

VARIATION IN MORPHOLOGY AND MATING SYSTEM AMONG ISLAND POPULATIONS OF GALÁPAGOS HAWKS

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Abstract. Interspecific variation in sexual size dimorphism has commonly been attributed to variation in social mating system, with dimorphism increasing as intrasexual competition for mates increases. In birds, overall body size has also been found to correlate positively with size dimorphism. In this study, we describe variation in morphology and mating system across six populations of the endemic Galápagos Hawk (*Buteo galapagoensis*). Galápagos Hawks exhibit cooperative polyandry, a mating system in which long-term social groups contain a single female and multiple males. Comparisons among islands revealed significant differences in overall body size for both adults and immatures. Populations ranged from completely monogamous to completely polyandrous, with varying mean group sizes. Data did not support our prediction that sexual size dimorphism would increase with the degree of polyandry (number of males per group) or with body size; there was no correlation between mating system and sexual dimorphism. We did find a significant negative relationship between degree of polyandry and body size among islands, opposite of the pattern predicted.

Key words: *body size, Buteo galapagoensis, cooperative polyandry, Galápagos Hawk, principal components analysis, sexual size dimorphism.*

Variación en Morfología y Sistema de Apareamiento entre Poblaciones de *Buteo galapagoensis*

Resumen. Variación interespecífica en dimorfismo sexual ha sido atribuida comúnmente a variaciones del sistema social de apareamiento, de tal manera que el dimorfismo aumenta conforme aumenta la competencia intrasexual por parejas reproductivas. También se ha encontrado que el tamaño corporal se correlaciona positivamente con el dimorfismo. En este estudio describimos la variación morfológica y el grado de poliandria de seis poblaciones de *Buteo galapagoensis*, una especie que exhibe un sistema de apareamiento denominado poliandria cooperativa. En este sistema los grupos de individuos reproductivos incluyen una sola hembra y múltiples machos. Se comprobó que existen diferencias significativas en el tamaño del cuerpo de adultos y juveniles entre islas. Las poblaciones muestreadas variaron entre monógamas y completamente poliándricas, y el tamaño promedio de los grupos fue variable. Los datos no apoyaron las predicciones establecidas inicialmente pues el grado de dimorfismo sexual no aumentó con el nivel de poliandria (número de machos por grupo) ni con el tamaño corporal, ni hubo una correlación entre el sistema de apareamiento y el dimorfismo sexual. La relación entre el tamaño corporal y el sistema de apareamiento fue contraria a la que se predijo: hubo una correlación negativa significativa entre el grado de poliandria y el tamaño corporal entre islas.

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INTRODUCTION

Morphological variation among species or populations is driven by a number of factors, one of which is sexual selection. Interspecific variation in sexual size dimorphism has commonly been attributed to variation in social mating system and differences in parental care (Darwin 1871, Andersson 1994). The high levels of intrasexual competition for mates characteristic of polygamous systems may result in large body size in the competitive sex. Increased sexual size dimorphism was found to be associated with increased polygyny in the New World blackbirds (Icterinae; Webster 1992) and increased polygyny and polyandry (reverse size dimorphism) within the Charadrii (Székely et al. 2000). Among 73 species, Owens and Hartley (1998) found a significant positive relationship between sexual size dimorphism in body mass and degree of polygamy, while in a larger analysis ($n = 1031$ species), Dunn et al. (2001) found a similar relationship, with polygynous and lek species being more dimorphic than monogamous species.

Across taxa, species with greater size dimorphism also tend to be larger in overall body size. Webster (1992) reviewed 11 hypotheses that have been proposed to explain this relationship, all of which are based on males competing for females in polygynous systems. Four of these ideas are based on intrasexual competition as the cause of sexual size dimorphism. They predict that the association with body size results from polygyny being more likely among large-bodied species, larger females being favored as better competitors, genetic correlations increasing female body size as male size increases, or the change in male body size being greater in larger species. Other hypotheses predict that while sexual selection drives dimorphism, larger species may have fewer ecological or energetic constraints on body size, or only the female is constrained to a smaller body size. Still other hypotheses argue that larger species may be more dimorphic because of increased niche partitioning, male predator defense, differences in genetic variation among the sexes, or allometric growth, with sexual selection having no effect.

Among the New World blackbirds, Webster (1992) found that sexual size dimorphism correlated with body size but less strongly so than with polygyny. The effect of body size on sexual

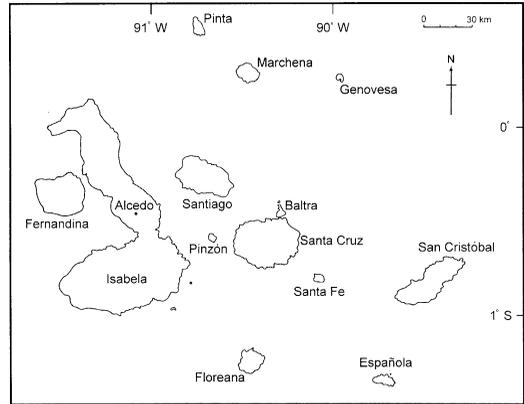


FIGURE 1. Map of the Galápagos archipelago showing islands where we acquired morphological measurements and group sizes for Galápagos Hawks: Volcan Alcedo on Isabela, Santiago, Pinta, Marchena, Santa Fe, and Española. The entire range of the Galápagos Hawk is limited to nine islands: the six mentioned above, Santa Cruz, Pinzón, and Fernandina.

size dimorphism disappeared after controlling for mating system, which Webster interpreted to mean that body size affects dimorphism indirectly through its effects on mating system. In their study, Dunn et al. (2001) also found a positive relationship between sexual size dimorphism and body size.

In this study, we look at the relationship between morphology and mating system in the Galápagos Hawk (*Buteo galapagoensis*), which is endemic to the Galápagos archipelago (Fig. 1). In addition to forming pairs, the Galápagos Hawk exhibits cooperative polyandry, in which one female mates with up to eight males (usually two or three), and all aid in the care of a single brood (Faaborg and Patterson 1981, DeLay et al. 1996). Group members are unrelated (Faaborg et al. 1995) and highly territorial, defending year-round, all-purpose territories (de Vries 1975). Observations of marked birds indicate that group membership is stable across years, especially for males (Faaborg et al. 1980, Donaghy Cannon 2001).

Immunatures are not territorial, and live in the floater population until they are at least three years old and able to secure a position in a territorial group. In addition to immunatures, non-breeding adult-plumaged hawks also occur in the floater population. On Santiago, adult male floaters are rarely seen; however, adult females account for a sizeable proportion of the floaters

(~17%; Donaghy Cannon 2001). Our observations between 1998 and 2002 suggest that competition among females for breeding spots may be high: (1) there is higher turnover among territorial females than males (Donaghy Cannon 2001); (2) four new territories carved out of area defended by existing groups were established by floater females and 1–3 males, never by males alone (Donaghy Cannon 2001); and (3) we have observed floater females fighting each other (JLB, pers. obs.).

Island populations tend to be small and isolated, which fosters genetic and phenotypic differentiation among them (Grant 1998, Whittaker 1998). Similar to most buteos, Galápagos Hawks are reluctant to cross wide expanses of water where thermals are not reliably present (Kerlinger 1985); thus, their populations are likely to be genetically isolated, with only a rare exchange of individuals between islands. Consistent with this suggestion, some authors have described morphological and behavioral differences across islands: larger hawks on Española (Swarth 1931, de Vries 1973) and variation in the frequency of polyandry (de Vries 1975, Faaborg et al. 1980).

Here, we quantify variation in morphology and mating system across six populations of the Galápagos Hawk. First, we use principal components analysis to assess morphological differences among adult and immature hawks from different islands. Second, we characterize the mating system on each of the islands based on the mean group size for each population. Finally, we look at whether there are relationships between morphology and mating system across populations. We test the prediction that the degree of sexual size dimorphism should be positively related to the degree of cooperative polyandry. If a greater frequency of polyandry is associated with more competition among females for access to males, then we would expect an increase in female body size, which would result in increased sexual dimorphism. We also test the predictions that body size will be positively related to sexual size dimorphism and to the degree of polyandry, as has been shown among polygynous species (Webster 1992).

METHODS

FIELD METHODS

Fieldwork was conducted in the Galápagos Islands between May and August of 1998–2001.

Hawks were caught on six islands (Fig. 1): Santa Fe ($n = 23$), Española (19), Santiago (223), Volcan Alcedo on Isabela (91), Pinta (12), and Marchena (25). The hawks were caught using two methods: a bal-chatri trap (Berger and Mueller 1959), baited with live prey such as a rat (*Rattus* spp.), and a rope noose on a stick (Faaborg et al. 1980). Each hawk was banded with either an aluminum or anodized color band bearing an alphanumeric code, or with both types of bands. The following morphological measurements were taken: wing chord (unflattened, to the nearest mm), tail length (posterior base of uropygial gland to tip of central rectrices, to nearest mm), cranium (posterior of cranium to tip of mandible, to nearest 0.1 mm), culmen (anterior edge of cere to tip of mandible, to nearest 0.1 mm), bill depth (vertical distance from dorsal to ventral surfaces of mandibles at anterior edge of cere, to nearest 0.1 mm), hallux claw (chord from proximal to distal extent of claw, to nearest 0.1 mm), foreclaw (as measured for hallux), and mass to nearest 10 g.

Given the large degree of reverse sexual size dimorphism present in the Galápagos Hawk, we were able to identify sex in the field. We used a PCR-based genetic sexing technique (Fridolfsson and Ellegren 1999) to confirm sex assignments for 328 of 330 birds (two Santiago immatures identified as males were found to be females). We were also able to place the birds into age classes, because their plumage gets progressively dark until they achieve adult plumage at five years of age (de Vries 1973).

Mating system was characterized by counting the number of adults present in each territory. We counted individuals during observations of chick provisioning at nests and when the nest or territory was being defended during our banding visits. All members of a group aggressively protected the young when we approached nests. Most territories were visited multiple times, so we feel confident that recorded group sizes were accurate.

STATISTICAL ANALYSES

Principal components analysis (PCA) was used to describe morphological differences among populations. Components with eigenvalues greater than one were retained, and eigenvectors were rotated using varimax rotation. Analyses were performed on log-transformed data. Females are on average 31% larger in mass than

males across populations (Table 1), and so the sexes were analyzed separately to prevent the variance due to sexual dimorphism from masking variation among populations. All analyses were done using SPSS 10.0.5 for Windows (SPSS Inc. 1999).

We conducted four PCAs: separate analyses on adult females, adult males, immature females, and immature males. The last two analyses were restricted to individuals from three populations because only single immature individuals of the same sex were captured on the other islands. Kruskal-Wallis tests were performed on the PC scores to test for significant differences among populations within sex and age classes.

We captured birds over a period of four years (1998–2001), so it is possible that year effects could have influenced our results. To test this, we performed Kruskal-Wallis tests on PC scores from adult females and males captured on Santiago in different years, as well as Mann-Whitney *U*-tests on PC scores from second-year females from two different years on Santiago. Sample sizes from other islands and other age classes were not large enough from multiple years to permit analysis.

We calculated a sexual size dimorphism index (Lovich and Gibbons 1992) as follows: sexual size dimorphism = (female measurement/male measurement) – 1. We evaluated whether there were significant differences in degree of sexual size dimorphism in overall body size across populations by testing for differences in degree of dimorphism in wing length and mass, the two variables that most strongly predicted overall adult body size according to the PCAs. We randomly paired the data from males and females within each population using all the adults, and calculated a size dimorphism index for each pairing. We conducted 100 randomizations for each population using the PopTools (v. 2.5.3; Hood 2002) add-in for Microsoft Excel. We assumed that our sampled individuals were representative of their populations, although our sample sizes were limited. Because the distributions did not have equal variances, a Kruskal-Wallis test was used to test for significant differences among populations in degree of wing and mass dimorphism. Additionally, overall size dimorphism indices were calculated for all eight variables for each population using the mean measurements for males and females. The val-

ues reported in the Results section are means \pm SD.

RESULTS

ADULTS

In general, birds from Española were the largest, then those from Isabela, Santa Fe, Santiago, Pinta, and Marchena; however, there was some variation in this order among the different measurements (Table 1). The PCAs yielded two components for both the females and males, explaining 63% of the total variance in both cases. The first principal component (PC1) for both sexes described overall body size, correlating positively and highly with all variables except the claw measurements (Table 2). Hallux and foreclaw loaded heavily onto the second component (PC2) in both sexes (Table 2).

Kruskal-Wallis tests performed on PC1 showed that the populations are significantly different in size for both females ($\chi^2_5 = 54.7$, $P < 0.001$; Fig. 2a) and males ($\chi^2_5 = 69.3$, $P < 0.001$; Fig. 2b). PC2 was also different among females ($\chi^2_5 = 29.5$, $P < 0.001$; Fig. 2a) and males ($\chi^2_5 = 26.1$, $P < 0.001$; Fig. 2b). These results indicate that there is a significant amount of morphological divergence among populations of Galápagos Hawks.

IMMATURES

For the immature females, individuals from Isabela, Santiago, and Marchena were used, and for immature males, individuals from Santa Fe, Isabela, and Santiago were used. Three components were kept in each analysis, explaining 74% of the total variance in females and 73% in males. The variables loaded similarly in both sexes (Table 2): hallux and foreclaw correlated highly with PC1, the head measurements (cranium, culmen, and bill depth) all loaded on PC2, and wing and tail length correlated most closely with PC3.

For the females, Kruskal-Wallis tests on PC1 ($\chi^2_2 = 9.9$, $P = 0.007$), PC2 ($\chi^2_2 = 26.9$, $P < 0.001$), and PC3 ($\chi^2_2 = 11.5$, $P = 0.003$) showed significant differences among islands (Fig. 2c). For the males, PC1 did not differ significantly ($\chi^2_2 = 5.1$, $P = 0.08$), while PC2 ($\chi^2_2 = 46.6$, $P < 0.001$) and PC3 ($\chi^2_2 = 7.8$, $P = 0.02$) did show significant differences among populations (Fig. 2d). These results indicate that, as in the adults, there are significant morphological dif-

TABLE 1. Means \pm SD (n) for eight measurements taken on adult female and male Galápagos Hawks from six islands. All measurements are in mm except for mass, which is in g.

Island Sex	Wing chord	Tail length	Cranium length	Culmen length	Bill depth	Hallux chord	Foreclaw chord	Body mass
Española								
Female	458 \pm 7 (10)	257 \pm 6 (10)	91.6 \pm 2.1 (10)	32.6 \pm 0.6 (10)	21.1 \pm 0.3 (9)	31.0 \pm 1.0 (10)	31.0 \pm 0.8 (8)	1578 \pm 83 (10)
Male	415 \pm 3 (8)	233 \pm 3 (8)	85.0 \pm 1.5 (9)	28.8 \pm 0.8 (8)	19.5 \pm 0.5 (8)	27.5 \pm 0.6 (9)	28.0 \pm 1.0 (7)	1137 \pm 37 (9)
Isabela								
Female	439 \pm 8 (11)	255 \pm 3 (10)	91.1 \pm 1.0 (9)	32.6 \pm 0.7 (11)	20.9 \pm 0.7 (10)	31.4 \pm 1.0 (11)	30.0 \pm 0.6 (10)	1494 \pm 96 (9)
Male	400 \pm 8 (8)	228 \pm 8 (8)	84.3 \pm 0.8 (7)	28.1 \pm 0.5 (7)	18.6 \pm 0.4 (8)	27.4 \pm 0.4 (7)	27.3 \pm 0.5 (8)	1013 \pm 59 (6)
Santa Fe								
Female	440 \pm 11 (8)	253 \pm 8 (9)	90.9 \pm 3.7 (8)	31.5 \pm 0.7 (8)	21.5 \pm 0.5 (9)	31.4 \pm 0.9 (9)	30.2 \pm 1.0 (6)	1354 \pm 64 (8)
Male	399 \pm 7 (9)	228 \pm 8 (8)	83.5 \pm 0.9 (9)	26.8 \pm 0.5 (8)	18.5 \pm 0.4 (9)	27.7 \pm 0.5 (9)	27.4 \pm 0.4 (7)	873 \pm 63 (9)
Santiago								
Female	429 \pm 8 (51)	245 \pm 6 (54)	91.2 \pm 2.0 (53)	32.0 \pm 0.9 (52)	20.7 \pm 0.6 (54)	32.0 \pm 1.3 (54)	31.5 \pm 1.0 (54)	1295 \pm 91 (53)
Male	392 \pm 10 (71)	224 \pm 6 (72)	83.4 \pm 1.5 (73)	27.8 \pm 0.8 (74)	18.0 \pm 0.4 (71)	27.8 \pm 1.1 (74)	27.7 \pm 1.0 (75)	903 \pm 54 (74)
Marchena								
Female	424 \pm 5 (4)	239 \pm 7 (4)	87.6 \pm 0.8 (4)	30.6 \pm 0.5 (4)	20.0 \pm 0.4 (4)	30.3 \pm 0.8 (4)	29.3 \pm 1.0 (4)	1223 \pm 107 (4)
Male	381 \pm 5 (16)	216 \pm 6 (17)	80.5 \pm 1.0 (17)	26.3 \pm 0.5 (17)	17.6 \pm 0.3 (17)	27.1 \pm 0.8 (17)	27.0 \pm 0.9 (17)	844 \pm 75 (17)
Pinta								
Female	417 \pm 9 (3)	239 \pm 1 (2)	88.1 \pm 2.1 (3)	29.2 \pm 0.2 (3)	20.0 \pm 0.3 (3)	31.4 \pm 2.2 (3)	29.7 \pm 0.4 (2)	1235 \pm 118 (3)
Male	381 \pm 11 (9)	214 \pm 5 (8)	81.8 \pm 1.2 (8)	26.1 \pm 0.8 (9)	18.2 \pm 0.3 (8)	26.0 \pm 0.4 (6)	26.1 \pm 1.1 (9)	891 \pm 33 (8)

TABLE 2. Results of four separate principal components (PC) analyses of Galápagos Hawks: adult and immature males and females. Numbers are variable loadings on each significant axis and percentage of total variance explained. We analyzed sexes separately because of the considerable sexual dimorphism in this species. In both immature analyses, we omitted body mass as a variable because we lacked this measurement for many individuals from Isabela. Variable loadings were similar within age groups, but quite different between age groups.

Variable	Adult females			Adult males			Immature females			Immature males		
	PC1	PC2	PC3	PC1	PC2	PC3	PC1	PC2	PC3	PC1	PC2	PC3
Wing chord	0.83	-0.05	0.75	0.32	0.29	0.65	0.33	0.32	0.65	0.52	0.07	0.57
Tail length	0.78	-0.01	0.67	0.31	0.08	0.87	-0.04	0.31	0.87	-0.21	-0.03	0.85
Cranium length	0.47	0.45	0.65	0.10	-0.18	0.34	0.68	0.10	0.34	-0.24	0.62	0.38
Culmen length	0.60	0.41	0.58	0.47	0.22	-0.07	0.81	0.47	-0.07	0.29	0.79	-0.15
Bill depth	0.67	0.21	0.81	-0.04	0.28	0.08	0.78	-0.04	0.08	0.06	0.87	-0.02
Hallux chord	-0.07	0.88	0.08	0.89	0.93	0.04	0.15	0.89	0.04	0.92	0.04	-0.04
Foreclaw chord	0.03	0.91	0.15	0.88	0.88	0.28	0.13	0.88	0.28	0.88	0.10	-0.15
Body mass	0.81	-0.12	0.79	0.07	0.46	0.46	0.17	0.07	0.46	0.33	0.24	0.16
% Variance explained	40	24	46	17	40	15	18	17	15	33	24	16

ferences among immature hawks from different islands.

YEAR EFFECTS

Kruskal-Wallis tests on the PC scores for Santiago adult females ($n = 53$) captured in four different years showed no significant differences among years (both $\chi^2_3 \leq 2.4, P > 0.5$). The same was true for the adult males ($n = 72$) from Santiago (both $\chi^2_3 \leq 3.7, P > 0.8$). Second-year females on Santiago, however, did show a significant difference between two years. Individuals caught in 1999 ($n = 9$) were significantly larger at PC1 ($U = 14, P = 0.01$) and smaller at PC2 ($U = 17, P = 0.02$) than those caught in 1998 ($n = 10$).

VARIATION IN MATING SYSTEM AND SEXUAL SIZE DIMORPHISM

The degree of polyandry varied greatly across islands, from 0% of territories sampled on Española to 100% of territories sampled on Pinta, Marchena, and Isabela (Table 3). The mean number of males per group varied significantly across islands (Kruskal-Wallis test: $\chi^2_5 = 32.5, P < 0.001$). Islands with larger mean group sizes tended to have a higher proportion of polyandrous groups as well, although our sample sizes from some of the islands were low (Table 3).

There was some variation in the degree of sexual size dimorphism among islands (Table 4). The degree of wing and mass dimorphism of males and females randomly assigned to pairs showed significant differences among populations (Kruskal-Wallis: $\chi^2_5 = 26.6, P < 0.001$ and $\chi^2_5 = 119.3, P < 0.001$, respectively). However, there was no relationship for any measurement between degree of dimorphism (as calculated from population means for each sex) and degree of polyandry across islands (all $r \leq 0.65, P > 0.16$), nor was there a relationship between dimorphism and overall body size as measured by mean male (all $r \leq 0.54, P > 0.27$) and female (all $r \leq 0.51, P > 0.30$) PC1 scores.

There was, however, a strong relationship between overall body size and mating system. Body size (PC1) of both adult females ($r = -0.72, P < 0.001$; Fig. 3a) and males ($r = -0.69, P < 0.001$; Fig. 3b) was significantly negatively correlated with degree of polyandry. PC2 was not significantly related to mating system ($r = -0.09, P = 0.41$) in females, but it

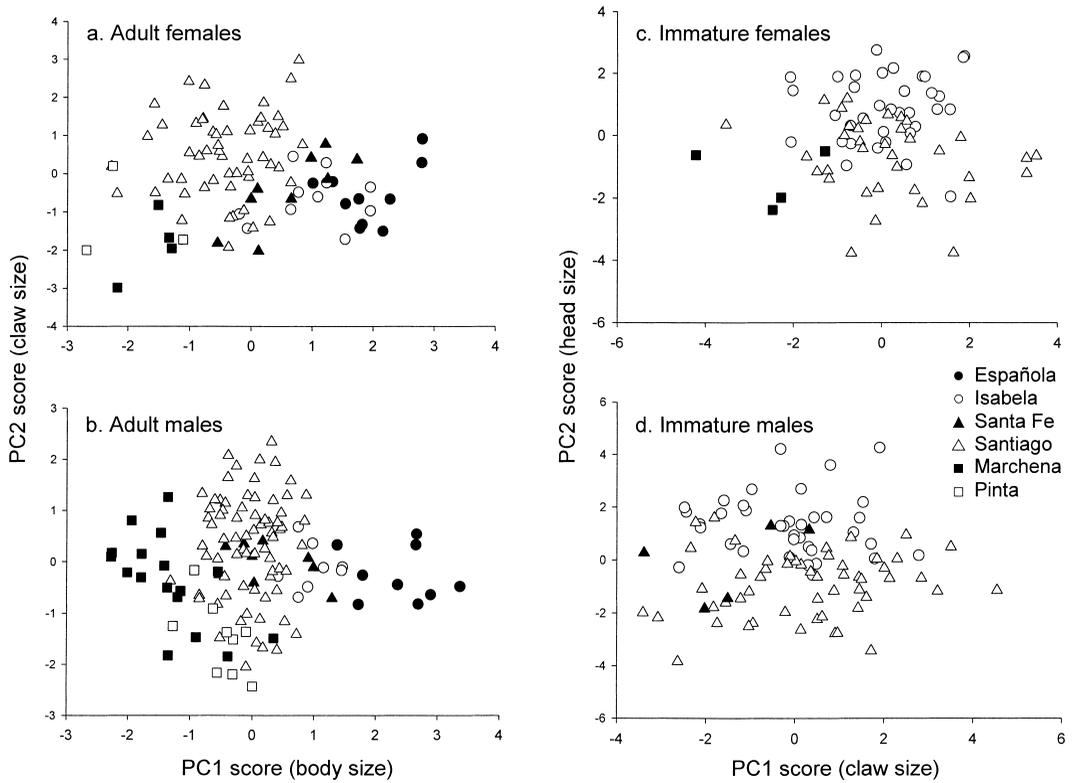


FIGURE 2. Principal components (PC) analysis of Galápagos Hawk morphology. Results are from four separate analyses. Variable loadings were similar between sexes but different between ages (see axis descriptions). Analyses were conducted on (a) 91 adult females, (b) 127 adult males, (c) 75 immature females, and (d) 95 immature males from six (adults) or three (immatures) different islands.

was in males ($r = -0.20, P = 0.03$), despite a large degree of scatter.

DISCUSSION

We sampled Galápagos Hawks on six of the nine islands they inhabit, and found that they varied greatly in morphology and mating system. The principal components analyses described significant differences among populations in overall

body size and claw size. The degree of polyandry also varied widely across populations. We had predicted that the degree of sexual size dimorphism would increase with increasing polyandry and body size because of potential intra-sexual competition (Webster 1992). Although the degree of sexual size dimorphism differed somewhat across islands, there was no relationship between size dimorphism and polyandry or

TABLE 3. Island area and degree of polyandry found in Galápagos Hawks breeding on six islands.

Island	Area (ha) ^a	No. of territories sampled	Percent polyandrous	Mean ± SD no. of males per territory
Española	6048	11	0	1.0 ± 0.0
Santa Fe	2413	6	50	1.5 ± 0.6
Santiago	58 465	32	89	2.3 ± 0.8
Isabela	458 812	3	100	2.3 ± 0.6
Marchena	12 996	6	100	2.8 ± 1.0
Pinta	5940	6	100	3.5 ± 1.6

^a Black 1973.

TABLE 4. Sexual size dimorphism indices for eight measurements taken from six Galápagos Hawk populations. The indices were calculated as the female population mean divided by the male population mean minus one. All variables are measured in mm except for body mass (g).

	Wing chord	Tail length	Cranium length	Culmen length	Bill depth	Hallux chord	Foreclaw chord	Body mass
Española	0.10	0.10	0.08	0.14	0.09	0.13	0.11	0.39
Santa Fe	0.10	0.11	0.09	0.18	0.16	0.13	0.10	0.55
Isabela	0.10	0.12	0.08	0.15	0.12	0.14	0.11	0.47
Santiago	0.10	0.09	0.09	0.16	0.14	0.15	0.14	0.47
Marchena	0.11	0.11	0.09	0.16	0.14	0.12	0.09	0.45
Pinta	0.09	0.12	0.08	0.12	0.10	0.20	0.14	0.39

body size. There was, however, a strong negative correlation between body size and degree of polyandry.

There were some potential sources of error in the morphological analyses. The majority of birds were measured once, so we lack data on measurement repeatability. Also, measurements

were taken over a span of four field seasons. Immature females caught in different years on Santiago differed significantly in size, but there were no differences among adults. We doubt that year effects greatly affected the analyses of the immatures, because the majority of immature males from Santiago (20 of 24), females from Isabela (33 of 36), and males from Isabela (29 of 35) were captured during a single year, 1998. A third source of error was variation in sample size; certain age and sex categories from some of the islands had limited sample sizes.

VARIATION IN MATING SYSTEM

The mating system of the hawks ranged from monogamous pairs to large polyandrous groups. Our sample of groups from Santa Fe was small, but the level of polyandry we observed (50% of territories) is similar to previous estimates. In 1969 and 1979, 47% of territories ($n = 15$; 1.5 ± 0.6 [SD] males per territory) and 50% of territories ($n = 16$; 1.7 ± 0.8 males per territory; Faaborg et al. 1980) held polyandrous groups, respectively. The current absence of polyandry on Española is similar to what de Vries (1975) found in 1970, when he recorded only one trio in 10 territories. Similarly, on Santiago Faaborg et al. (1980) found that 85% of territories in 1979 were polyandrous compared to our finding of 89% in 2000. There are no previous mating-system data for Marchena, Pinta, or Isabela. We found 100% polyandry on each of these islands. While our sample sizes from Santa Fe, Marchena, and Pinta are much smaller than our sample from Santiago, their populations are also much smaller, so the proportion of territories sampled may actually be larger. Our characterization of mating system on Isabela, however, is clearly preliminary. Given the large size of Isabela, mating system and morphology may vary across

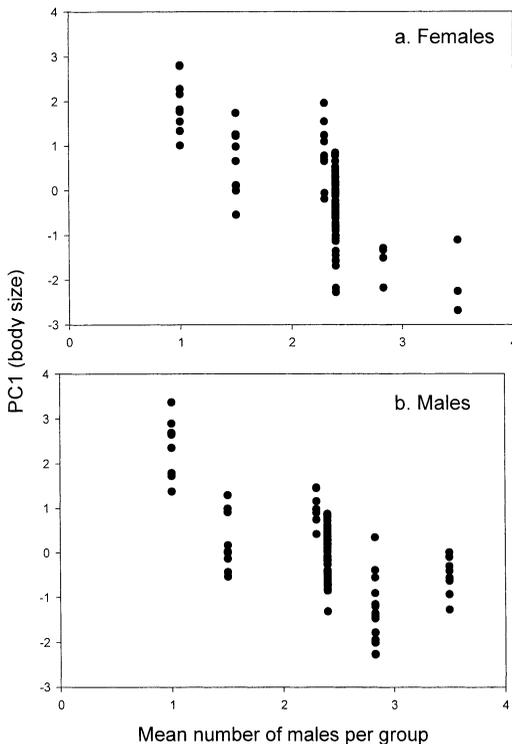


FIGURE 3. The relationship between body size and degree of polyandry in Galápagos Hawks on six islands. Body size was measured as the first principal component in individual analyses of (a) adult females and (b) adult males. Degree of polyandry was measured as the mean number of adult males per territorial group for each of six islands.

the island, and our characterization may be just for hawks on Volcan Alcedo and not Isabela as a whole.

This variation in degree of polyandry across islands could be related to variation in sex ratio, survivorship, and ecology. Polyandry may arise from male-biased sex ratios; however, the presence of large numbers of adult female floaters on Santiago (Donaghy Cannon 2001) suggests that mates are not limiting for male Galápagos Hawks on this island. Sex ratio has not yet been studied on the other islands. Across species, cooperative breeding is associated with high annual adult survivorship, which leads to low turnover of breeders on territories (Arnold and Owens 1998). Faaborg et al. (1980) hypothesized that the variation in degree of polyandry among Galápagos Hawk populations may result from interisland variation in survival of both adult male floaters and territorial males. Annual survivorship of nonterritorial hawks on Santiago (50–58%) is greater than on Santa Fe (0–33%), where there is less polyandry (Faaborg 1986, Donaghy Cannon 2001), which suggests that more “excess” nonbreeders accumulate in the floater population of Santiago. As another alternative, polyandry may have arisen in the Galápagos Hawk due to a limitation in suitable breeding territories (Faaborg and Bednarz 1990). The number of suitable territories, and hence the degree of such limitation, probably varies as a result of ecological factors peculiar to each island (Arnold and Owens 1999, Hatchwell and Komdeur 2000).

SEXUAL DIMORPHISM AND POLYANDRY

The degree of sexual size dimorphism was not related to variation in polyandry, a finding for which there are a number of possible explanations. Sexual selection may be weaker when females (as opposed to males) compete for mates, because females generally experience lower variance in reproductive success (Payne 1984). Although studies have shown that classically polyandrous species are more dimorphic than monogamous species (Székely et al. 2000, Dunn et al. 2001), intraspecific variance in female reproductive success among Galápagos Hawk populations may be too weak to drive changes in size dimorphism. In addition, factors other than sexual selection can drive sexual size dimorphism (Hedrick and Temeles 1989), and different se-

lective forces may be acting on the two sexes (Price 1984).

On average, female Galápagos Hawks are 31% heavier than males, making them one of the most dimorphic *Buteo* species (of 22 species compared; Paton et al. 1994). Aside from mating system, other factors may play a role in producing this large degree of dimorphism. Diurnal raptor species that pursue aerial or high-speed prey are generally more dimorphic (Reynolds 1972, Wheeler and Greenwood 1983), although Galápagos Hawks mostly capture their prey on the ground (de Vries 1976). Alternatively, size dimorphism may minimize intrasexual competition for food (Storer 1966). Island species may evolve greater sexual dimorphism due to decreased interspecific competition or increased intraspecific competition from high population densities (Stamps et al. 1997). Among closely related *buteos* (Riesing et al. 2003), the island-dwelling Hawaiian Hawk (*Buteo solitarius*) is similarly dimorphic (Paton et al. 1994, Clarkson and Laniawe 2000), while the mainland Swainson's Hawk (*Buteo swainsoni*), is less so (Friedmann 1950, England et al. 1997).

BODY SIZE AND POLYANDRY

There was a strong relationship of decreasing body size with increasing degree of polyandry across populations. Our prediction, made from the female point of view, was the reverse: as intrasexual competition for mates increases, body size should increase. Taking the male point of view, though, we might have predicted this result. Among hawks, smaller males are more agile (Andersson and Norberg 1981) and may be favored in aerial fights. We could speculate, then, that as mean group size increases, the level of competition for limited space also increases. Territory defense should become more difficult (especially for smaller groups neighboring larger ones), thus selecting for smaller body size, perhaps in both males and females.

Alternatively, the correlation between polyandry and body size is not causal, but is the result of a third, unknown factor. For example, a number of studies have attributed interisland morphological differentiation to variation in available resources, presence of competitors, or predation pressure across islands (Schwaner 1985, Freeman-Gallant 1996, Yasushi et al. 1999). Schoener (1969) and Schwaner and Sarre (1990) predicted that optimal body size should

be related to prey size or availability. At this time we do not know enough about the different island populations to evaluate the influence of these factors on body size.

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