

## ARE INSULAR POPULATIONS OF THE PHILIPPINE FALCONET (*MICROHIERAX ERYTHROGENYS*) STEPS IN A CLINE?

TODD E. KATZNER<sup>1,2,5</sup> AND NIGEL J. COLLAR<sup>3,4</sup>

<sup>1</sup>Division of Forestry and Natural Resources, West Virginia University, Morgantown, WV 26506-6125

<sup>2</sup>USDA Forest Service, Timber and Watershed Laboratory, Parsons, WV

<sup>3</sup>BirdLife International, Cambridge CB3 0NA, UK

<sup>4</sup>Natural History Museum, Tring, Herts HP23 6AP, UK

**Abstract.** Founder effects, new environments, and competition often produce changes in species colonizing islands, although the resulting endemism sometimes requires molecular identification. One method to identify fruitful areas for more detailed genetic study is through comparative morphological analyses. We measured 210 museum specimens to evaluate the potential morphological consequences of colonization across the Philippine archipelago by the Philippine Falconet (*Microhierax erythrogenys*). Measurements of both males and females differed clearly from island to island. Univariate and multivariate analysis of characteristics showed a latitudinal gradient, with the bill, wing, and tail of southern birds being larger than those of northern birds, forming the pattern of a stepped cline across a succession of islands. The stepped gradient in morphology and extensive differences between islands we observed provide evidence for multiple perspectives on phylogeny, including concordance with aggregate complexes expected on the basis of sea-level fluctuations. However, calculation of diagnosability indices did not support subspecific designations. Sex-specific dominance and dispersal patterns may explain this unusual south-to-north stepped cline, and they also provide a useful format for understanding biogeographical patterns by island. Finally, these morphological data suggest a potentially fruitful area for future genetic studies.

**Key words:** colonization, dispersal, *Microhierax*, Philippines, stepped clines, tropical raptors.

### ¿Son las Poblaciones Insulares de *Microhierax erythrogenys* Escalones en una Clina?

**Resumen.** Los efectos de fundador, los nuevos ambientes y la competencia producen a menudo cambios en la colonización de especies en las islas, aunque el endemismo resultante a veces requiere la identificación molecular. Un método para identificar áreas fructíferas para estudios genéticos más detallados es a través de análisis morfológicos comparativos. Medimos 210 especímenes de museo para evaluar las consecuencias morfológicas potenciales de la colonización de *Microhierax erythrogenys* a lo largo del archipiélago filipino. Las mediciones de machos y hembras difirieron claramente de isla a isla. Análisis univariados y mutivariados de las características mostraron un gradiente latitudinal, siendo el pico, el ala y la cola de las aves del sur más grandes que las de las aves del norte, formando el patrón de una clina escalonada a lo largo de una sucesión de islas. El gradiente escalonado en la morfología y las amplias diferencias entre islas que observamos brindan evidencia de múltiples perspectivas en filogenia, incluyendo concordancia con complejos agregados basados en el nivel del mar. Sin embargo, el cálculo de índices de diagnóstico no apoyó la designación de subespecies. La dominancia específica del sexo y los patrones de dispersión pueden explicar esta clina escalonada inusual de sur a norte, y también brindan un formato útil para entender los patrones biogeográficos por isla. Finalmente, estos datos morfológicos sugieren un área potencialmente fructífera para futuros estudios genéticos.

## INTRODUCTION

Species colonizing islands often undergo significant changes from their parent stock in response to founder effects, new environments and competition (Paulay and Meyer 2002). Dispersal in variable environments accompanied by these changes can result in the formation of morphological and genetic clines. Smooth clines characterize populations that vary continuously along a gradient. Stepped clines, in contrast, typify populations

that show abrupt shifts in morphology that correspond to sharp geographical boundaries, but the shifts may be small enough in magnitude that the populations do not achieve the status of subspecies (e.g., Patten and Unitt 2002). Such clines are regularly observed among populations of terrestrial species on islands separated by distinct and challenging oceanic barriers (Salomon 2002). In these conditions, populations may diverge and eventually speciate allopatrically (Thorpe et al. 2010).

Manuscript received 22 April 2012; accepted 14 November 2012.

<sup>5</sup>E-mail: [todd.katzner@mail.wvu.edu](mailto:todd.katzner@mail.wvu.edu)

In Pacific archipelagos, the consequences of these processes of colonization and diversification are poorly understood. Recent work across taxa has suggested that the Philippine Islands may contain high numbers of so-called cryptic species, morphologically similar but genetically distinct (Lohman et al. 2010). This finding is important because the Philippines are a hotspot of biodiversity and their unique species are also highly imperiled (Catibog-Sinha and Heaney 2006). In the Philippines, studies of phylogenetic relationships within species groups show a surprising taxonomic diversity (Jones and Kennedy 2008, Moyle et al. 2011). However, even the most detailed of these studies (Lohman et al. 2010) focused on only seven species of passerines not endemic to Philippines, leaving large taxonomic groups unevaluated.

The Philippine Falconet (*Microhierax erythrogenys*) is a forest-dwelling raptor endemic to the Philippine archipelago, where it is known from the islands of Bohol, Calicoan, Catanduanes, Cebu, Leyte, Luzon, Mindanao, Mindoro, Negros, and Samar (Dickinson et al. 1991), with the recent addition of Panay (M. Lagerqvist, pers. obs.). The nominotypical subspecies *M. e. erythrogenys* is found on the northern Philippine islands (Bohol, Catanduanes, Luzon, Mindoro, and Negros). Southern populations (those on Calicoan, Cebu, Leyte, Mindanao, and Samar, although curiously not on Bohol) have been widely recognized as constituting a separate subspecies *M. e. meridionalis* (McGregor 1909–1910, Peters 1931, Stresemann and Amadon 1979, Dickinson et al. 1991, Clark 1994, Kennedy et al. 2000, Dickinson 2003, Clements 2007).

Ogilvie-Grant (1897) based the original description of *M. e. meridionalis* on two morphological characteristics, greater size in both sexes and all-black rather than white-barred inner webs of the primaries in males. McGregor (1909–1910) pointed out that the latter character is “due to immaturity” and that adult males of both subspecies possess all-black primaries. The disjunction in size between the northern and southern specimens of the Philippine Falconet prompted Peterson (2006) to suggest that two species might be involved. Initial review recognized no species-level differentiation owing to inconstant and peculiar patterns in both plumage and distribution (Ferguson-Lees and Christie 2001), although more recent work tentatively supported this position (Collar 2007).

Although genetics is an essential component of modern taxonomic studies, morphology is still important, especially because it can identify directions for future study. The specific goals of our study were (1) to use a range of approaches to evaluate the taxonomic status of subpopulations of the Philippine Falconet across a broad swath of its range in the Philippines, with a specific focus on proposed subspecific designations and on differences among islands and island groups, and (2) to evaluate potential mechanisms for the patterns we observed. To do this, we examined the morphology of a large sample of museum specimens and analyzed this dataset for possible trends within populations. On the basis of these data we also evaluated historical characterizations of subspecies

and inter-island patterns and advance a testable behavioral hypothesis to explain the microevolutionary clinal divergence we observed. Finally, we considered our results in the context of their value as the foundation for future genetic study.

## METHODS

### MEASUREMENT OF BIRDS

We used digital calipers sensitive to 0.01 mm to measure (in mm) the exposed culmen, unflattened wing, and tail (from tip to point of insertion) of 210 (101 males, 103 female, 6 sex unknown) Philippine Falconets labeled with a provenance. Specimens included all samples with sufficient information from the American Museum of Natural History (AMNH; 25 m, 15 f, 2 u), (British) Natural History Museum (BMNH; 6 m, 14 f, 2 u), Carnegie Museum of Natural History (CM; 3 m, 2 f), Delaware Museum of Natural History (DMNH; 30 m, 34 f, 1 u), Museum of Comparative Zoology (MCZ; 4 m, 6 f), Muséum National d'Histoire Naturelle (MNHN; 2 f), Philippines National Museum (PNM; 22 m, 18 f, 1 u), and United States National Museum of Natural History (USNM; 11 m, 12 f). These specimens were from Luzon (90; 39 m, 48 f, 3 u), Catanduanes (15; 9 m, 6 f), Mindoro (15; 8 m, 7 f), Negros (2; 2 m), Cebu (2; 1 m, 1 f), Samar (20; 9 m, 10 f, 1 u), Leyte (7; 3 m, 4 f), and Mindanao (59; 30 m, 27 f, 2 u); no specimens were found from either Bohol or Calicoan. Most museum records provided only the island of collection, not the exact collection location on each island.

### STATISTICAL ANALYSES

We used several univariate statistical tools to understand inter-island variability in morphometric traits of the Philippine Falconet in the context of previous univariate assessments of this species. First, we calculated within-island and overall averages and variances for the morphometric measurements we recorded. We did this for all islands, regardless of sample size. Second, focusing only on islands from which we had at least five specimens, we used an analysis of variance to compare differences among islands in measurements of the bill, tail, and wing. When the ANOVA indicated significant differences among islands, we used a conservative multiple comparison (Scheffe's test) to delineate those differences.

We also used two multivariate statistical approaches simultaneously to characterize overall differences among islands in all three measurements. First, we used a multivariate analysis of variance (MANOVA; Wilks'  $\Lambda$ ) to compare covariation in mean differences among islands. Second, we used a principal components analysis (PCA) to identify suites of morphometric features that separated birds from different islands. We then used an ANOVA and Scheffe's test to compare differences in factor scores for principal components that accounted for the majority of variability (>40%) within the PCA.

We also evaluated morphological variation (1) between the two putative subspecies (as defined in the introduction);

(2) within each subspecies, among islands; and (3) among the seven predicted “Philippine aggregate island complexes” (PAICs; Heaney 1985, Evans et al. 2003). In this case the analytical tools we used (ANOVA on single traits, MANOVA and a PCA on multiple traits with an ANOVA on factor scores) were the same as in the preceding analyses but the treatment groups were subspecies, islands within those subspecies, or the three PAICs for which we had data sufficient for comparison.

Finally, we used a *D* statistic (Patten and Unitt 2002) to evaluate the diagnosability of the currently described subspecies. We calculated *D* statistics in a univariate manner, for each of the three morphological characteristics we measured: bill, wing, and tail.

For statistical analyses we used SAS version 9.2 (SAS Institute, Inc., Cary, NC) or a spreadsheet (Microsoft Excel 2007).

## RESULTS

### INDIVIDUAL MORPHOMETRIC TRAITS

There were clear differences among islands in measurements of both male and female Philippine Falconets (Table 1). These differences generally followed a south–north gradient, with southern birds being larger and northern birds smaller. Furthermore, these trends followed a remarkably consistent pattern of small changes between most islands,

resulting in an extended, gently stepped cline. Interestingly, birds from islands that overlap latitudinally (Mindoro, Luzon, and Catanduanes) are less distinct, thus generally supporting the cline concept (smaller steps between less geographically separated sites).

Measurements of females from islands for which the sample exceeded 5 were different (bill:  $F_{4,89} = 21.89$ ,  $P < 0.0001$ ; wing:  $F_{4,89} = 6.08$ ,  $P = 0.0002$ ; tail:  $F_{4,89} = 10.97$ ,  $P < 0.0001$ ). Scheffe’s tests for females’ bill and tail lengths supported the south–north gradient in morphology (Table 1). The same test was unable to detect differences among islands in wing length of females.

Measurements of males from islands for which the sample exceeded 5 were also different (bill:  $F_{4,87} = 35.59$ ,  $P < 0.0001$ ; wing:  $F_{4,87} = 13.22$ ,  $P < 0.0001$ ; and tail:  $F_{4,87} = 16.39$ ,  $P < 0.0001$ ). Scheffe’s test for differences in males’ bill size suggested strong differences, grouping Mindanao and Samar together and separate from all other islands (Table 1). This test also supported the inter-island differences that create the south–north gradient in morphology for differences in males’ wing chord and tail length.

### COVARIATION AMONG SUITES OF MORPHOMETRIC CHARACTERISTICS

When all characteristics were considered together, the morphometrics of the Philippine Falconet, both females ( $F_{12,230,47} =$

TABLE 1. Measurements (mean  $\pm$  SD) of female and male Philippine Falconets by island. Islands are organized generally north to south, with Catanduanes grouped with Samar and Leyte. Groupings designated by capital letters are according to the output of a post-hoc comparison (Scheffe’s test); islands for which  $n \leq 5$  were not compared.

Island	<i>n</i>	Bill	Wing	Tail
Females				
Luzon	46	11.61 $\pm$ 0.58 <sup>Z</sup>	108.22 $\pm$ 4.00 <sup>X</sup>	66.09 $\pm$ 3.67 <sup>Y</sup>
Mindoro	7	12.00 $\pm$ 1.00 <sup>Y,Z</sup>	110.14 $\pm$ 6.04 <sup>X</sup>	67.86 $\pm$ 3.46 <sup>X,Y</sup>
Catanduanes	6	12.16 $\pm$ 0.75 <sup>Y,Z</sup>	109.16 $\pm$ 1.72 <sup>X</sup>	68.00 $\pm$ 2.90 <sup>X,Y</sup>
Samar	10	12.80 $\pm$ 0.42 <sup>X,Y</sup>	111.80 $\pm$ 5.49 <sup>X</sup>	67.50 $\pm$ 3.86 <sup>X,Y</sup>
Leyte	4	13.00 $\pm$ 0.00	111.75 $\pm$ 4.11	66.75 $\pm$ 2.87
Cebu	1	13.00 $\pm$ 0.00	117.00 $\pm$ 0.00	70.00 $\pm$ 0.00
Mindanao	27	13.19 $\pm$ 0.88 <sup>X</sup>	113.81 $\pm$ 5.41 <sup>X</sup>	71.56 $\pm$ 3.46 <sup>X</sup>
Grand mean	7	<b>12.53 <math>\pm</math> 0.23</b>	<b>111.70 <math>\pm</math> 1.13</b>	<b>68.25 <math>\pm</math> 0.72</b>
Males				
Luzon	39	10.64 $\pm$ 0.58 <sup>Y</sup>	103.13 $\pm$ 3.67 <sup>Y</sup>	62.54 $\pm$ 2.94 <sup>Y</sup>
Mindoro	8	11.14 $\pm$ 0.69 <sup>a Y</sup>	104.13 $\pm$ 2.53 <sup>Y</sup>	65.37 $\pm$ 2.56 <sup>X,Y</sup>
Catanduanes	9	10.89 $\pm$ 0.33 <sup>Y</sup>	102.78 $\pm$ 3.15 <sup>Y</sup>	63.22 $\pm$ 2.95 <sup>Y</sup>
Samar	9	12.00 $\pm$ 0.53 <sup>b X</sup>	108.11 $\pm$ 3.98 <sup>X,Y</sup>	65.11 $\pm$ 4.24 <sup>Y</sup>
Leyte	3	12.00 $\pm$ 0.00	112.00 $\pm$ 3.46	63.00 $\pm$ 3.00
Cebu	1	12.00 $\pm$ 0.00	114.00 $\pm$ 0.00	66.00 $\pm$ 0.00
Negros	2	12.00 $\pm$ 0.00	108.00 $\pm$ 1.41	67.00 $\pm$ 4.24
Mindanao	30	12.21 $\pm$ 0.49 <sup>c X</sup>	109.67 $\pm$ 4.63 <sup>X</sup>	68.40 $\pm$ 3.25 <sup>Y</sup>
Grand mean	8	<b>11.61 <math>\pm</math> 0.22</b>	<b>107.73 <math>\pm</math> 1.46</b>	<b>65.08 <math>\pm</math> 0.73</b>

<sup>a</sup>*n* = 7.

<sup>b</sup>*n* = 8.

<sup>c</sup>*n* = 29.

7.03,  $P < 0.0001$ ) and males ( $F_{12,225.18} = 11.88$ ,  $P < 0.0001$ ), differed by island.

Our PCA delineated relationships among correlated morphological variables. Scores for PCA factors 1 and 2 clearly demonstrated the south–north gradient in morphometrics, for both females (Fig. 1a, 2) and males (Fig. 1b, 2). Principal component 1 (PC1) accounted for 67.8% of the variability in the data for females and for 73.2% of the variability in those for males. This factor was composed of roughly equal contributions by each of the three variables, whose variances were, by and large, positively correlated with each other (Table 2).

Analysis of variance suggested that for females PC1 varied strongly by island ( $F_{4,89} = 21.26$ ,  $P < 0.0001$ ). The Scheffe's test found no difference in factor scores from Mindanao and Samar and among Samar, Catanduanes, Mindoro, and Luzon, indicating a lack of distinct groupings among islands.

PC1 for males also varied strongly by island ( $F_{4,87} = 36.93$ ,  $P < 0.0001$ ), and males from different islands were grouped more distinctly than were females. There were no differences between Mindanao and Samar, Samar and Mindoro, and Mindoro, Catanduanes, and Luzon.

#### DIFFERENTIATION AMONG SUBSPECIES AND PAIC REGIONS

Analyses of morphology of Philippine Falconet specimens showed consistent and strong (>75%; e.g., Amadon 1949, Mayr 1969) differences between the two putative subspecies that meet a high level of statistical differentiation. Univariate analyses

TABLE 2. Patterns of factors from principal components analysis of measurements of bill, wing, and tail of museum specimens of the Philippine Falconet by sex.

	Factor 1	Factor 2
Females		
Bill	0.849	−0.254
Wing	0.76	0.630
Tail	0.842	−0.315
Males		
Bill	0.853	−0.414
Wing	0.884	−0.103
Tail	0.830	−0.535

detected differences in measurements for bill, tail, and wing between the two subspecies, in both males and females ( $P < 0.0001$ ;  $df = 1,92$ ;  $F$  statistics varied with the test). MANOVA results provided additional support for this differentiation (females:  $F_{3,90} = 27.66$ ,  $P < 0.0001$ ; males:  $F_{3,88} = 53.98$ ,  $P < 0.0001$ ), as did analysis of factor scores (females:  $F_{1,92} = 66.94$ ,  $P < 0.0001$ ; males:  $F_{1,90} = 121.97$ ,  $P < 0.0001$ ).

Confusingly, however, our analysis suggested inter-island variation *within* each subspecies, at a level of statistical significance (95%) similar to that observed between subspecies. There were no differences between males or females of *M. e. erythrogenys*, either with regard to univariate or our two

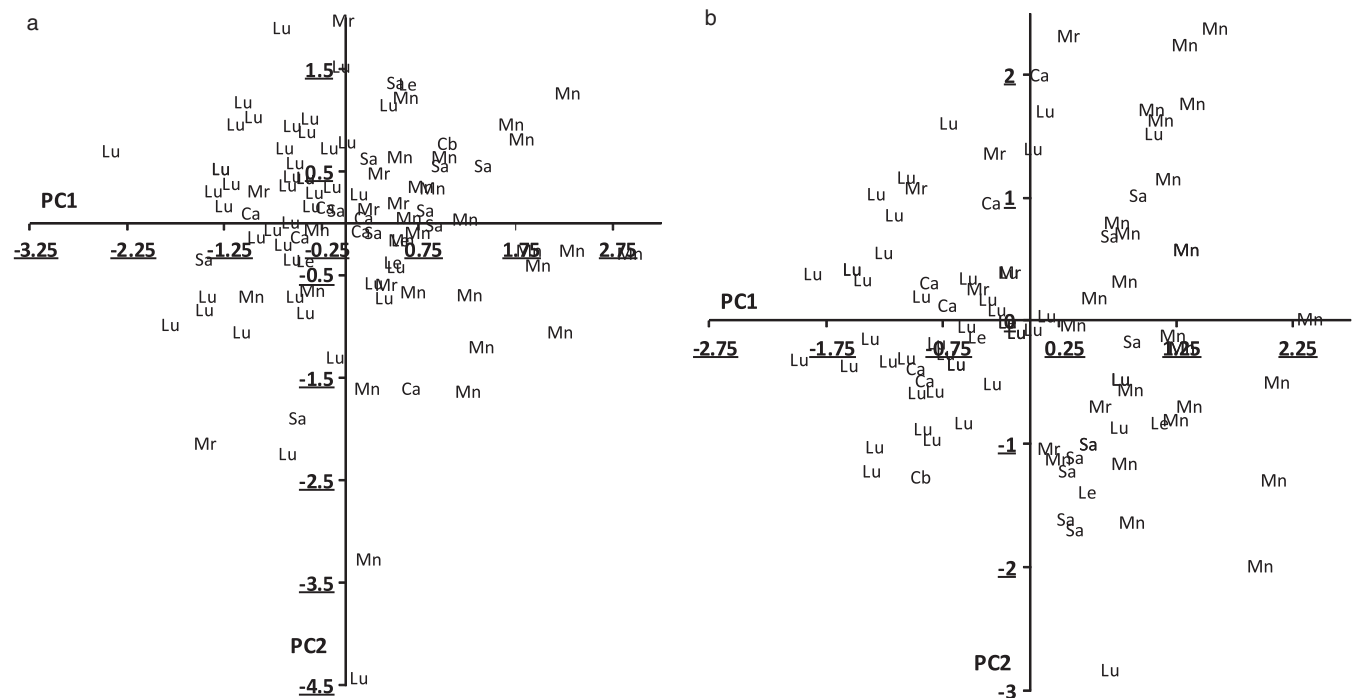


FIGURE 1. Plot of primary factor scores of a principal components analysis of measurements of bill, wing, and tail of (a) female, and (b) male Philippine Falconets. Islands are Lu = Luzon, Mr = Mindoro, Ca = Catanduanes, Cb = Cebu, Sa = Samar, Le = Leyte, and Mn = Mindanao.

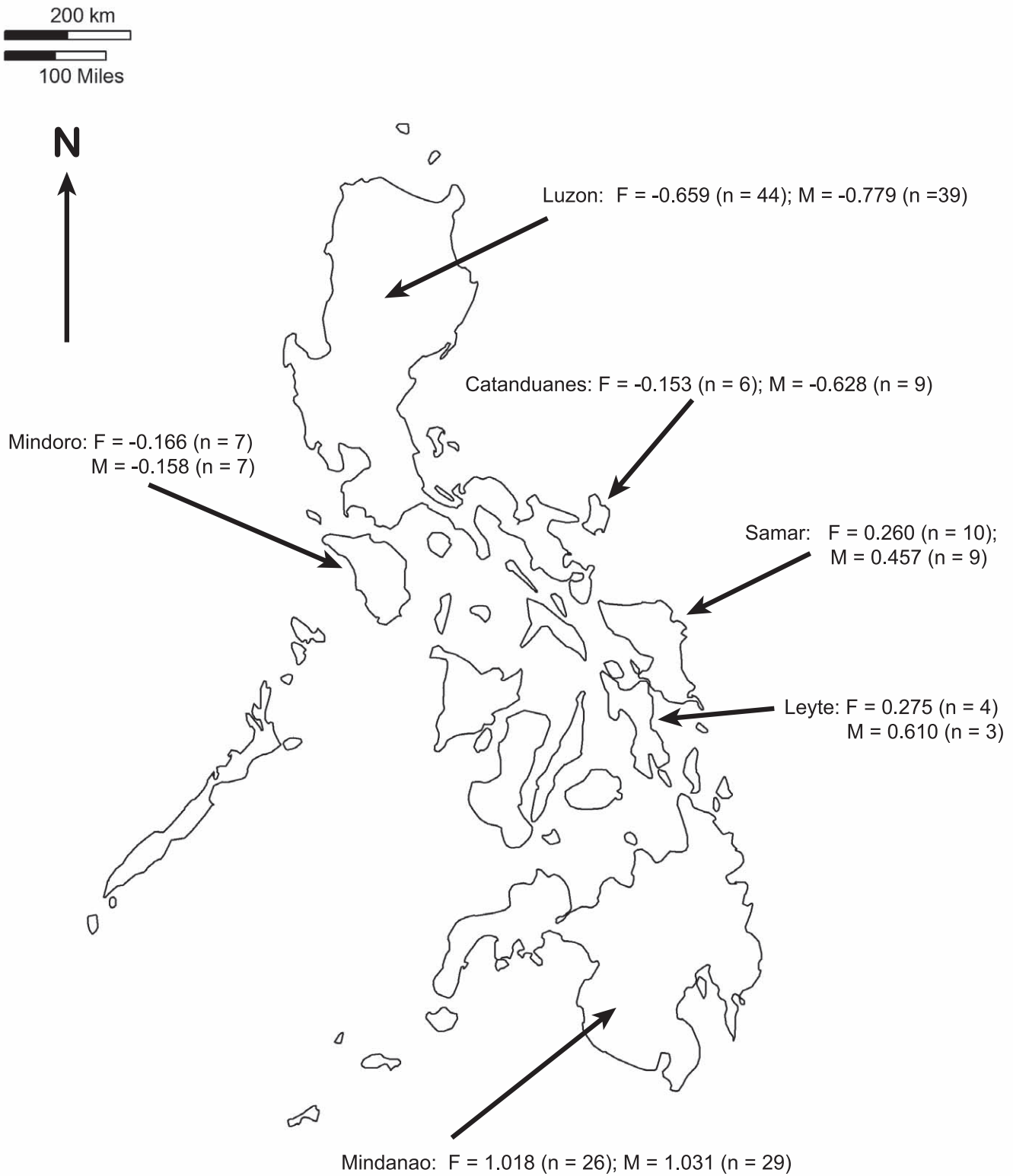


FIGURE 2. Mean factor scores and number of individuals measured, by island, for factor 1 from a principal components analysis of bill, tail and wing measurements of Philippine Falconets. Factor scores show the general south-to-north gradient in the species' size; only islands for which  $n \geq 5$  are included.

multivariate analyses ( $P > 0.05$ ). However, males and females of *M. e. meridionalis* from different islands were morphologically different. For females, this was driven by substantial differences in tail measurements ( $F_{1,34} = 10.38$ ,  $P < 0.0028$ ). Our multivariate analyses supported this interpretation (MANOVA:  $F_{3,32} = 3.71$ ,  $P < 0.0213$ ; ANOVA, PC1:  $F_{1,34} = 5.03$ ,  $P < 0.0315$ ). Males showed similar trends in differences in tail measurements ( $F_{1,35} = 10.87$ ,  $P < 0.0023$ ), which were also supported by our multivariate analyses (MANOVA:  $F_{3,33} = 4.02$ ,  $P < 0.0152$ ; ANOVA, PC1:  $F_{1,35} = 7.58$ ,  $P < 0.0093$ ).

Given the degree of differentiation within each subspecies, it is therefore not surprising that results of tests for differences among PAIC regions were similar to those for inter-island differences. Univariate analyses detected differences in measurements of bill, tail, and wing between the three PAIC regions for which samples exceeded five, for both males and females ( $P < 0.0001$ ;  $df = 2,95$  [females],  $2,92$  [males];  $F$  statistics varied with the test). MANOVA results provided additional support for this differentiation (females:  $F_{6,186} = 12.72$ ,  $P < 0.0001$ ; males:  $F_{6,180} = 20.09$ ,  $P < 0.0001$ ), as did analysis of factor scores (females:  $F_{2,95} = 34.46$ ,  $P < 0.0001$ ; males:  $F_{2,92} = 70.21$ ,  $P < 0.0001$ ).

Finally, our tests for diagnosability provided further corroboration that there is limited differentiation between currently proposed subspecies. Values of  $D$  were strongly negative (indicating that populations are not diagnosable), with the highest values being for bill measurements in both females ( $D_{e,m} = -0.75$ ,  $D_{m,e} = -0.90$ ) and males ( $D_{e,m} = -0.45$ ,  $D_{m,e} = -0.22$ ). Values for wing and tail were higher, for both females (wing:  $D_{e,m} = -8.75$ ,  $D_{m,e} = -10.88$ ; tail:  $D_{e,m} = -7.37$ ,  $D_{m,e} = -8.31$ ) and males (wing:  $D_{e,m} = -5.13$ ,  $D_{m,e} = -6.89$ ; tail:  $D_{e,m} = -5.77$ ,  $D_{m,e} = -6.75$ ).

## DISCUSSION

We observed small directional and progressive changes in morphology in discontinuous but adjacent populations of the Philippine Falconet. Specifically, birds on southern Philippine islands were significantly larger than birds on more northern islands. However, statistical tests failed to distinguish between birds on geographically neighboring islands, suggesting an overall size gradient that we verified by examination of each morphological trait. While we were able to differentiate between subspecies with statistical analyses of morphometrics, statistically significant differences in morphology also existed within the putative subspecies, and the subspecies were not diagnosable by a nonstatistical test following a “75% rule of overlap” (as described in Patten and Unitt 2002).

Although the trends we observed may be confusing with regard to current taxonomic status, they are concordant with those predicted by hypothesized PAICs, i.e., a classical Wallacean biogeographical explanation suggesting that only those

islands currently separated by shallow water were aggregated in the Pleistocene (Heaney 1985, Evans et al. 2003). PAIC-induced patterns may therefore explain the less distinct differences between birds from geographically closer islands (especially, for example, Catanduanes, Luzon, and Mindoro, which overlap latitudinally and a drop in sea level may have joined (e.g., Fig. 1 in Evans et al. 2003), resulting in gene flow between populations. Such differences likely do not rise to the level of subspecific status, since larger aggregates are not diagnosable.

In spite of the concordance we observed with PAIC patterns, the stepped cline we observed appears to be previously unrecorded for a tropical bird species with a relatively constrained geographical range (here 6–18° N). A casualty of this finding is the taxon *meridionalis*. Our statistical analyses largely undermine the taxonomic viability of this subspecies, with the range defined previously (e.g., Dickinson et al. 1991, Kennedy et al. 2000). This conclusion is further supported by our evaluation of diagnosability of this subspecies (Patten and Unitt 2002). In essence our analyses suggest that the variability around mean measurements (Table 1) is sufficiently extensive within the insular subpopulations we sampled that none of the birds on any island can be easily distinguished taxonomically.

Recent work with other Philippine birds shows the complexity of patterns of diversity and evolution within species and across islands (e.g., Sheldon et al. 2009, Lim et al. 2010, Moyle et al. 2011). These studies with genetic markers showed exceptional degrees of endemism in Philippine birds and an unusual level of distinctness from mainland and other island populations scaled to time since colonization. Without complementary genetic information, the stepped cline in morphology of the Philippine Falconet is difficult to explain. It is too consistent to be attributable to the random processes of genetic drift. However, it seems equally unlikely to indicate selective pressure for reduction in size with increasing latitude. Such a trend contradicts Bergmann's rule, although the rule's effects on body size are unlikely within so narrow a tropical latitudinal range. Furthermore, there is no obvious link between size of bird and size of island, which (since smaller islands may possess fewer competitors and predators) might otherwise explain size variation in terms of niche width and predation pressure. An effect of elevation, if southern birds are confined to mountain peaks and northern birds to lowlands, is unlikely because such a distribution has not been noted in the fairly extensive literature on Philippine birds.

The Philippine Falconet is the easternmost representative of *Microhierax*; its closest relative, geographically and (on morphological grounds probably also) phylogenetically, is the White-fronted Falconet (*M. latifrons*) of northern Borneo. The absence of the Philippine Falconet from Palawan and neighboring islands suggests that the invading ancestors

of *M. erythrogyne* may have followed the line of the Sulu Islands to Mindanao, then progressed north through Leyte, Samar, and tiny Calicoan to reach Luzon. Over roughly the same time scale they could also have spread west from Leyte to Bohol, Cebu, Negros, and Panay, and colonized Mindoro from Panay or southern Luzon.

One novel, but admittedly speculative, possible explanation of this pattern combines the likely circumstances of colonization of the Philippines by *Microhierax* with the pronounced reverse sexual dimorphism of the Falconidae. If the colonization process was driven by internal population pressures forcing dispersal, one would expect the dispersers to be less dominant individuals. Moreover, the pronounced sexual size dimorphism in falcons is thought to be the result of selection among females for competitive ability and hence larger size, and of selection among males, as sole providers of food to the nest, for agility and hence smaller size (White et al. 1994). If this explanation is accurate, it is plausible that females forced to disperse would have been smaller individuals. Males forced to disperse would not necessarily differ in size, since males that dispersed to find mates might be larger (females might select smaller, more agile males), but males forced by other males to disperse might be smaller (larger males might dominate them). Thus the displacement of incrementally smaller females from one island to the next, only partly tempered by neutral selection for size of males, could have produced and maintained the pattern of microevolutionary divergence in morphometrics we observed.

Evolution of this pattern requires only that dispersal not be immediate and that dominance hierarchies not be age-related. This is plausible for a small tropical raptor without an extended pre-adult life stage. There are a number of ways for this hypothesis of internal population pressure driving the development of a stepped cline in morphology to be tested. One method may be concurrent telemetry and morphological studies to evaluate differential dispersal of hatch-year falconets of known size. Another approach may be to use genetic evidence to evaluate molecular clocks, divergence, and age of colonizers (Woltmann et al. 2012).

Regardless of the mechanism, however, since Huxley (1938, 1939 in Salomon 2002) proposed the concept of the stepped cline evidence for this pattern has rarely been found. Our analysis suggests such a pattern and should encourage others to look for similar trends in populations of other, similarly labile and diverse tropical species. A limitation of our study is that it is focused exclusively on morphology. However, recent research has highlighted the value of combining morphological and genetic studies with knowledge of aggregations of islands in clarifying phylogeography (Jones and Kennedy 2008). Most previous work on avian island phylogeography in the Philippines has focused on passerines. Our morphological studies suggest that nonpasserine genera such as *Microhierax* may also be fruitful for future genetic studies.

## ACKNOWLEDGMENTS

We thank Paul Sweet (AMNH), Robert Prys-Jones (BMNH), Steve Rogers (CM), Jean Woods (DMNH), Jeremiah Trimble (MCZ), Eric Pasquet (MNHN), Lourdes Alvarez (PNM), and James Dean (USNM), who allowed access to the bird specimens in their care. Markus Lagerqvist permitted use of his recent record from Panay. Adam Duerr, Maria Wheeler, Claire Spottiswoode, J. Ignacio Areta, and several anonymous reviewers made helpful comments on earlier versions of the manuscript, and Tricia Miller assisted with the figure.

## LITERATURE CITED

- AMADON, D. 1949. The seventy-five percent rule for subspecies. *Condor* 51:250–258.
- CATIBOG-SINHA, C. C., AND L. R. HEANEY. 2006. Philippine biodiversity, principles and practice. Haribon Foundation, Manila.
- CLARK, W. S. 1994. Philippine Falconet *Microhierax erythrogyne*, p. 256. In J. del Hoyo, A. Elliott, and J. Sargatal [EDS.], *Handbook of the birds of the world*, vol 2. Lynx Edicions, Barcelona.
- CLEMENTS, J. F. 2007. *The Clements checklist of birds of the world*, 6th ed. Comstock, Ithaca, NY.
- COLLAR, N. J. 2007. Philippine bird taxonomy and conservation: a commentary on Peterson (2006). *Bird Conservation International* 17:103–113.
- DICKINSON, E. C. [ED.]. 2003. *The Howard and Moore complete checklist of the birds of the world*, 3rd ed. Christopher Helm, London.
- DICKINSON, E. C., R. S. KENNEDY, AND K. C. PARKES. 1991. *The birds of the Philippines: an annotated check-list*. British Ornithologists' Union (Check-list 12), Tring, UK.
- EVANS, B. J., R. M. BROWN, J. A. MCGUIRE, J. SUPRIATNA, N. ANDAYANI, A. DIESMOS, D. ISKANDAR, D. J. MELNICK AND D. C. CANNATELLA. 2003. Phylogenetics of fanged frogs: testing biogeographical hypotheses at the interface of the Asian and Australian faunal zones. *Systematic Biology* 52:794–819.
- FERGUSON-LEES, J., AND D. A. CHRISTIE. 2001. *Raptors of the world*. Christopher Helm, London.
- HEANEY, L. R. 1985. Zoogeographic evidence for middle and late Pleistocene land bridges to the Philippine Islands. *Modern Quaternary Research in Southeast Asia* 9:127–165.
- JONES, A. W., AND R. S. KENNEDY. 2008. Plumage convergence and evolutionary history of the Island Thrush in the Philippines. *Condor* 110: 35–44.
- KENNEDY, R. S., P. C. GONZALES, E. C. DICKINSON, H. C. MIRANDA AND T. H. FISHER. 2000. *A guide to the birds of the Philippines*. Oxford University Press, Oxford, UK.
- LIM, H. C., F. ZOU, S. S. TAYLOR, B. D. MARKS, R. G. MOYLE, G. VOELKER AND F. H. SHELDON. 2010. Phylogeny of magpie-robins and shamas (Aves: Turdidae: *Copsychus* and *Trichixos*): implications for island biogeography in Southeast Asia. *Journal of Biogeography* 37:1894–1906.
- LOHMAN, D. J., K. K. INGRAM, D. M. PRAWIRADILAGA, K. WINKER, F. H. SHELDON, R. G. MOYLE, P. K. L. NG, P. S. ONG, L. K. WANG, T. M. BRAILE, D. ASTUTI, AND R. MEIER. 2010. Cryptic genetic diversity in “widespread” Southeast Asian birds suggests that Philippine avian endemism is gravely underestimated. *Biological Conservation* 143: 1885–1890.
- MAYR, E. 1969. *Principles of systematic zoology*. McGraw-Hill, New York.
- MCGREGOR, R. C. 1909–1910. *A manual of Philippine birds*. Bureau of Printing, Manila.
- MOYLE, R. G., S. S. TAYLOR, C. H. OLIVEROS, H. C. LIM, C. L. HAINES, M. A. RAHMAN, AND F. H. SHELDON. 2011. Diversification of an endemic southeast Asian genus: phylogenetic relationships

- of the spiderhunters (Nectariniidae: Arachnothera). *Auk* 128: 777–788.
- OGILVIE-GRANT, W. R. 1897. On the birds of the Philippine Islands. Part IX. The islands of Samar and Leite. *Ibis* 3(ser. 7): 209–250.
- PATTEN, M. A., AND P. UNITT. 2002. Diagnosability versus mean differences of Sage Sparrow subspecies. *Auk* 119:26–35.
- PAULAY, G., AND C. MEYER. 2002. Diversification in the tropical Pacific: comparisons between marine and terrestrial systems and the importance of founder speciation. *Integrative and Comparative Biology* 42: 922–934.
- PETERS, J. L. 1931. Check-list of birds of the world, vol. 1. Museum of Comparative Zoology, Cambridge, MA.
- PETERSON, A. T. 2006. Taxonomy *is* important in conservation: a preliminary assessment of Philippine species-level bird taxonomy. *Bird Conservation International* 16: 155–173.
- SALOMON, M. 2002. A revised cline theory that can be used for quantified analyses of evolutionary processes without parapatric speciation. *Journal of Biogeography* 29: 509–517.
- SHELDON, F. H., D. J. LOHMAN, H. C. LIM, F. ZOU, S. M. GOODMAN, D. M. PRAWIRADILAGA, K. WINKER, T. M. BRAILE, AND R. G. MOYLE. 2009. Phylogeography of the magpie-robin species complex (Aves: Turridae: *Copsychus*) reveals a Philippine species, an interesting isolating barrier and unusual dispersal patterns in the Indian Ocean and southeast Asia. *Journal of Biogeography* 36: 1070–1083.
- STRESEMANN, E., AND D. AMADON. 1979. Order Falconiformes, p.271–425. In E. Mayr and G. W. Cottrell [EDS.], Check-list of birds of the world, vol. 1, 2nd ed. Museum of Comparative Zoology, Cambridge, MA.
- THORPE, R. S., Y. SURGET-GROBA, AND H. JOHANSSON [ONLINE]. 2010. Genetic tests for ecological and allopatric speciation in *Anoles* on an island archipelago. *PLoS Genetics* 6(4): e1000929. <<http://www.plosgenetics.org/article/info:doi/10.1371/journal.pgen.1000929>>.
- WHITE, C. M., P. D. OLSEN, AND L. F. KIFF. 1994. Family Falconidae (falcons and caracaras) family introduction. p.216–247. In J. del Hoyo, A. D. Elliott, and J. Sargatal [EDS.], *Handbook of birds of the world*, vol. 1. Lynx Edicions, Barcelona.
- WOLTMANN, S., T. W. SHERRY, AND B. R. KREISER. 2012. A genetic approach to estimating natal dispersal distances and self-recruitment in resident rainforest birds. *Journal of Avian Biology*. 43:33–42.