation + (1 | Sex)	2.71	0.003	0.081
Beak Shape (BL/BH) ~ Elevation + (1 | Sex)	3.73	<0.001	0.113
Wing length ~ Elevation + (1 | Sex)	0.09	0.465	-0.003
Tail length ~ Elevation + (1 | Sex)	0.44	0.331	0.008
PDL (Dorsal) ~ Elevation + (1 | Sex)	6.17	<0.001	0.13

Appendix 4: Summary of linear mixed models testing the relationship of tarsus length, beak shape, and proportion of downy section (dorsal) with elevation binned into 4 categories, >1000, 1000-2000, 2000-3000, >3000 to control for spatial autocorrelation.

	Estimate	Standard Error	df	t value	P
Tarsus length ~ Elevation + (1 | Location)					
Intercept	16.76	0.22	9.2	76.79	<0.001
Elevation>3000 m	0.73	0.33	8.8	2.23	0.05
2000-3000 m	0.32	0.37	12.8	0.87	0.40
1000-2000 m	0.32	0.32	8.2	1.01	0.34
Beak Shape (BL/BH) ~ Elevation + (1 | Location)					
Intercept	1.48	0.03	7.5	51.15	<0.001
Elevation>3000 m	0.17	0.04	7.1	3.78	0.007
2000-3000 m	-0.01	0.05	12.2	-0.39	0.08
1000-2000 m	0.09	0.04	6.5	2.10	0.71
PDL (Dorsal) ~ Elevation + (1 | Location)					
Intercept	0.67	0.01	6.3	133.22	<0.001
Elevation>3000 m	0.02	0.01	5.2	2.87	0.03
2000-3000 m	-0.01	0.01	13.9	-0.55	0.59
1000-2000 m	-0.01	0.01	4.4	-0.37	0.73