Integration and Modularity of Cranial and Postcranial Anatomy in Raptors

June Hohl, Shanta Hejmadi, Keith Barker

University of Minnesota-Twin Cities, Department of Ecology, Evolution and Behavior
University of Minnesota Undergraduate Research Opportunity Program (UROP)

Introduction

The study of integration and modularity of morphological traits offers a lens through which we evaluate how functional ecology has shaped the morphology of organisms. Birds, who show impressive variance in phenotypes, exemplify how different environments have impacted the form and function of individual species. Previous work has investigated skull integration and modularity in amphibians[1,2,3] archosaurs[7,8], and birds[4], but to date, no one has explored integration and modularity of cranial *and* postcranial anatomy in any of these groups.

Raptors are widespread, primarily carnivorous birds of prey in the orders Accipitriformes, Cathartiformes, and Falconiformes, and are highly diverse in size (Accipitriformes and Cathartiformes form a clade separate from Falconiformes). As apex predators and indicator species, they play a critical role in many ecosystem services[6,12], and give key insights into ecosystem health[11]. Raptors are also an excellent example of convergent evolution; these two clades show strikingly similar morphological and functional traits despite nearly 65 million years of independent evolutionary history[10]. One key difference between birds in these lineages is their different foraging styles. Accipitriformes generally use their strong feet and sharp claws to kill prey, Falconiformes tend to kill with their sharp beaks[9,14], and Cathartiformes are obligate scavengers. Their ecological importance, interesting evolutionary history, and functional differences make diurnal raptors an excellent system for studying integration and modularity in cranial and appendicular morphology.

Methods

Beak Data Collection and Processing

- Landmarked 3D rostral scans in Stratovan Checkpoint
- Performed Generalized Procrustes Analysis (GPA) to remove variation due to size, position, and orientation in R package *geomorph*[5].
- 93% sampling of all diurnal raptor species (309/333 species).
- Landmarks converted into an array for analysis, species without foot data were removed (306 final species).

Foot Data Collection and Processing

- Obtained linear measurements[13] of digits and claws; GPA was performed to remove variation due to size, position, and orientation.
- Measurements were converted to an array for analysis, species without beak data were removed. 306 total species were analyzed.

Analysis

- 3 datasets were created: all species, Falconiformes only, and Accipitriformes/Cathartiformes only.
- Integration and Modularity tests were performed in R package *geomorph*[5] for each dataset.

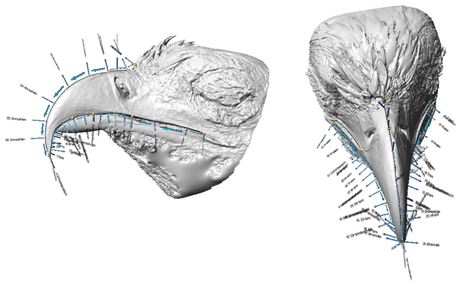
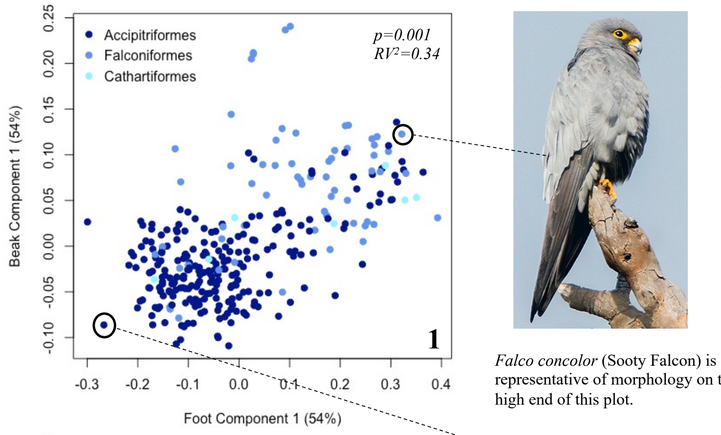


Figure 1: *Sagittarius serpentarius* (Secretarybird) landmarked in Stratovan Checkpoint.

Results: Integration and Modularity Tests



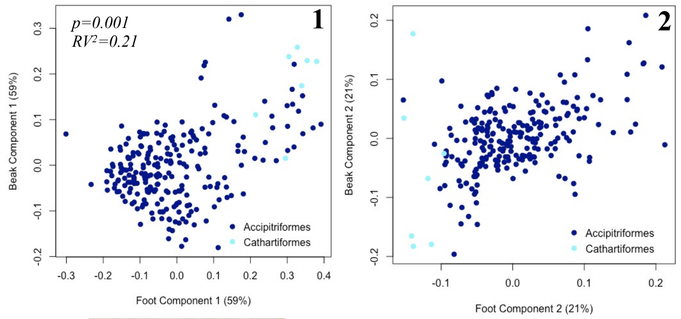
Falco concolor (Sooty Falcon) is representative of morphology on the high end of this plot.

Aquila africana (Cassin's Hawk-Eagle) is representative of morphology on the low end of this plot.

	P-Value	Covariance Ratio	Effect Size
All Species	0.001*	0.327	-27.868
Accipitriformes /Cathartiformes	0.001*	0.400	-14.959
Falconiformes	0.001*	0.2174	-14.3561

Table 1: Results of modularity tests. P-value, covariance ratio, and effect size shown for all species combined, Accipitriformes/Cathartiformes only, and Falconiformes only. * indicates significance of a p-value (P<0.05).

Figure 2: Results of integration tests on all species. Scores from beak and foot components are plotted. RV^2, P-values, and amount of covariance explained by each plot are shown.



Falco newtoni (Malagasy Kestrel) is a significant outlier in both plots 3 and 4. Closely related taxa *Falco alopex, Falco rupicolus, Falco rupicolpides, and Falco araeus* are also included in this outlying group.

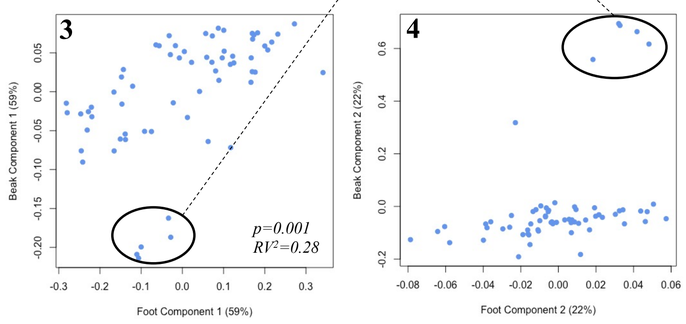


Figure 3: Results of integration tests on Falconiformes and Accipitriformes/Cathartiformes independently. Scores from beak and foot components are plotted. Plots 1 and 2 show distributions of Accipitriformes/Cathartiformes scores, plots 3 and 4 show distributions of Falconiformes scores. RV^2, P-values, and amount of covariance explained by each plot are shown. An example of an outlying species is also depicted.

Results

Integration

- In all datasets, low p-values ($p<0.05$) indicate that foot and beak morphologies are significantly integrated and therefore covary with each other.
- The somewhat low RV^2 values output from these analyses indicate that although significant, the integration between feet and beaks is somewhat weak.
- On the plots of all species and Accipitriformes/Cathartiformes only, a significant outlier is *Sagittarius serpentarius* (Secretarybird), pictured below (Figure 4).
- On the plots of all species and Falconiformes only, significant outliers are a handful of taxa in the genus *Falco* (Figure 3).

Modularity

- When grouped together, all species exhibited modularity with a relatively low covariance ratio, indicating that the beaks and feet of these birds are generally more correlated with themselves than each other.
- When analyzed alone, Accipitriformes/Cathartiformes and Falconiformes both exhibited significant modularity.

Figure 4: *Sagittarius serpentarius* (Secretarybird) with a fresh kill.

Discussion and Conclusions

- For all raptors, body parts involved in prey capture change predictably with one another.
- The integrated morphology in both clades suggests that there is some constraint on the evolution of these traits.
- However, modularity (strong within-module integration) of these two sets of traits suggests some degree of evolutionary independence of beak shape and foot shape.

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