Morphological Integration and Natural Selection in the Postcranium of Wild Verreaux's Sifaka (*Propithecus verreauxi verreauxi*)

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ABSTRACT   Morphological integration manifests as strong phenotypic covariation among interacting traits. In this study, a graph-theory approach is used to analyze patterns of morphological integration in a wild population of Verreaux's sifaka (*Propithecus verreauxi verreauxi*). The motivation for this study is to determine the relative roles of development versus function in shaping patterns of morphological integration in the sifaka postcranium. A developmental and a functional hypothesis of integration are compared with the observed pattern of integration and the fit of these hypotheses is assessed using information theoretic statistics. Correlational selection is also estimated on limb elements. Information theoretic statistics indicate that the developmental hypothesis fits the observed pattern of integration slightly better than the functional hypothesis. Only two pairs of traits experience correlational selection but neither of the traits within each pair are morphologically integrated. The observed pattern of integration contains several trait–trait associations that are specified by both the functional and developmental hypotheses. These results likely reflect the nested covariation structure in which a novel locomotor mode, vertical clinging and leaping, is derived from a primitive quadrupedal morphotype. Am J Phys Anthropol 136:204–213, 2008. © 2008 Wiley-Liss, Inc.

Morphological integration is the phenotypic association of particular sets of traits to the exclusion of other sets of traits (Olson and Miller, 1958; Cheverud, 1982; Magwene, 2001). Theory suggests that previously separate traits become interdependent because of either shared functional or shared developmental factors. Thus, over evolutionary time, traits that contribute to a common function or are specified by a common biochemical or epigenetic pathway, come to be coinherited and/or coselected (Lande, 1980; Cheverud, 1982, 1984; also see Felsenstein, 1988). The basic population genetic mechanisms that produce integration are thought to be correlational selection and pleiotropic mutations. Selection for two or more traits to function or develop in concert will favor the suppression of pleiotropic mutations among traits that do not interact with the functional/developmental set of traits, while promoting pleiotropic mutations among interacting traits. The resulting trait modules will evolve quasi-independently from other modules (Cheverud, 1996; Wagner, 1996; Wagner and Altenberg, 1996).

While the terms "function" and "development" are invariably used in the same breath, so to speak, when talking about morphological integration (e.g., Olson and Miller, 1958; Cheverud, 1982), traditionally these two topics have spawned alternative perspectives on the evolution of animal diversity (Amundson, 2007). A functional perspective on trait form is taken by population geneticists, functional anatomists, and behavioral ecologists. This group takes its influence from the modern synthesis and emphasizes the power of natural selection to modify a trait to serve a particular function. On the other hand, a structuralist perspective emphasizes the role of ontogeny and how architectural and epigenetic factors specify and constrain the final form of the trait. Thus, when phenotypically integrated traits are attrib-

uted to "... a common biological property related to function and/or development" (Olson and Miller, 1958, p. 1), it remains an open question as to whether the signature of trait covariation is due to functional *or* developmental factors (e.g., Young and Badyaev, 2006). This is a complex question, but it is hypothesized that developmental modules are evolved to match functional modules (Frazzetta, 1975; Riedl, 1978; Wagner and Altenberg, 1996; but see Raff, 1996). This idea has recently been described as the "matching hypothesis" (Breuker et al., 2007). It will require myriad experimental and comparative studies to test predictions of the matching hypothesis, but an immediate avenue to discovery is to a priori specify patterns of developmental and functional integration among the same set of traits within a species and compare these hypothetical patterns to the observed pattern.

Primates have served as a model system for investigating morphological integration since the pioneering study of Owl monkey teeth by Olson and Miller (1958). Since that time, different aspects of primate anatomy have been probed for their covariation structure (e.g., Cheverud, 1982, 1995; Marroig and Cheverud, 2001;

Marroig et al., 2004; Young, 2006; reviewed in Ackermann and Cheverud, 2004). As Young notes (2004), most of these studies focused on the primate skull because of the abundance of these materials in museum collections and the ability to a priori delineate functional and developmental modules. Far fewer studies have been conducted on the postcranium (see Hallgrimsson et al., 2002; Young, 2004, 2006; Young and Hallgrimsson, 2005). Recent synopses of limb development and evolution (e.g., Schwabe et al., 1998; Ruvinsky and Gibson-Brown, 2000; Chiu and Hamrick, 2002; Wilkins, 2002; Niswander, 2003) coupled with continuing studies of primate biomechanics and positional behavior make it possible to specify hypotheses about limb element covariation structure from developmental and functional perspectives.

Verreaux's sifaka, like other vertical clinging and leaping (VCL) indriids, are ideal animals to study morphological integration. Historically, the positional mode of VCL was viewed as the primitive locomotor and postural mode for primates (Napier and Walker, 1967). Studies conducted subsequent to Napier and Walker's proposal made two major points: 1) VCL was a very broad positional category and it covered up major myological and osteological differences among prosimian taxa and 2) VCL, as it concerns Malagasy strepsirhines, is more likely a specialized positional mode that derives from a more generalized quadrupedal morphotype (e.g., Cartmill, 1972; Stern and Oxnard, 1973; Godfrey, 1988; Anemone, 1990). In this regard, the pattern of VCL evidenced by the Indriidae is qualitatively and quantitatively different from other strepsirhines and this pattern evolved from a primitive morphotype that emphasizes quadrupedalism rather than orthograde leaping (Gebo and Dagosto, 1988; Godfrey, 1988). Whatever the selective (and possibly other evolutionary) forces that led to the evolution of VCL in the indriids, it is clear that novel patterns of limb element covariation must have been coselected and coinherited to functionally contribute to this new mode of positional behavior. Such functional interactions, in turn, help build phenotypic and genetic correlations among traits that, over evolutionary time, lead to morphological integration. As functional interactions become developmentally "entrenched" (or fixed), this results in a hierachical pattern of integration and modularity (Riedl, 1978; Wagner, 1996).

In this study, I test hypothetical patterns of morphological integration among postcranial elements that correspond to developmental and functional hypotheses. The overall goal is to determine if the observed pattern of integration in the sifaka locomotor skeleton retains more of a functional "signature" versus developmental "signature" of integration. Specifically, I use the graph-theory approach introduced by Magwene (2001) and test hypotheses about trait integration based on biomechanical and developmental models of limb development and function. I also estimate selection coefficients acting on postcranial elements to test predictions concerning the magnitude and type of selection that is expected to act on integrated traits. The data come from continuously monitored population of wild Verreaux's sifaka (*Propithecus verreauxi verreauxi*, hereafter "sifaka") at Beza Mahafaly Reserve, southwest Madagascar. Given that VCL is a derived positional mode, I predict that the signature of phenotypic covariation will be more in line with a functional model of limb element covariation rather than the developmental model, which is likely shared among all primates. Further, I predict that patterns of correlational selection will only be evident in traits that manifest strong integration, and selection pressures will be stronger for the functional trait interactions rather than the developmental trait interactions.

METHODS
Establishing developmental and functional hypotheses

Hypotheses of morphological integration can be represented by conditional independence graphs consisting of vertices and edges (Magwene, 2001). Vertices correspond to variables in the model and edges represent associations among variables. Traits that are conditionally independent do not share an edge, whereas traits that are mutually informative, conditional on all other traits under consideration, share an edge. There are numerous mathematical techniques that allow one to analyze the informational content and statistical associations among traits using conditional independence graphs (Edwards, 2000; Magwene, 2001; also see Methods). Here, I develop two different a priori hypotheses about how limb elements are predicted to covary, and I represent them as conditional independence graphs.

The first hypothesis is based on the work of Hallgrimsson and colleagues (Hallgrimsson et al., 2002; Young and Hallgrimsson, 2005). Specifically, looking at several taxa, they show that the strongest covariation occurs among homologous elements in the fore and hind limbs (i.e., femur-humerus, tibia-radius, and metatarsal-metacarpal), and less covariation occurs among elements within a limb (e.g., humerus-radius, radius-metacarpal, and humerus-metcarpal) (Young and Hallgrimsson, 2005). Young and Hallgrimsson's findings are rooted in developmental genetics. The molecular basis of limb development involves genes that encode transcription factors and genes that encode signaling proteins (Ruvinsky and Gibson-Brown, 2000). Both types of genes are involved in coding the spatial location of limb elements. Of relevance here is the finding that many families of genes overlap in their specification of limb elements (they are spatially "collinear"). This suggests that sets of genes, for example the *Hox* 9-13 paralogs, sequentially specify the initial limb positions, and they may also be involved in more "downstream" processes of morphogenesis (Ruvinsky and Gibson-Brown, 2000; Wilkins, 2002), implying a common genetic basis for fore and hindlimb bones. On the other hand, one family of transcription factors, the T-box genes, has members that specify either forelimb patterning (*Tbx*5) or hindlimb patterning (*Tbx*4) exclusively. To the extent that these gene products do not attenuate along the biochemical pathway corresponding to the proximal-distal limb axis, it is assumed that all within-limb elements (e.g., femur-tibia-foot or humerus-radius-hand) should exhibit positive covariation. In principle, there could be cases in which negative covariation is evident, (e.g., humerus length negatively covaries with metacarpal length, Young and Hallgrimsson, 2005) but the hypothesis developed here assumes otherwise. This is not to say that the elements must grow at the same rate—they do not (e.g., Gregory, 1912; Schultz, 1926; Davenport, 1933)—only that the overall pattern of phenotypic covariation will be positive among limb elements in the fore and hindlimb. Young and Hallgrimsson (2005) documented that the pattern of between-limb/within-limb covariation is found in several
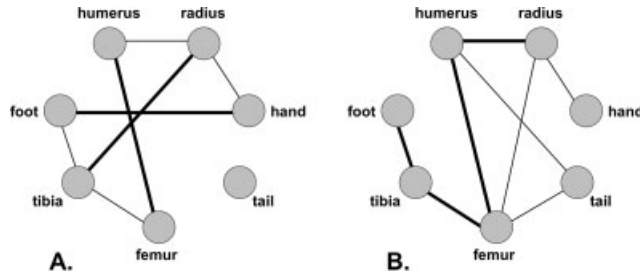
Fig. 1. Graphical models of the developmental hypothesis (**A**) and the functional hypothesis (**B**). Lines show hypothesized patterns of integration (or covariation) among variables. Thickness of lines gives predicted strength of covariation among variables (strong versus moderate) as discussed in the text.

mammalian taxa and reflects the consequences of conserved genetic pathways discussed above. Given that this pattern of limb development is likely primitive for primates, it is hypothesized that the developmental signal of limb element integration will manifest as strong covariation of homologous elements of the fore and hindlimb (humerus-femur, radius-tibia, and hand-foot), and relatively weaker covariation of elements within the forelimb and within the hindlimb. A graphic model reflecting the developmental hypothesis of integration is shown in Figure 1.

The second hypothesis of integration is derived from kinematic and biomechanical information as it pertains to sifaka locomotion. Sifaka are committed arboreal leapers and they exhibit numerous myological and osteological adaptations in their postcranium that facilitate orthograde, thigh-powered leaps from tree trunk to tree trunk (Demes et al., 1996, 1998; Gebo and Dagosto, 1988). Leaping, particularly orthograde leaping from vertical tree trunks, is a major locomotor mode of sifaka and accounts for over 50% of all locomotor behaviors in sifaka (Lawler, 2006). On the basis of kinematic data of sifaka leaping, a functional model of integration is proposed that emphasizes thigh-powered vertical leaps between substrates. This functional hypothesis does not take into account other locomotor or postural behaviors that most likely influence patterns of covariation (e.g., grasping, bipedal galloping, vertical clinging; a study examining multiple functional hypotheses will be presented elsewhere, Wunderlich and Lawler, submitted.). Demes et al., (1996) have documented the kinematics of trunk and limb elements during orthograde leaping. An orthograde leap starts with the animal clinging ventrally to the tree trunk with its backside facing the opposite "target" tree trunk. Looking over its shoulder, the animal pushes off the substrate at the deep cleft between the big toe and lateral toes. The majority of the propulsive force comes from the quadriceps and gluteal muscles, which cause the hip and knee to extend and push away from the trunk (Demes et al., 1996, 1998). The animal uses its arms and tail to rotate the body in mid air, and uses the deep cleft between its big toe and lateral digits to "catch" the incoming substrate.

Given the above, to leap safely between vertical substrates, sifaka need to do two things: 1) generate enough muscle force to propel the animal between tree trunks and 2) rotate in mid-air and land feet-first (Demes et al., 1996; Lawler, 2006). The length of the propulsive limbs are a major factor that influences jump distance (Biewener, 2003); for sifaka, this means the lengths of the

tibia and femur (and also foot; Demes et al., 1996) should coevolve to maximize jumping distance and jumping efficiency. In particular, having a long tibia and a long femur (and large angular excursions at the hip joint) increases the duration of time over which the sifaka can accelerate and thus produce momentum for the leap. In leaping animals, the distal joints such as the knee must move a larger proportion of body mass during extension relative to proximal joints such as the hip. Because muscle cross-sectional area (and therefore force) relative to body mass, decreases with increasing body mass, muscle forces at the knee are relatively weaker in heavier animals. To counter this, heavier animals often have relatively shorter tibias, and hence shorter load-arm lengths, to maintain mechanical similarity with smaller animals (Demes and Gunther, 1989). This is supported by the crural index in Verreaux's sifaka (87.5 in adult animals, Lawler, unpublished data) (see Table 2). This likely reflects the demands of maintaining a high mechanical advantage at the knee joint, while also maintaining a long hindlimb length. The femur and tibia, therefore, should positively covary (and possibly the foot, given it can contribute to push-off leverage and aids in landing; Demes et al., 1996; Lawler, 2006) to produce enough acceleration to leap distances of 3 m or more (Lawler, unpublished data).

Additionally, sifaka sometimes use their arms to help increase the push-off force as well as to rotate the body at take off and prior to landing (Demes et al., 1996), suggesting positive covariation between the humerus and radius. During take-off, one or both arms are coordinated with hindlimb extension to assist with push-off as well as trunk rotation around a vertical axis. During the mid-air phase of the leap, the tail is swung upward and the arms are swung forward and down as the hindlimbs are brought forward to receive the incoming substrate (Dunbar, 1988; Demes et al., 1996). Thus whole-body rotation prior to landing involves simultaneous flexion of the hip-joint, rotation of the shoulder joint, and dorsiflexion of the tail (see Fig. 1 in Demes et al., 1996). This suggests that the femur, humerus-radius, and tail should be functionally integrated to coordinate overall body position during the mid-air phase of the leap. Specifically, positive covariation among arm and leg elements (particularly the long bones) should be evident because the arms help rotate the body and maintain body positioning during the in-air phase of a leap. Under this scenario, increases in femur length (which contributes to propulsion as well as rotation prior to landing) should be "offset" by increases in the humerus and radius (plus the tail) length, thus increasing the moment of inertia of the arm and tail (assuming similar mass distribution within segments), thereby positively influencing initial rotation and counterbalancing angular momentum in order to facilitate hindlimb positioning prior to landing (see Demes et al., 1996).

One final point is worth mentioning. Rice (2000) has shown that in cases of three of more characters where selection acts on the sum of these characters (e.g., three different skull bones all contribute to covering the brain case), it is possible to have selection for "deintegration"; this means that selection "doesn't care" about the independent variation in each particular character (e.g., the size or shape of each skull bone) so long as they maintain a constant sum that produces a positive fitness effect. The functional integration model proposed above is predicated on functional interactions and does not rely

TABLE 1. Assumptions of the developmental and functional hypotheses

The developmental hypothesis assumes:
   Hox 9-13 paralogs specify homologous elements of the fore and hindlimb (e.g., humerus-femur, radius-tibia, and hand-foot)
   Tbx 4 and Tbx 5 specify within-limb elements of the fore and hindlimb
The functional hypothesis assumes:
   Lengths of femur, tibia, and foot are major contributors to propulsion
   Lengths of humerus, radius, and hand contribute to push-off phase of leap
   Lengths of arm elements and tail contribute to body rotation during in-air phase
   Tail, humerus, radius are integrated with flexion of hip joint (via femur) to coordinate body rotation

TABLE 2. Description of the variables and their mean and standard deviation (n = 107)

Variable	Description	Mean (cm)	Standard deviation
Humerus	Acromion process on scapula to lateral epicondyle on humerus	9.64	0.65
Radius	Lateral epicondyle on humerus to radial styloid on radius	10.06	0.55
Hand	Base of palm to tip of longest digit	9.19	0.50
Femur	Greater trochanter on femur to lateral epicondyle of tibia	16.96	0.93
Tibia	Lateral epicondyle of tibia to lateral malleolus of fibula	14.91	0.76
Foot	Back of calcaneus to tip of longest digit	12.38	0.64
Tail	Base of tail at spine to tip of distal caudal vertebrae	48.06	3.06

on the summed fitness effect of phenotypic traits, as in Rice's model. A graphical model reflecting the functional hypothesis of integration is shown in Figure 1 and Table 1 provides a list of the assumptions made by both the developmental and functional hypotheses.

Estimation procedures

In this study, patterns of morphological integration are investigated using measurements collected on 107 adult animals. Since sifaka long-bone growth ends at age 5 (Richard et al., 2002) and sexual maturity begins around age 3 for females and age 4–5 for males (Brockman, 1999; Lawler et al., 2003), only animals of age 5 or above were included in the analysis. Seven linear measurements are examined for their pattern of covariation: femur length, tibia length, foot length, humerus length, radius length, hand length and tail length. When the same animal was recaptured on more than one occasion, measurements from the latest capture occasion were used (i.e., measurements corresponding to an older animal). Table 2 provides summary statistics for these measurements. All measurements were taken on the left side of each animal. Sifaka males and females at Beza Mahafaly do not exhibit sexual dimorphism in body mass (Richard et al., 2000), so allometric differences among sexes are not a confounding factor. Measurements were not size corrected following the recommendations of Magwene (2001), since the elements of the partial correlation matrix are conditioned on every other variable, and conditioning on all other variables implicitly estimates size (also see Whitaker, 1990).

Conditional independence graphs were constructed for each hypothesis of integration (see Fig. 1) based on the developmental and functional considerations. These graphs (interchangeably referred to as models or hypotheses) will be compared with the observed pattern of integration found in the sifaka postcranium. To determine the observed pattern of integration, the partial correlation matrix was calculated from the data; entries that are zero in this partial correlation matrix are conditionally independent and are not connected by an edge in the conditional independence graph. The partial correlation matrix implies a conditional independence matrix,

which is a symbolic matrix where zeros reflect weak partial correlations and asterisks denote strong partial correlations (Magwene, 2001). Edge exclusion deviance was calculated for each edge to ascertain the statistical significance of each edge. Edges that had a deviance of below 3.84 were discarded because this value is the 5% cut-off using a chi-square distribution with one degree of freedom (Magwene, 2001). Edge exclusion deviance was measured as

$$-N\ln(1-\rho_{ij}) \qquad (1)$$

where N is the number of individuals in the sample and ρ is the partial correlation among variables i and j with all others held constant. The resulting partial correlation matrix (with additional edges excluded based on deviance) gives the observed pattern of integration. To get a better feel for the strength of the association between variables, edge strength was calculated. Edge strength is a measure of information among variables conditional on all the rest of the variables. This calculation allows one to rank-order associations among traits if all associations are significant (Magwene, 2001). The information that X_i provides about X_j and vice versa, conditional on all other variables (X_k) is calculated as

$$\text{Inf}(X_i \perp X_j \,|X_k) = -0.5\ln(1-\rho_{ij}) \qquad (2)$$

Edge strength allows for the testing of strong versus moderate covariation among variables. In Figure 1, bold lines denote predicted stronger edge strengths and thin lines denote predicted weaker edge strengths. I used Matlab (Mathworks) and MIM 2.1 (Hypergraph, Roskilde Denmark) software to perform graphic modeling calculations (see Edwards, 2000). I use Akaike's information criterion (AIC) (Burnham and Anderson, 2002) to compare the two conditional independence graphs with the observed conditional independence graph (i.e., the observed pattern of integration) where AIC $= -2 \log L_i + 2 k_i$ and L_i and k_i are the likelihood and the number of parameters of model i, respectively. This equation balances model complexity with model simplicity; the model with the lowest AIC value is the model that provides the

most parsimonious description of the data. Δ-AIC is used to provide the relative information content of models ($\Delta\text{-AIC}_i = \text{AIC}_i - \text{min AIC}$). Models with lower Δ-AIC better fit the observed data. In general, models with a Δ-AIC below 10 are deemed informative (Burnham and Anderson, 2002). For comparison, I also calculate these statistics for a "saturated model" in which all variables in the conditional independence model are connected by an edge, as well as an "independent model" in which none of the variables in the conditional independence model are connected by an edge. These latter models reflect total versus no integration, respectively.

The sample size for estimating correlational selection consisted of 73 adult animals that were marked and censused between 1985 and 2001. These animals are a complete subset of the sample used for the studies of integration. I use Lande and Arnold's (1983) method for estimating multivariate correlational selection. I regress relative fitness against postcranial traits standardized to have a mean of 0 and a standard deviation of 1. The measure of fitness was "years survived" (ranging from 5 to 28, mean = 14.08 years) divided by the mean years alive. I estimated correlational selection using the following equation:

$$w = c + \sum \beta_1 z_i + 0.5 \sum \gamma_2 z_i^2 + \sum \gamma_3 z_{ij} \qquad (3)$$

where w is relative fitness, c is the intercept, β_1 is the linear selection coefficient (measuring directional selection), γ_2 is the nonlinear selection coefficient (measuring stabilizing and disruptive selection), γ_3 is the correlational selection coefficient; z_i represents limb element trait i, and z_{ij} represents the cross-product for pairs of traits i and j. As many of the animals are still alive, this method will underestimate selection strength, since it is possible that an animal currently alive will later die in a manner that is causally related to the trait values it possesses. Significance is set at $\alpha = 0.05$. It should be noted that the sample size is relatively low and thus issues of statistical power are bound to arise. To aid in interpretation, I report the least significant number (LSN), an analysis that gives the required sample size to detect a significant difference when an actual difference truly exists. When LSN equals the sample size this represents a borderline case of significance, whereas when LSN is below the sample size the parameter estimate is deemed significant.

RESULTS

Table 3 lists the partial correlation matrix and conditional independence matrix for the observed covariance structure among limb elements. In Table 3, some of the largest partial correlation values are found among humerus-radius, hand-foot, femur-tibia, and femur-foot. Table 4 provides information on what "near-zero" means from a statistical viewpoint. The above-diagonal elements in Table 4 contain edge deviances. As discussed above, any edge deviance that is below 3.84 is statistically insignificant at the $\alpha = 0.5$ significance level [see Eq. (1)]. Edge strength values [Eq. (2)] are provided on the below-diagonal matrix. Edge strengths provide additional information about the information content of integrated traits when their edge deviance is bordering on 3.84. No values of edge deviance are borderline and all cases of edge strengths are either very low (corre-

TABLE 3. Conditional independence matrix (above diagonal) and partial correlation matrix (below diagonal) for observed correlation structure among limb elements

	Hu	Ra	Ha	Fe	Ti	Fo	Ta
Hu	1	*	0	0	0	0	*
Ra	0.312	1	0	*	*	*	*
Ha	0.048	0.078	1	*	*	*	*
Fe	0.066	0.205	0.124	1	*	*	*
Ti	0.050	0.133	0.127	0.312	1	0	0
Fo	0.041	0.123	0.320	0.296	−0.060	1	0
Ta	0.116	−0.117	0.239	0.195	−0.075	0.031	1

Hu, humerus; Ra, radius; Ha, hand; Fe, femur; Ti, tibia; Fo, foot; Ta, tail.

TABLE 4. Matrix of edge deviances (above diagonal) and edge strengths (below diagonal) calculated from the partial correlation matrix in Table 3

	Hu	Ra	Ha	Fe	Ti	Fo	Ta
Hu	–	10.985	0.249	0.464	0.272	0.183	1.460
Ra	0.051	–	0.658	4.589	1.900	1.629	1.462
Ha	0.001	0.003	–	1.652	1.748	11.577	6.311
Fe	0.002	0.021	0.008	–	11.151	9.793	4.132
Ti	0.001	0.009	0.008	0.052	–	0.390	0.611
Fo	0.001	0.008	0.054	0.046	0.002	–	0.099
Ta	0.007	0.007	0.030	0.019	0.003	0.000	–

Variables are defined in Table 3.

sponding to nonsignificant interactions) or very high (corresponding to significant interactions).

A graphical model of the observed pattern of morphological integration is shown in Figure 2. This model was developed from Tables 3 and 4, taking into account significant trait–trait interactions based on edge strengths and edge deviances. Two versions of the graphical model are shown. In version A, all traits with an edge strength above 0.050 are connected by a bold line, while traits with an edge strength of below 0.050 are connected by a thin line; in B, all traits with an edge strength above 0.025 are connected by a bold line and all traits with an edge strength below 0.025 are connected by a thin line. Comparing Figure 2A,B with Figure 1 suggests that neither the developmental nor functional model exclusively matches the observed pattern of integration. Instead, the observed pattern of integration contains trait covariances from both hypotheses. Table 5 provides information theoretic statistics calculated from each graphical model. As is evident from Table 5, the developmental hypothesis has a lower AIC and Δ-AIC value indicating that it provides a relatively better fit to the observed pattern of integration relative to the functional hypothesis; however, the Δ-AIC values for both the functional and developmental hypotheses are quite large, suggesting that other hypothetical models would be a better match to the observed pattern of integration (Burnham and Anderson, 2002). In fact, using Δ-AIC, the saturated model provides a better fit the observed pattern of covariation than either the functional or the developmental hypothesis (Table 5). Note that "model deviance" compares models with the saturated model, hence the saturated model has a deviance of 0.

Magwene (2001, p. 1743) defines a "strong" morphological module as: "A module is a maximal subset of traits for which all pairs of traits within the subset are mutually informative, conditional on all other traits under
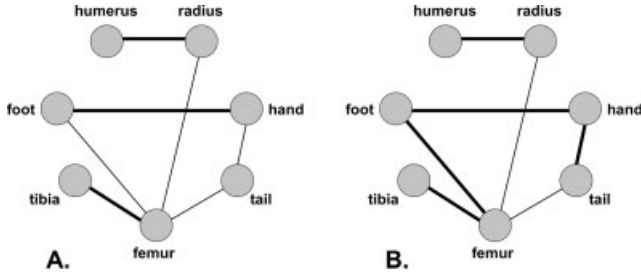
Fig. 2. Graphical model of the observed pattern of morphological integration. Lines show significant patterns of integration (or covariation) as determined by edge deviance. In graph **A**, bold lines denote edge strength values of 0.050 and above. In graph **B**, bold lines denote edge strength values of 0.025 and above (see below diagonal matrix in Table 4).

TABLE 5. *Statistics of conditional independence graphs shown in Figures 1 and 2*

Model	Deviance	df	AIC	Δ-AIC
Observed	23.23	14	1698.02	0.00
Saturated	0.00	0	1702.82	4.8
Developmental	65.21	14	1740.04	42.02
Functional	76.08	13	1752.91	54.89
Independent	187.45	21	1848.27	150.25

Statistics are also presented for the saturated model and the independent model. The models are ranked by Δ-AIC.

consideration." On an independence graph, modules constitute a subset of traits whose vertices are all adjacent (i.e., connected) and the addition of an additional trait will render some vertices in the subset as nonadjacent. In the language of conditional independence graphs, maximal subsets of adjacent vertices are called cliques. For example, the clique consisting of humerus-radius-femur in Figure 1B constitutes a morphological module. Looking at Figure 2 and using the definition of strong modularity, no morphological modules are evident in the observed covariation structure of the limb elements.

In Table 6, the estimates of the selection gradient analysis are presented. No traits are experiencing significant nonlinear selection (i.e., the quadratic coefficients). Only one trait, the radius, experiences near-significant negative directional selection ($\beta_1 = -0.112$; $P = 0.06$) although the least significant number (LSN = 79) suggests this is a borderline case. Two pairs of traits, the humerus-hand and humerus-femur appear to be experiencing correlational selection. Both of these pairs of traits had LCNs below the sample size used in the analysis. The humerus-hand experiences significant negative correlational selection ($\gamma_3 = -0.225$, $P = 0.04$, LSN = 65), while humerus-femur experiences near-significant positive correlational selection ($\gamma_3 = 0.204$, $P = 0.06$, LSN = 78). Neither of these traits is connected by an edge (i.e., integrated) as is evidenced by the observed pattern of integration shown in Figure 2.

DISCUSSION

Numerous studies have sought to characterize patterns of morphological integration in primates and then compare the resulting covariance structure against a variety of biological factors. Such factors include body mass, phylogenetic and morphological distance, dietary

TABLE 6. *Estimates of linear, quadratic, and correlational selection coefficients estimated from Eq. (3)*

	Humerus	Radius	Hand	Femur	Tibia	Foot	Tail
Linear coefficients	0.084 (0.14/93)	−0.112 (0.06/79)	0.014 (0.82/4957)	0.038 (0.61/1065)	0.025 (0.66/410)	0.025 (0.70/639)	−0.039 (0.44/289)
Quadratic coefficients	−0.104 (0.13/118)	0.031 (0.66/1414)	−0.049 (0.58/914)	−0.246 (0.07/82)	0.066 (0.27/230)	0.025 (0.80/4503)	0.065 (0.31/267)
Correlational coefficients							
Humerus	—	0.030 (0.83/5931)	−0.225 (0.04/65)	0.204 (0.06/78)	0.020 (0.81/4656)	−0.040 (0.80/4124)	−0.013 (0.89/13642)
Radius		—	0.015 (0.88/12806)	−0.090 (0.54/722)	0.037 (0.77/3234)	−0.050 (0.66/1686)	−0.161 (0.10/100)
Hand			—	0.003 (0.98/735755)	0.010 (0.94/46839)	−0.017 (0.85/8186)	−0.122 (0.30/255)
Femur				—	0.170 (0.14/126)	0.134 (0.51/634)	0.098 (0.33/295)
Tibia					—	−0.195 (0.08/91)	0.222 (0.07/84)
Foot						—	−0.125 (0.31/269)

Statistical P-values and least significant number are given in parentheses (P-value/least significant number).

and locomotor information, as well as models of expected change under selection and drift (e.g., Cheverud, 1995; Marroig and Cheverud, 2001, 2004; Marroig et al., 2004; Young, 2004, 2006; Vinyard, 2007). Many studies find that patterns of integration are correlated with numerous of the aforementioned factors, not just one of them. For example, Marroig and Cheverud (2001) found that the covariance structure of numerous craniofacial landmarks across platyrrhine species were associated with major dietary guilds. These authors also found that there was a common pattern of covariance structure across all species, implying that there is an underlying developmental unity of New World monkey craniofacial growth. Similarly, in a study of the hominoid scapula, Young (2004) found that patterns of trait covariation were associated with functional similarity (matrices containing information on the proportion of locomotor behaviors) and morphological distance, but only weakly with phylogenetic distance (Young notes that functional and phylogenetic distances, themselves, were highly correlated).

The major finding from these studies, and others, suggest that integration patterns reflect a combination of stability (i.e., covariation structure is invariant across related species) and function (i.e., covariance structure often maps onto aspects of lifestyle). Thus across a variety of primate taxa patterns of integration often manifest a mixture of primitive (as specified by symplesiomorphic developmental pathways) and derived signals (as specified by auta- and synapomorphic functional requirements). And this is to be expected if modularity enhances evolvability in lineages (e.g., Frazzetta, 1975; Lewontin, 1978; Wagner, 1996; Wagner and Altenberg, 1996). Primitive beneficial modules are preserved and inherited across species resulting in clade-specific patterns (Wagner, 1996), yet quasi-independence among modules allows for the evolution of new modules or modification of existing modules. In the context of the two hypotheses proposed for the sifaka postcranium, the developmental hypothesis is primitive for all primates (and most likely all tetrapods), while the functional hypothesis likely reflects the derived lifestyle of VCL among the Indriidae. More simply, "... the differences between ancestral and derived patterns of integration are expected to reflect the pattern of character coevolution during the evolution of the clade" (Wagner, 1996, p. 42). This likely explains the dual signatures of development and function evident when comparing Figure 2 with the two different hypotheses shown in Figure 1.

The fact that some integrated traits remain invariant across evolutionary time and phylogenetic clades begs the question of what maintains such invariance. There are two schools of thought concerning the issue of stasis, and these views harken back to the difference between functionalists and structuralists described in the introduction. The vast literature on this question (e.g., Gould and Eldredge, 1977; Charlesworth et al., 1982; Maynard Smith, 1983; Hansen and Houle, 2004; Estes and Arnold, 2007) shows that researchers often take one of two positions: 1) stasis can be explained by stabilizing selection or 2) stasis is due to some sort of genetic/ontogenetic constraint. Recent views, however, point out the paradox of this dichotomy: some form of selection is necessary to produce the "nonselective" constraint that is invoked to explain stasis (Hansen and Houle, 2004; Schwenk and Wagner, 2004; Estes and Arnold, 2007). One way out of this paradox is to note a distinction between external

and internal selection (Reidl, 1978; Wagner and Schwenk, 2000). External selection refers to traditional Darwinian selection, where fitness is determined by environmental, ecological and social pressures. Internal selection, on the other hand, recognizes that an organism is an evolved dynamic system comprised of numerous characters that are interrelated to various degrees. When two or more characters interact to fulfill a particular task, some form of internal selection is required to maintain character interdependency. Internal stabilizing selection is the likely factor, and it works to suppress variation among the interacting parts within the developing phenotype. In this perspective, stabilizing selection still maintains a prominent role in explaining stasis but it is not potentiated by abiotic selection pressures, rather, it is a necessary outcome of physiological and functional interdependencies that emerge during the evolution of ontogeny (Frazzetta, 1975; Wagner, 1996).

The present study did not find strong evidence for correlational selection except for the humerus-hand and humerus-femur. These trait pairs experience negative and positive correlational selection, respectively. The negative correlational selection experienced by the humerus-hand was not predicted by the functional or developmental model. Both models predicted correlational selection between the humerus-femur, but neither this pair of traits, nor the humerus-hand, are integrated to any degree (Tables 3 and 4; Fig. 2). The fact that no integrated traits in the sifaka postcranium experience significant correlational selection might be indicative of some form of internal stabilizing selection. It is interesting to note that only two pairs of un-integrated traits are experiencing correlational selection, suggesting that the integrated traits do not manifest adaptively relevant (co)variation. If the patterns of integration represent fixed characters this lack of variation might represent a form of internal stabilizing selection that suppresses the amount of variation made available to selection (Riedl, 1978; Wagner, 1988). That said, sifaka limb bones contain adaptively relevant variation in the form of additive genetic variation for length (Lawler, 2006); thus the likely explanation for the lack of correlational selection pressures is either that covariation in limb elements is not causally linked to variation in survivorship or there is insufficient statistical power to rigorously estimate selection. Studies of natural selection in the wild continue to be hampered by sample size (Hersch and Phillips, 2004). This problem is compounded when studying wild primates because collecting phenotypic and fitness data from individual primates involves the manipulation of highly-encephalized, slow-growing, mostly arboreal creatures. This latter point is neither new nor trivial (Morris, 1967). At present, our understanding of the relationship between fitness and skeletal/dental variation in wild primate populations comes from only a handful of studies (e.g., DeGusta et al., 2003; Lawler et al., 2005; Lawler, 2006; Caillaud et al., 2007).

The observed pattern of integration contained several trait covariances that were predicted by the developmental hypothesis. Many of these covariances pertain to within-limb elements, apart from the hand-foot covariation. The hand-foot covariation was, as predicted, strong and positive. Hallgrimsson et al., (2002) note that any substantial covariation between the hand and foot would require strong selection to individually modify each of these distal limb elements if they need to fill different

biological roles. In sifaka, the foot fills a different functional role during orthograde leaping, retains a qualitatively different anatomy, and experiences different selection pressures than the hand (Gebo, 1985; Gebo and Dagosto, 1988; Demes et al., 1996; Lawler, 2006). This indicates that the indriid foot was able to be modified in an adaptive manner despite its functional integration with other traits. Possible selection pressures acting on hands and feet in sifaka might involve the changing roles of these organs during locomotor ontogeny (Lawler, 2006). Wagner (1988) showed that the ability to evolve new configurations is enhanced if the covariation among characters follows a "corridor model," where many traits experience stabilizing selection except for those under directional selection. When functionally integrated traits contain developmental properties that allocate variation in an adaptively advantageous way for some traits, while restricting variation in other characters, this allows all traits to evolve in a manner that enhances fitness (Riedl, 1978; Wagner, 1988). The hand and foot are positively integrated with the tail and femur, respectively, and all of the covariation among these elements is strong and positive, conditional on all other traits (Table 2). The positive covariation among the hand and foot allows them to adapt to different functional roles likely because many of the differences between hands and feet of sifakas appear to be simple changes in carpal/tarsal and digit lengths (Ravosa et al., 1993; Lemelin and Jungers, 2007), apart from the orientation of the hallux (Gebo, 1985). In addition, while the foot and hand fulfill different roles during orthograde leaping, they fill a similar grasping role during vertical clinging; thus the strong covariation between these organs might relate to vertical postures and not vertical leaping (Lawler and Wunderlich, in preparation).

The functional hypothesis of covariation a priori specified two modules: humerus-radius-femur and humerus-femur-tail (see Fig. 1B) yet the present study did not identify any morphological modules according to the definition of strong modularity. That said, a number of hypothesized trait covariances from the functional hypothesis were contained within the hypothesized modules, including the humerus-radius, femur-tibia, and femur-tail. Tail length positively covaries with femur length suggesting a role for body repositioning during the in-air phase of a leap, as documented by Demes et al., 1996. However, tail length was not integrated with the humerus as predicted; instead, somewhat puzzlingly, tail length is integrated with hand length. The functional basis for this association is difficult to envision. Future studies should examine how the tail length covaries with other elements of the postcranium across the indriids (and across ontogeny), particularly since tail length varies substantially across this clade suggesting a role for allometric effects (Ravosa et al., 1993). On the whole, the covariance structure of the sifaka postcranium contains a slightly stronger developmental signature than a functional one (Tables 5). It is worth pointing out however, obvious as it seems, that the functional hypothesis relies on a number of biomechanical assumptions that need to be verified experimentally and empirically (see Table 1). It is possible that the functional hypothesis is mis-specified and this contributes to its poor fit against the observed data. Similarly, it is possible to come up with a functional explanation that fits the developmental hypothesis; for example, the model shown in Figure 1A could reflect the phylogenetic legacy of a grasping/suspensory mode of locomotion in the Indriids (see Godfrey and Jungers, 2003).

In this analysis, I utilized information theoretic statistics, rather than model deviance, to assess how a priori hypotheses of integration compare with the observed pattern of integration. Magwene (2001) suggests that in the context of hypothesis testing one can compute the model deviance of any two models (so long as they are a subset of each other) to assess their fit against the saturated model (which, by definition, has a deviance of zero). In this regard, the saturated model serves as a null model. It is interesting to note that in this study the "saturated" model, where all postcranial elements are integrated, provides a better fit to the observed pattern of integration than does either the functional or developmental models. For sifaka, the fact that the saturated model provides a decent approximation to the observed covariance structure suggests that "global" integration provides a more informative "picture" of postcranial evolution in this taxa, rather than viewing each postcranial trait as an independently evolving element. It would be illuminating to know which model, the saturated model (i.e., total integration) versus the independent model (i.e., no integration), provides a better fit to the observed integration structure across a variety of primate taxa. If the saturated model proves to be a closer fit to the observed data across a variety of species, this would have implications for how we go about investigating the adaptive basis of trait complexes versus independent traits. Methodologically, this suggests that a priori hypothesis specification might begin with the saturated model and then ask the following question: What trait *disassociations* need to occur in order to produce a particular functional or developmental pattern of trait covariance?

Studies of morphological integration are a good first step in identifying biologically relevant patterns of phenotypic covariation in primate populations. In this study, a large-sample analysis of morphological integration was carried out using wild-caught adult animals from a single population. The results presented above have research implications for many field and lab-based studies. For example, why does radius length, but not humerus length, positively covary with femur length? Is this pattern due to body rotation during leaping (as discussed above), climbing and clinging efficiency (see Cartmill, 1985), or does this pattern reflect the ontogenetic signature of neonatal selection for grasping ability (see Ravosa et al., 1993; Lawler, 2006)? In addition, it would be helpful to know if the pattern of hand-tail covariation is rooted in some sort of pleiotropic developmental pathway or does it have a functional basis? Furthermore, how does the covariation pattern in the hindlimb differ between thigh-powered and foot-powered VCL taxa? Finally, determining the degree to which the covariation patterns observed here are found in non-VCL species will help to disentangle the signature of derived locomotor function from the signature specified by primitive developmental pathways.

Overall, the safest interpretation of the above results is that the sifaka postcranium manifests a mosaic of developmentally and functionally integrated traits. This pattern is similar to the pattern found in other primates (e.g., Marroig and Cheverud, 2001; Young, 2004). These covariation patterns reflect the interplay of developmental processes and functional requirements that coevolve across evolutionary timescales. Gould (2002) has argued

that evolutionary biologists tend to focus on one of three factors—history, structure, or function—often at the expense of the other two. The results presented above indicate that the signature of structure and function are intertwined and may only become apparent by adding a historical dimension via the comparative method (e.g., Autumn et al., 2002; Young and Hallgrimmsson, 2005), or by specifying a priori structural and functional hypotheses and comparing their predictions with the observed data. The challenge regarding the latter approach is to delineate sufficiently different hypotheses such that the evolutionary patterns can, in fact, be disentangled—a challenge that has only been partially met here.

ACKNOWLEDGMENTS

I thank the government of Madagascar for permission to conduct this research. I also thank the Beza Mahafaly monitoring team and their coordinator Dr. Joelisoa Ratsirarson; I thank David Watts, Marion Schwartz, Diane Brockman, Laurie Godfrey, Bob Dewar, Joel Ratsirarson, and Alison Richard for contributing to this study in numerous direct and indirect ways. I thank Bob Dewar, Jennifer Wernegreen, and especially Roshna Wunderlich for commenting on this manuscript during its gestation. Campbell Rolian also prereviewed this manuscript and provided many helpful comments. Moxie is thanked for helping me understand limb function in agile, energetic quadrupeds. I learned a lot about multi-model inference from the Mathematical Ecology Group at the Woods Hole Oceanographic Institution, and in particular, Hal Caswell. P. Magwene kindly provided Python code which was used as a template for developing Matlab files. Two anonymous reviewers, particularly reviewer numero dos, provided lots of constructive criticism that greatly improved and shortened the final draft. I also thank the editor and associate editor at AJPA for offering suggestions about how to improve this manuscript.

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