Ecological effects on morphometric development of the Indian Eagle Owl *Bubo bengalensis*

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Abstract: Univariate analysis based on logistic growth curve fitting and multivariate analysis using principle component analysis (PCA) were used to analyze complex patterns and correlations in morphometric data from 16 individuals of the Indian Eagle Owl *Bubo bengalensis* from the Deccan Plateau. Wing chord length, tarsus length, claw length, beak length, tail length and weight were measured from hatching until fledging (1-58 days old) . A logistic growth curve showed a good fit for all characters. Different characters showed different growth patterns according to their function in the developing nestling. PCA analysis revealed that different morphological characters are loosely coupled together during growth, and this could be attributed to the behavioural ecology of nestlings. By comparing the patterns in our data with data published from southern India, we also show that there is plasticity in the development in these geographically isolated populations.

Keywords: *Bubo bengalensis*, development, morphometry, principle component analysis

INTRODUCTION

Growth rates are subject to selection based on the ecological and environmental factors. Interspecific variations in growth rates are often attributed to a trade-off between growth and yield rate in terms of biomass (Ricklefs 1979; Urban 2007). Fast-growing organisms spend more energy per unit time and thus contribute to less biomass or offspring size; however, they are vulnerable to predators for shorter periods. On the other hand, slow-growing organisms require less energy per unit time and thereby permit larger family size; however, they are more prone to predation. Even within a particular species, there could be different growth patterns, and these could be related to geographical locations (Caley & Schwarzkopf 2004), nutritional stress (Negro et al. 1994) and other environmental factors (Ricklefs 1979; King & Hubbard 1981). It has been previously observed that within the same individual, different body parts have different rate of growth (Springer 1979; Bortolotti 1984; Kristan et al. 1996; Nagarajan et al. 2002; Penteriani et al. 2005) and this is often attributed to the compromise between allocation of tissue to embryonic and mature functions (Ricklefs 1979). There are population variations in growth patterns, and different body parts also differ in their growth rates. This fact suggests that within the same species, growth patterns of different body parts in different populations can differ. This plasticity in the development is gaining increased attention (Yearsley et al. 2004), as it can shed light on the ecology of growth and help in understanding stressors in the conservation of threatened species.

Studies on the development of nestlings, their ecological interpretations and plasticity in development are relatively rare for Indian birds. In the current study we have focused on these aspects of development in the Indian Eagle Owl *Bubo bengalensis* (Franklin), until recently considered a subspecies of the Eurasian Eagle Owl *Bubo bubo* (Linnaeus) but now recognized as a species in its own right (Wink & Heidrich 1999; Penhallurick 2003). The distribution of the Indian Eagle Owl is restricted to outer hills of the western Himalayas to about 1500m, and rarely up to 2400m altitude, and extends from western and central Nepal to the entire Indian peninsula (Ali & Ripley 1969; Pande et al. 2003). Detailed information is available concering feeding behaviour (Ramanujam 2006), intimidating behaviour in nestlings (Ramanujam 2003a) and adults (Ramanujam 2004), calling behaviour (Ramanujam 2003b) and other acoustic and visual traits (Ramanujam 2007). However, a detailed account of nestling development is not available, although some preliminary observations on nesting (Eates 1937), parental care (Dharmakukarsinhji 1940) and development of the young (Ramanujam & Murugavel 2009) do exist.

In this study we have undertaken a detailed quantitative analysis of nestling development from hatching to fledging of Indian Eagle Owls from the Deccan Plateau of India. We have tried to correlate the patterns in development of different body parts with the ecology of the organism. We have also compared the patterns in development observed in our study with those observed in the study by Ramanujam & Murugavel (2009) to better understand the plasticity in development of *B. bengalensis* in western and southern Indian populations.

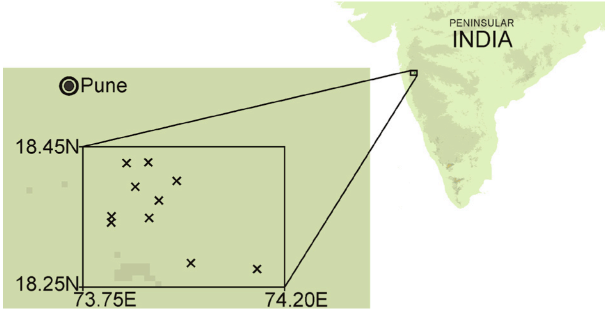

Figure 1. Point locality map for the 10 nests used for this study from western Maharashtra, India. Nest sites are depicted by cross.

METHODS

We studied 10 nests south of Pune (Fig. 1). Morphometry of 16 nestlings from hatching till fledging at 58 days was recorded, with data entered serially for each nestling identified by a numbered aluminium ring placed on the tarsus. At around 25 days of age nestlings leave the nest even when unable to fly, but despite roosting away from the nest they remain dependent on their parents for food. Thus it was not possible to get data from all 16 individuals, and as a result the sample size decreased after 33 days of age (Table 1) and a total of 319 measurements were available for each of the six characters, namely, wing chord length (carpal joint to the tip of the longest primary with the wing in neutral position), tarsus length (ankle joint to the attachment of toes where measurements were taken using flexion at proximal and distal joints), tail length (from the root of tail to the tip by flexing the tail upwards), beak length (the exposed part of the culmen from the cere to the tip), claw length (middle claw from insertion to tip) and body mass. We used Vernier calipers (least count 0.001mm), wing-stop and tail rulers (least count 0.1mm) for measurements and Pesola spring scales (least count 0.1g) to determine the body mass. Body mass was taken at sunset, allowing the Indian Eagle Owl forages at dusk or at night, this assured an empty stomach, which minimized the effect of meals. This also caused minimal disturbance to the nestling and assured uniformity in methodology.

To each biometric character we fitted a logistic model to understand its growth pattern and growth rate (Ricklefs 1979). The logistic equation is:

$$\text{Character value} = \frac{a}{1 + b \cdot \exp(-c \cdot \text{Age})}$$

Where a, b and c are positive constants. Constant a is the maximum possible value of the character, constant b is the delay in growth associated with the lag phase and constant c is the growth rate. The goodness of fit was determined by coefficient of determination, R^2.

Univariate analysis based on the logistic regression was capable of depicting the growth pattern in a given character. However, to understand the simultaneous development of different characters we used multivariate technique called Principle Component Analysis (PCA). PCA is a statistical technique that reduces the dimensionality of the multivariate data while retaining most of the variation in the data set. It can be used as an effective method to understand the structure in the data and relationships between various variables. To account for the unit and scale differences between different morphological characters we used PCA on the correlation matrix of the variables. We performed Bartlett's sphericity test with the null hypothesis that there is no correlation significantly different from zero between the variables and alternative hypothesis that at least one of the correlations between the variables is significantly different from zero (Harris 2001). Correlation biplot was plotted to visualize PCA results (Legendre & Legendre 1998). All statistical analysis were performed in Statistica 10® and figures were prepared in Microsoft EXCEL 2003® and CorelDraw X4®.

In the current study we have applied PCA in a different manner than what has been already suggested. Research focusing on the evolution of ontogenic patterns and understanding the allometric relationships in growth have often used modified PCA using covariance matrix for each age group separately so as to remove the effect of size and shape from the final analysis (Anderson 1963; Klingenberg 1996; Badyaev & Martin 2000). Even though these techniques are more robust to the scale differences they are mathematically rigorous and relatively difficult to interpret. On the other hand we have used the PCA technique for a different purpose. We have used PCA and the resulting biplot simply as a convenient way to understand the simultaneous effect of different variables on the growth pattern. To nullify the size and scale effect we have used PCA on the correlation matrix rather than the covariance matrix as suggested by Sommers (1986). An important reason why we do not use the alternate PCA method is that when comparing the growth patterns in our study with the previous study by Ramanujam & Murugavel (2009) we only have the information about the mean value of the character at a given age. As a result PCA method suggested by Anderson (1963), Klingenberg (1996) and Badyaev & Martin (2000) cannot be used for the data provided in Ramanujam & Murugavel (2009).

RESULTS AND DISCUSSION

Average value of various morphometric characters at different ages are given in Table 1. The plots of character value against age (Fig. 2) showed good fit to the logistic growth curve equation (all regressions were significant at $p < 0.001$). The parameters for the logistic growth model are given in Table 2, where we observe that the growth rates of different morphological characters increase in the ascending order from beak, tail, tarsus, wing, claw to weight. Growth patterns of Indian Eagle Owl are comparable to the growth patterns observed for other raptors (Springer 1979; Bortolotti 1984; Kristan et al. 1996; Nagarajan et al. 2002; Penteriani et al. 2005), but there are subtle differences which could be attributed to the ecology of Indian Eagle Owl.

Beak length was about 40% of its asymptotic value at hatching. This could be because of the possible role of the beak in breaking the egg shell. Beak underwent less lag phase and increased rapidly till 20 days of age and then its growth slowed down. At hatching, tarsus was about 20% of its asymptotic value. It underwent a lag phase for first four days after hatching and then it increased rapidly till about 30 days of age and then its growth slowed down. Claws were completely absent at birth but they appeared in two to four days. Their growth followed short lag till first five days then they grew very rapidly till 20 days of age after which their growth slowed down. Rapid growth and early maturation of above three characters, namely beak, tarsus and claw, reflects their early functioning in nestling development. As the ground dwelling nestlings desert the nest by walking out of the nest at about 25 days of age and roost away from the nest, the early development of tarsi is essential for its survival.

At hatching, wing length was about 6% of its asymptotic length and it underwent a long lag phase till about 25 days of age after which it grew rapidly till fledging. Tail was completely absent at hatching and it also went a long lag phase of growth for about first 30 days after which it grew rapidly till fledging. At hatching the weight was about 4% of the asymptotic weight. It underwent some lag phase in growth for first 11 days after which it grew rapidly till 30 days of age and then the growth rate decreased. For the weight, even though logistic growth curve shows a good fit, there is a sudden break in the growth pattern at about

Table 1. Average values of morphometric characters at different age of Indian Eagle Owl

Age (days)	n	Average value of the character (standard deviation)					
		Beak length (mm)	Tarsus length (mm)	Claw length (mm)	Wing length (mm)	Tail length (mm)	Weight (g)
1	16	13.98 (0.31)	19.03 (0.25)	0.00 (0.00)	19.41 (0.59)	0.00 (0.00)	33.41 (0.80)
2	16	14.36 (0.29)	19.46 (0.23)	2.00 (0.00)	20.31 (0.63)	1.78 (0.25)	38.59 (0.79)
3	16	14.93 (0.25)	20.87 (0.31)	4.86 (0.14)	21.34 (0.63)	3.78 (0.43)	56.21 (2.59)
5	16	15.33 (0.29)	22.96 (0.73)	5.86 (0.13)	26.25 (0.59)	5.72 (0.39)	129.69 (4.71)
6	16	15.49 (0.34)	26.43 (0.59)	6.40 (0.13)	34.56 (0.70)	7.72 (0.31)	184.63 (7.23)
7	16	20.06 (0.82)	27.51 (0.73)	6.89 (0.13)	37.75 (0.61)	9.81 (0.39)	207.00 (7.11)
8	16	20.59 (0.41)	29.59 (0.72)	7.19 (0.12)	38.91 (0.71)	10.59 (0.40)	217.69 (5.74)
9	16	21.76 (0.44)	33.46 (0.80)	7.45 (0.09)	41.34 (0.79)	11.09 (0.44)	232.06 (4.32)
10	16	22.14 (0.39)	36.35 (0.78)	8.43 (0.13)	44.25 (0.87)	11.91 (0.48)	245.38 (3.67)
12	16	22.99 (0.34)	39.49 (0.52)	8.93 (0.10)	46.09 (0.76)	14.97 (0.48)	269.38 (3.67)
15	16	24.57 (0.45)	50.14 (0.35)	9.95 (0.09)	51.59 (0.73)	20.81 (1.13)	290.06 (4.48)
18	16	29.36 (0.75)	53.26 (0.21)	10.95 (0.07)	69.16 (1.43)	44.81 (2.88)	348.88 (5.94)
20	16	30.61 (0.46)	57.74 (0.26)	13.91 (0.11)	90.47 (2.23)	55.38 (2.37)	533.69 (7.38)
23	16	31.06 (0.47)	63.81 (0.21)	14.91 (0.09)	105.50 (2.72)	62.19 (2.29)	617.25 (9.97)
25	16	31.41 (0.54)	66.23 (0.85)	15.45 (0.06)	127.75 (2.88)	65.81 (2.10)	649.25 (9.51)
28	16	31.96 (0.51)	67.81 (0.29)	15.69 (0.06)	189.63 (4.36)	70.00 (1.66)	702.63 (9.12)
30	16	33.20 (0.49)	72.89 (0.12)	16.68 (0.09)	210.13 (4.09)	80.63 (2.12)	724.75 (8.16)
33	16	34.74 (0.54)	74.91 (0.10)	17.56 (0.09)	234.50 (4.35)	93.25 (2.56)	730.94 (7.55)
37	11	37.28 (0.80)	77.86 (0.32)	17.94 (0.09)	240.18 (2.48)	107.36 (2.57)	745.09 (6.08)
43	7	38.03 (0.71)	82.66 (0.26)	18.26 (0.07)	280.00 (4.14)	144.71 (3.73)	771.57 (5.42)
50	7	38.24 (0.41)	86.00 (0.37)	18.41 (0.06)	310.14 (2.99)	164.86 (3.31)	828.57 (4.14)
58	6	38.27 (0.33)	87.03 (0.59)	18.55 (0.08)	339.83 (4.41)	182.00 (4.04)	888.17 (4.63)

20 days of age (Fig. 2f). This sudden decrease in the weight could be attributed to the stress faced by the nestling, which deserts the nest at this age, and roosts away from it.

PCA could depict the complex patterns of morphological changes with growth. PCA extracted only one significant factor, with eigenvalue more than unity, which explained 94.90% of the total variability in the data. Second factor had an eigenvalue 0.212 and it explained 3.56% of the total variation in the data. Together, the first two factors explained 98.46% of the total variability in the data. Bartlett's sphericity test suggested that the correlation between variables was significantly different from zero ($\chi^2 = 4905.778$, df = 15, $p < 0.0001$). Correlation biplot of PCA is given in Fig. 2. On the first PCA factor, the scores of observations increased with age indicating that the first factor depicted overall increase in the size. This was further supported by positive factor loading on F1 axis for all different morphological variables indicating all characters increased in size with age. On the second factor, however, both factor scores for observations and different variables showed positive and negative factor loading indicating that different morphological characters showed different growth patterns.

We could see that claw and beak growth were coupled together and their growth was rapid in early days of the development. Both the characters had short lag period and they grew rapidly till 20 to 25 days of age after which their growth rate decreased. Both characters are essential during the early development of the nestlings. While the beak is essential for breaking of the egg shell and during feeding, claws are essential for defence during nestling competition, thus coupled growth of these characters could be justified. Growth of tarsus and weight were loosely coupled together and they had slightly more lag phase than beak and claw. Tarsus and weight grew rapidly up to 25 to 30 days of age and then they grew very slowly. Coupled growth of tarsus and weight can be attributed to the

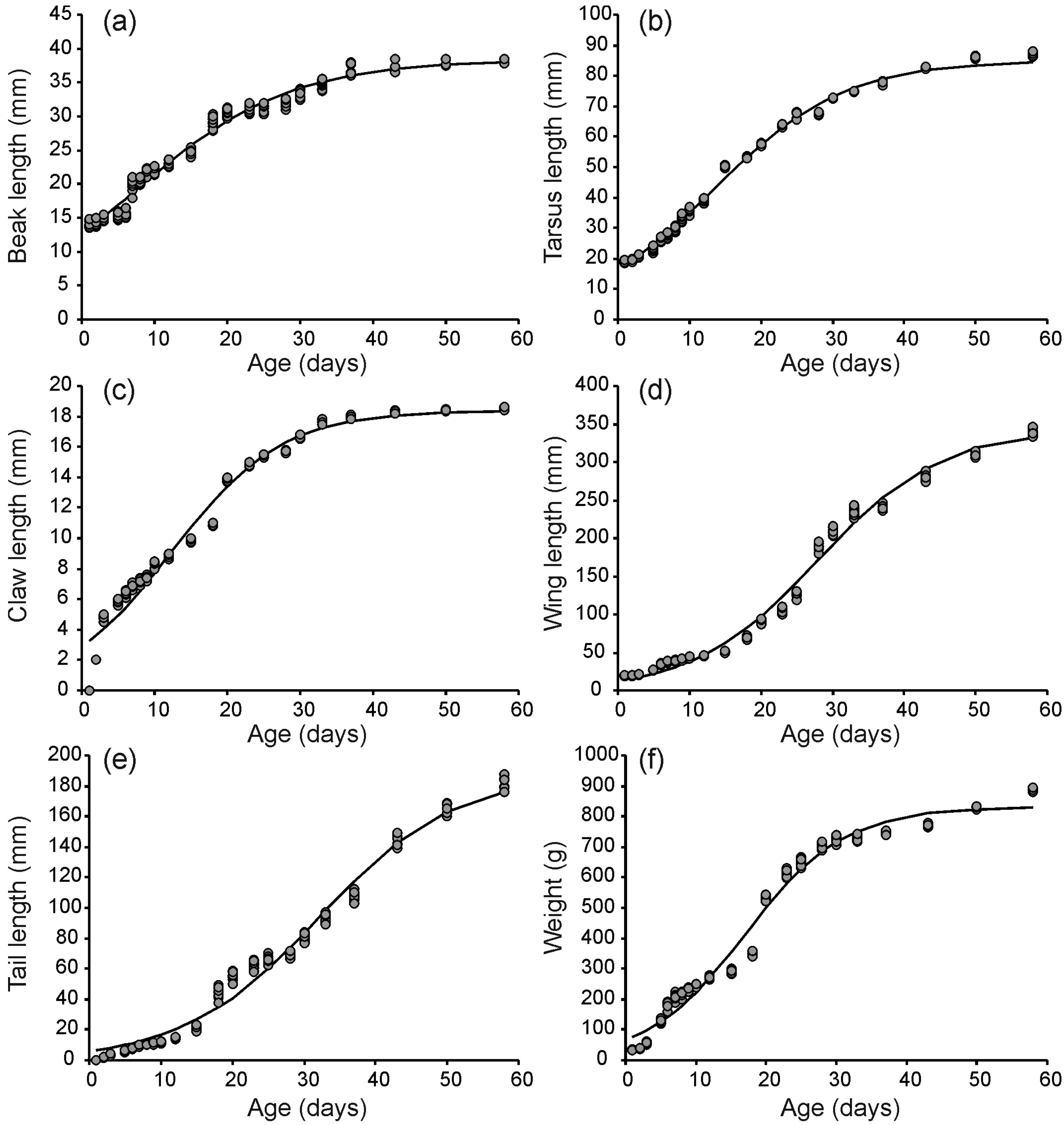

Figure 2. Logistic growth curve fitted to six different characters (a) beak length, (b) tarsus length, (c) claw length, (d) wing length, (e) tail length and (f) weight of Indian Eagle Owl. All regressions are significant at p < 0.001.

behavioural ecology of Indian Eagle Owl. The nest of Indian Eagle Owl is made on the ground and we observed that after 20 to 25 days of age the nestling leaves the nest by walking out. This explains why tarsus growth is rapid till 20 to 25 days of age. The coupling of increased weight with tarsus length perhaps enable the nestling to move from place to place by walking, because during this period nestlings cannot fly. During this phase, the nestling is still dependent on the parents for food and it is stressed. After a long period of lag, wing and tail growth starts. These two characters are coupled together and it is obvious because both the wing and tail are required for flight. The differential pattern in development of the tarsus and wing depicts an effective method of resource allocation for growth. Nestling Eagle Owl leaves the nest before it can fly.

Character	Parameters of logistic growth curve					
	Western Indian population (This study)			Southern Indian population (Ramanujam & Murugavel 2009)		
	*a**	*b*	*c*	*a*	*b*	*c*
Beak length	38.2727	2.0178	0.0944	42.9611	2.0259	0.0271
Tarsus length	85.0858	4.1909	0.1080	69.3262	2.9571	0.0683
Claw length	18.3599	5.2819	0.1333	-	-	-
Wing length	342.5934	25.5547	0.1161	355.3626	9.4882	0.0854
Tail length	187.6243	29.6824	0.1056	-	-	-
Weight	830.5012	11.3443	0.1419	986.2860	10.3488	0.1104

Table 2. Parameters of logistic growth model 'character value = *a*/[1+*b*·exp(-*c*·Age)]' fitted to the data in this study and the work of Ramanujam & Murugavel (2009).

Therefore, tarsus, which is required for walking, develops rapidly before wings within the first 25 days, while wing development shows a long lag phase of about 25 days after which it starts growing rapidly.

In the above arguments we focused on the ecological effects on differential growth patterns in different morphological characters of Indian Eagle Owl. Even though we justified our findings with the observed ecology of the bird it is likely that the same species inhabiting different environments may have different patterns in growth. To check out whether such plasticity exists in development of the Indian Eagle Owl we compared the findings of our study, a western Indian population of Indian Eagle Owl from Deccan plateau, with the study by Ramanujam & Murugavel (2009), a southern Indian population of Indian Eagle Owl from coastal region. This comparison, however, should be taken with caution because Ramanujam & Murugavel's (2009) study is preliminary and has a smaller sample size. Nevertheless, there are some interesting findings emerging from this comparison which can be explored further.

Comparison of logistic growth curve parameters for both the studies is given in Table 2. All the morphological characters had smaller growth rate and less lag phase in southern Indian population than the western Indian population. To understand whether the growth rates affect the size at fledging we compared different morphological characters using unpaired t test assuming unequal variance. Except for beak length, which was marginally larger in the western Indian population ($t = 13.1025$, $p = 0.0485$), no other character, namely tarsus, wing and weight, differed significantly between the two populations (tail was not measured in the southern population). The asymptotic weight of southern Indian population was higher than that of western Indian population (ca. 19% larger). This finding coupled with the fact that growth rate of weight was lesser in southern Indian population than in western Indian population, possibly reflects the growth rate versus yield tradeoff, which suggests that higher growth rate is coupled with lower yield and vice versa (Gadgil & Bossert 1970). This trade off is an outcome of natural selection acting on partitioning the resources either to increase growth rate or yield but not both (Gadgil & Bossert 1970). An interesting outcome of this comparison is that even though the growth rates of characters in southern Indian population were lower than the western Indian population, both achieved maturity at same time, and this could be attributed to the smaller lag phases in southern Indian population.

A more direct comparison can be done based on the PCA analysis of growth (Fig. 4). To keep minimum discrepancies in comparisons we considered only a subset of our data from 10 days onwards. For both populations, PCA was done on mean values of the characters as actual data was not available for Ramanujam & Murugavel (2009). Similar to the western Indian population, southern Indian population showed correlated growth among tarsus and weight. However, the pattern in growth for wing and beak was different. Unlike in the western Indian population, the beak length, in southern Indian population, increased till fledging, while wing grew along with tarsus and weight, with relatively shorter lag period than in the western Indian population. This has a significant contribution on the behavioural ecology of the nestling and explains the development plasticity in the two populations.

Behaviour of the nestling regarding the nest abandonment prior to gaining the ability of flight is

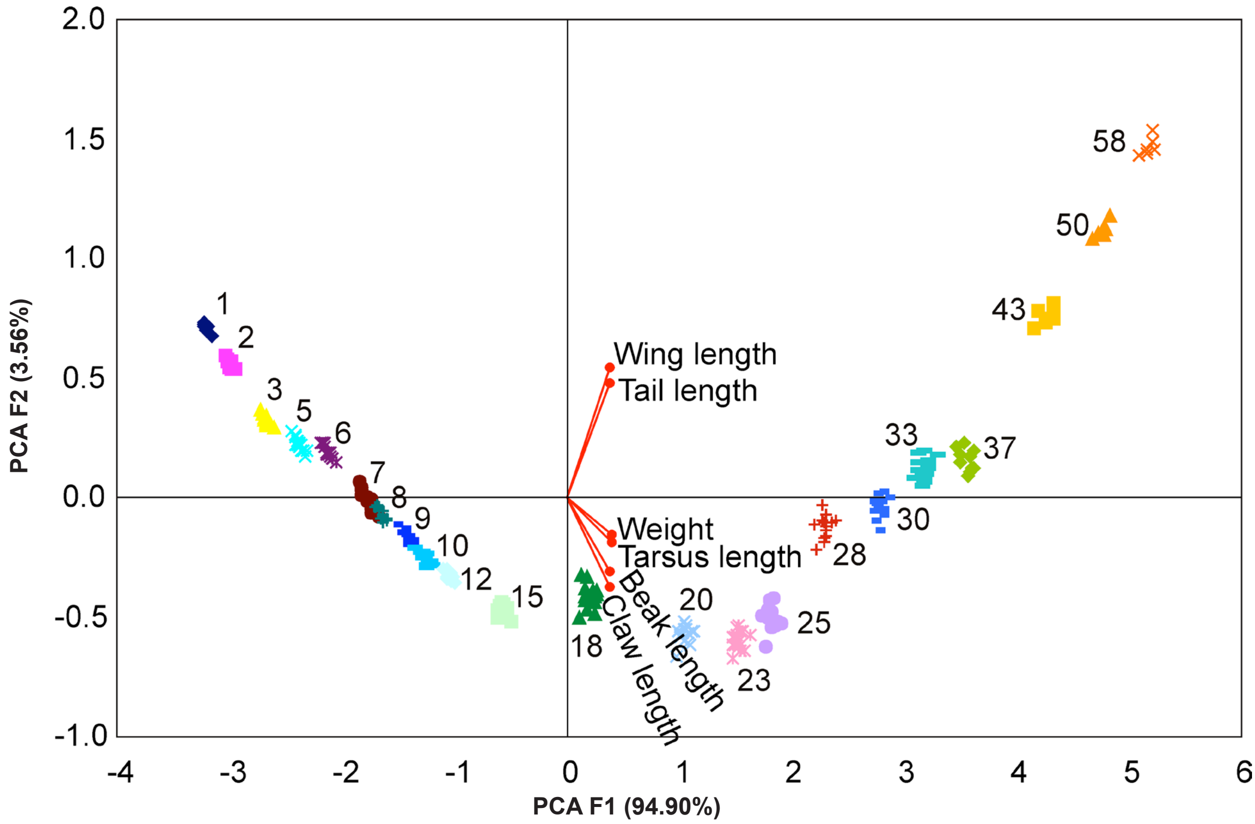

Figure 3. Principle Component Analysis (PCA) of developmental morphometry based on all six characters in our study of western Indian population of Indian Eagle Owl. Graph shows the biplot of eigenvectors, shown by red lines, and factor scores, shown by colored points. Numbers besides the factor scores gives the age of Indian Eagle Owl. Percentage in parenthesis is the variation explained by each PCA factor.

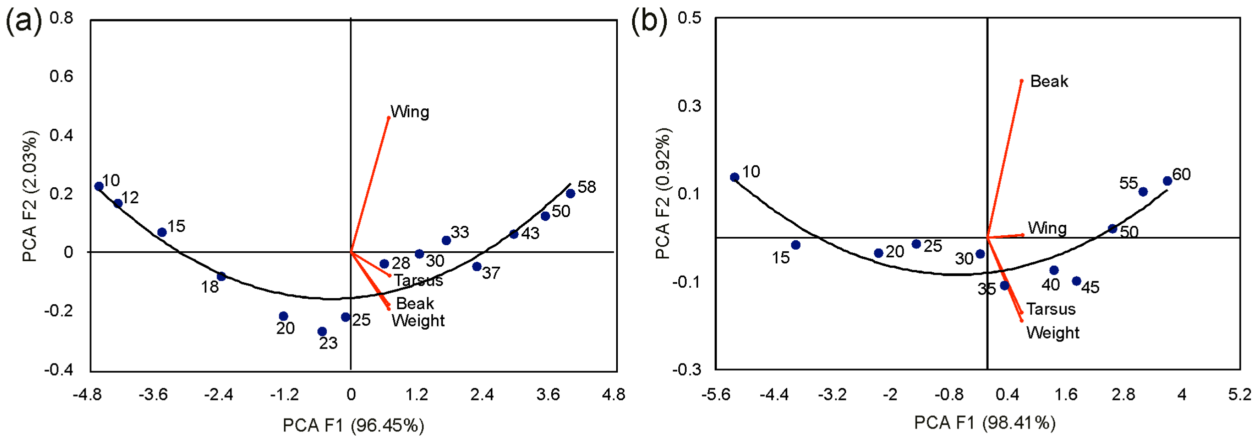

Figure 4. Comparison of growth patterns in (a) western Indian, based on this study, and (b) southern Indian, based on study by Ramanujam & Murugavel (2009), population of Indian Eagle Owl. PCA is performed for mean values of each character for four of them, namely wing chord length, weight, tarsus length and beak length, which were common to both the studies. Percentages in parenthesis are variation explained by each PCA factor. Solid black line is a best fit polynomial to the factor scores drawn just to eyeball the pattern in PCA.

an important stage in the life of several owl nestlings (Duncan 2003; Austing & Holt 1966). In the western Indian population, we observed that between 23 and 28 days from hatching the chicks abandon the nest and move a few meters away from it which could be possibly attributed to the adaptive strategy of the nestling to escape predation from ground predators and avoid the poor nest hygiene. Dharamkumarsinhaji's (1940) bewildering experience of mysterious disappearance of the Indian Eagle Owl chick around 23rd day in his observation from Saurashtra could be the same phenomenon which points out to the fact that the age at which the nestling deserts the nest is same. Surprisingly, in the southern Indian population, the nestlings leave the nest much later on 35 days of age (Ramanujam & Murugavel 2009). Furthermore, we observed that since the wing development in western Indian populations starts rapidly only at the age of 25 days, the nestling that deserts the nest at 25 days of age cannot fly at all. They fly only from the age of 58 days. This is also consistent with the observations made on Great Horned Owl *Bubo virginianus*, which leaves the nest around 21 days of age but can fly only at the age of 60 days (Austing & Holt 1966). Surprisingly, in the southern Indian population, as the lag phase of wing growth is less (Table 2), the nestling that deserts the nest around 35 days of age is capable of gliding (Ramanujam & Murugavel 2009). These differences between the western Indian and southern Indian populations reflect the plasticity in development of the Indian Eagle Owl.

Even though it is difficult to pinpoint the exact reasons for the differences in the growth patterns in western and southern Indian populations, habitat characteristics and food availability may be playing an important role. Ramanujam & Murugavel (2009) have stated that their study area is an environmental disaster with severe habitat degradation. On the contrary, our study area in the western India is relatively undisturbed with rocky areas, grasslands and agricultural fields that sustain high rodent populations, which is the preferred prey of the Indian Eagle Owl (Ramanujam 2006). Such constraint on the availability of energy to the nestling is considered as a major limiting factor for its growth (Ricklefs 1984).

In conclusion, in this study we have given a detailed quantitative account of growth patterns in different morphological characters of Indian Eagle Owl. We also tried to correlate the growth patterns with relevant ecological observations. We further showed that growth patterns in southern Indian and western Indian populations vary suggesting that there is plasticity in the development of this owl. However, our reasoning of ecological effects on growth is still limited because we have not considered other factors like predation, population size and density (Ricklefs 1984) that may have profound effects on growth and growth rate.

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