

ALTITUDINAL VARIATION IN BOLIVIAN BIRDS

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It has long been recognized that there is frequently an increase in wing length in birds correlated with an increase in latitude or altitude. However, increase with altitude has not been studied quantitatively except for Rand's (Am. Mus. Nov. No. 890, 1936: 1-14) report on altitudinal variation among the birds of New Guinea. The present report embodies the results of a study of altitudinal variation among Bolivian birds, undertaken to determine if birds of the Andes show an increase in wing length to the same extent as those of New Guinea. That some increase in size takes place with altitude was noted long ago by Taczanowski (Ornith. du Perou, 1, 1884:59): "*Les formes des plaines sont plus petites que celles des montagnes. Comme ces differences ne changent pas la valeur specifique, le fait meme ne perd rien de son importance.*" But apparently no one has previously attempted to study the phenomenon quantitatively. I would like at this time to express my appreciation to Dr. A. L. Rand of the Chicago Natural History Museum for his constant help and encouragement.

The material used in the present study was a large collection of birds from the departments of Santa Cruz and Cochabamba, Bolivia, made by Francisco Steinbach during the 1930's. Tropical localities, up to 500 meters, were all within the vicinity of Buenavista, Santa Cruz. Subtropical and temperate localities, from 1600 to 3600 meters were all in the region to the north and east of the city of Cochabamba. Birds from the Puna zone come from a collection made by Steinbach in 1941 in the vicinity of Mount Sajama, Oruro, at altitudes from 3900 to 4200 meters.

The following criteria were used in selecting the species for study. A minimum of eight specimens was necessary, representing localities separated by at least 1000 meters of altitude, and of the eight specimens at least two were from each extreme of altitude. These were considered the minimum series that could be expected to indicate altitudinal variation; in most instances the series was much more extensive. Only one species, *Spinus magellanicus*, was included on the basis of a series of less than eight specimens; in this form the tropical race *santaecrucis* is characterized by smaller size, and the single available specimen amply demonstrated this difference. The wing measurements were made with the wing flattened.

Altogether, forty-two species representing sixteen families were available in sufficient series and with sufficient altitudinal range to be studied. In thirty of these the same currently recognized subspecies occupies the whole vertical range of the species; in each of the other twelve, two subspecies are included. Of the forty-two species, nineteen, or forty-five per cent, showed an increase in wing length with increase in altitude; twenty-two, or fifty-three per cent, showed no change; and one species, or two per cent, showed a slight decrease. Of most significance is the fact that out of twenty species which showed a wing variation with altitude, nineteen, or ninety-five per cent, showed an increase and only one a decrease.

ALTITUDINAL SUBSPECIES

Of the twelve species in which there are two generally recognized subspecies, ten showed a significant increase in wing length in the form of higher altitude. In some of these wing length alone is sufficient to separate the two races, but in others it is only a supplementary character. In no instance are the two subspecies merely the ends of a gradual size cline; where the change is not abrupt and clearly marked, there are color

characters which differentiate the two forms. The ten species showing an increase in wing length (with the altitudinally lower race listed first) are:

Aratinga acuticaudata acuticaudata and *neumanni* (parrot)
Pyrrhura molinae restricta and *molinae* (parrot)
Brotogeris versicolurus chiriri and *behni* (parrot)
Colaptes rupicola rupicola and *puna* (flicker)
Asthenes d'orbignyi d'orbignyi and *arequipae* (oven-bird)
Pitangus sulfuratus maximiliani and *bolivianus* (flycatcher)
Myiarchus tuberculifer tuberculifer and *atriceps* (flycatcher)
Cyclarhis gujanensis viridis and *dorsalis* (pepper shrike)
Spinus magellanicus santaecrucis and *bolivianus* (goldfinch)
Zonotrichia capensis hypoleuca and *pulacayensis* (sparrow)

The two species which failed to show altitudinal variation in size are:

Lepidocolaptes angustirostris bivittatus and *hellmayri* (woodhewer)
Compsothlypis pitiayumi pitiayumi and *melanogenys* (warbler)

An example of variation in which the smaller form inhabits the tropics and the larger the subtropics is the flycatcher *Pitangus sulfuratus*. The elevations are in meters.

	Elevation	Males	Females
<i>bolivianus</i>	2750	129, 130, 131, 133	125
	2500	135	-----
	1600	-----	122
<i>maximiliani</i>	400	115, 115, 117, 120, 122	108, 111

Similar variation is shown between temperate and Puna-zone birds, as demonstrated by the measurements of the oven-bird *Asthenes d'orbignyi*.

	Elevation	Males	Females
<i>arequipae</i>	4200	73, 76	69
	3900	74, 74, 76, 76, 78, 78, 79	71, 71, 72, 74
<i>d'orbignyi</i>	3800	63	-----
	3300	67, 67, 67, 71	66, 69
	2700	66, 67, 68, 68, 69, 70, 70	68
	2500	61, 63, 64, 64, 65, 66	62, 65, 66, 68, 68

Except for the single female of *A. d. arequipae*, there is no overlap in measurements between these samples of the races of either *Pitangus* or *Asthenes*, and they could be separated on size alone. In other species, there is some overlap in wing lengths, but color characters permit the separation of subspecies. An example of this type of variation is the parrot *Pyrrhura molinae*. No females of *restricta* were available.

	Elevation	Males
<i>molinae</i>	2800	143, 147
	2500	131, 138
	2000	129, 140, 140
	1500	129, 134
<i>restricta</i>	500	126, 137

ALTITUDINAL VARIATION WITHIN SUBSPECIES

In the thirty species studied in which only one recognized subspecies covers the entire altitudinal range of species, nine, or thirty per cent, showed an increase in wing size with altitude. Only one, or three per cent, showed a decrease.

The species showing an increase in wing length are:

<i>Chlorostilbon a. aureoventris</i> (hummingbird)	<i>Turdus amaurochalinus</i> (thrush)
<i>Phacellodomus s. striaticeps</i> (oven-bird)	<i>Vireo olivaceus chivi</i> (vireo)
<i>Furnarius rufus commersoni</i> (oven-bird)	<i>Thraupis sayaca obscura</i> (tanager)
<i>Cinclodes fuscus albiventris</i> (oven-bird)	<i>Sicalis flaveola pelzelni</i> (ground finch)
<i>Suiriri suiriri</i> (flycatcher)	

Species showing no change in wing length with altitude are:

<i>Leucippus chionogaster hypoleucus</i> (hummingbird)	<i>Diglossa c. carbonaria</i> (honey-creeper)
<i>Xiphorhynchus brevirostris ocellatus</i> (wood-hewer)	<i>Molothrus b. bonariensis</i> (cowbird)
<i>Upucerthia validirostris pallida</i> (oven-bird)	<i>Icterus cayanensis</i> (oriole)
<i>Cinclodes a. atacamensis</i> (oven-bird)	<i>Tanagra musica aureata</i> (tanager)
<i>Pyriglena leuconota hellmayri</i> (antbird)	<i>Tanagra chlorotica serrirostris</i> (tanager)
<i>Myrmeciza h. hemimelaena</i> (antbird)	<i>Tangara schrankii</i> (tanager)
<i>Pipra chloromeros</i> (manakin)	<i>Thraupis b. bonariensis</i> (tanager)
<i>Myiodynastes maculatus solitarius</i> (flycatcher)	<i>Ramphocelus carbo atrosericeus</i> (tanager)
<i>Serpophaga munda</i> (flycatcher)	<i>Tachyphonus l. luctuosus</i> (tanager)
<i>Diglossa baritula sittioides</i> (honey-creeper)	<i>Catamenia a. analis</i> (seed-eater)

The single species which shows a decrease in size is *Habia rubica amabilis* (tanager).

The most striking example of increase is found in the flycatcher *Suiriri suiriri*:

<i>Suiriri suiriri</i> :	Elevation	Males	Females
	3100	82
	2500	75, 77, 77, 77, 81	76, 77, 80
	2150	77, 79, 79, 81, 83	74, 80, 80
	500	69, 70, 71, 74	70, 70, 72, 74, 74

Out of the seventeen birds from 2150 meters and above, only a single female overlaps the measurements of the tropical birds. However, a series of fifteen specimens from Tucuman, in northern Argentina, exhibits a range of wing measurements from 70-80, which is intermediate to the ranges shown by the two Bolivian samples. Without this intergradation it might be possible to separate a highland Bolivian race; but at present, it is evident that the two Bolivian populations are merely the ends of a U-shaped size cline. The smaller extreme of the cline is found in the Bolivian and Paraguayan chaco; it is connected by intergrading populations south through northern Argentina and then north along the edge of the Andes to the larger extreme in the highlands of eastern Bolivia.

A species which suggests a more gradual increase in wing size with increased altitude is *Vireo olivaceus chivi*:

Elevation	Males	Females
2700	70, 77	73
2500	71
2000	67, 68, 73, 73	69
1600	71, 71
500	67, 68	65, 65

The measurements of the single species that shows a decrease in wing size with increased altitude are given below. They are not entirely convincing, but since this is the only species that showed any decrease, the measurements are of interest. Only males were available.

<i>Habia rubica amabilis</i>	Elevation	Males
	2000	92, 93, 95, 95, 96, 96, 96
	400	93, 96, 96, 96, 98, 99, 100

Further series may well show that this decrease was merely due to sampling error. The importance of these measurements lies in the fact that they show the only decrease among the species examined, and if the difference in this case is not significant, then not one of the forty-two species examined showed a decrease in wing size with increased altitude.

DISCUSSION

It is interesting to compare Rand's (*op. cit.*) figures for the birds of New Guinea with those from Bolivia.

	<i>Bolivia</i>		<i>New Guinea</i>	
	Number	Per cent	Number	Per cent
Total species	42		69	
Increase	19	45	23	33
No change	22	53	45	66
Decrease	1	2	1	1
Species with representative subspecies	12		9	
Increase	10	83	8	89
No change	2	17	1	11
Species with a single subspecies	30		60	
Increase	9	30	15	25
No change	20	67	44	73
Decrease	1	3	1	2

The figures for Bolivia and New Guinea show remarkably close agreement and amply demonstrate that the same response to altitude is shown by the avifaunas of the two regions. Although one-third more of the Bolivian birds studied show an increase in wing length than the New Guinea birds, 45 per cent as against 33 per cent, it is doubtful that this difference is particularly significant, since the species studied represent only small parts of their respective faunas and they were selected solely on the basis of their abundance in collections.

Of most significance is the fact that in the two dissimilar avifaunas inhabiting the two most distinct zoogeographical regions, the Australasian and the Neotropical, between a third and a half of the species studied showed an increase in wing length with altitude and only a single species in each group showed a decrease. These similarities greatly outweigh the differences in percentages and demonstrate that this response to increased altitude is not restricted to a given region or group of birds, but is found wherever the appropriate conditions exist.

The causes of increase in wing size are not readily apparent. It is often stated that this increase is evidence for Bergmann's rule, that animals increase in size with an increase in altitude and latitude. This increase is believed to be a response to the lower temperatures at higher altitudes and latitudes, and is based on the principle that a larger body is more efficient at lower temperatures because of its proportionately smaller radiating surface. This principle, however, can not be applied directly to wing length, because that part of the wing that is measured is primarily dead, non-radiating, tissue. The increase in wing size may eventually be shown to be a reflection of a general increase in body size, but there are at present no data on the body weights of Andean birds which could be used to determine this.

Chicago Natural History Museum, Chicago, Illinois, January 9, 1950.