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EXTREME SEXUAL DIMORPHISM IN GREEN WOODHOOPOE (*PHOENICULUS PURPUREUS*) BILL LENGTH: A CASE OF SEXUAL SELECTION?

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ABSTRACT.—Adult male Green Woodhoopoes (*Phoeniculus purpureus*) are only 5–8% larger than adult females in most linear measures but have 36% longer bills. Such sexual dimorphism may result from sexual selection, reproductive role division, or ecological separation. Here, we show that there is little evidence that sexual selection is currently acting on bill dimorphism in the Green Woodhoopoe. (1) Breeding males did not have longer bills than nonbreeding males. (2) There was no significant relationship between bill length and reproductive success of breeding males. (3) Although there was greater variation in male than in female bill length, the coefficient of variation (5.3%) fell within the range of those for naturally selected traits. (4) Although male bill length was found to be positively allometric with body mass, female bill length followed a similar relationship and there was no significant difference between the allometric slopes of the two sexes. Maintenance of the bill dimorphism by reproductive role division also seems unlikely when considering the nesting and provisioning characteristics of the species. We therefore conclude that the extreme sexual dimorphism in Green Woodhoopoe bill length is maintained by ecological separation to reduce foraging competition. We cannot, however, rule out the possibility that the sexual dimorphism initially evolved as a consequence of sexual selection. *Received 23 January 2003, accepted 5 October 2003.*

RESUMEN.— Los machos adultos de la especie *Phoeniculus purpureus* son sólo un 5–8% más grandes que las hembras adultas en la mayoría de mediciones lineales, pero tienen picos que son un 36% más largos. Este dimorfismo sexual podría ser el resultado de selección sexual, de división de las tareas reproductivas o de separación ecológica. En este estudio, demostramos que existe poca evidencia de que la selección sexual esté operando en la actualidad sobre el dimorfismo sexual en *P. purpureus*. (1) Los machos reproductivos no tuvieron picos más largos que los machos que no se reprodujeron. (2) No hubo una relación significativa entre la longitud del pico y el éxito reproductivo de los machos que se reprodujeron. (3) Aunque hubo mayor variación en la longitud del pico en los machos que en las hembras, el coeficiente de variación (5.3%) estuvo en el rango observado en caracteres que son objeto de selección natural. (4) Aunque se encontró que la longitud del pico de los machos tiene una relación alométrica positiva con la masa corporal, la longitud del pico de las hembras mostró una relación similar, y las pendientes alométricas de los dos sexos no fueron significativamente diferentes. El mantenimiento del dimorfismo en el pico por la división de tareas reproductivas también parece poco probable, considerando las características de nidificación y aprovisionamiento de la especie. Por lo tanto, concluimos que el dimorfismo sexual extremo en la longitud del pico en *P. purpureus* es mantenido por separación ecológica para reducir la competencia en el forrajeo. Sin embargo, no podemos descartar la posibilidad de que el dimorfismo sexual haya evolucionado inicialmente como consecuencia de selección sexual.

AMONG BIRDS, THE most extreme case of bill dimorphism was in the extinct Huia (*Heteralocha acutirostris*): males were 5–7% larger than females in tarsus, wing, and tail length, but females had 60% longer bills (Burton 1974). Three main hypotheses have been proposed as the evolutionary cause of such sexual dimorphism (Hedrick and Temeles 1989, Shine 1989): (1) sexual selection for enhanced courtship or combat ability, (2) reproductive role division, and (3) ecological separation.

Green (also known as Red-billed) Woodhoopoes (*Phoeniculus purpureus*) are cooperatively breeding birds that live in groups of 2 to 12 individuals (du Plessis 1991). Adult males are 5–8% larger than adult females in wing, tail, and tarsus length, as well as cube root mass, but

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have 36% longer bills (Radford and du Plessis 2003). All individuals within a group forage together, creating opportunities for conflict over food resources. Intersexual competition is reduced by the specialization of each sex for different foraging techniques, each suited to their particular bill length (Radford and du Plessis 2003). Ecological separation therefore plays a role in maintaining the bill-length dimorphism apparent today. However, body traits may be influenced by both natural and sexual selection (Price 1984, Buchanan and Evans 2000).

If sexual selection is also important in the maintenance of bill-length dimorphism, the following general predictions can be made. First, breeding males should have longer bills than nonbreeding males. Second, males with longer bills should have greater reproductive success (RS). Third, variation in male bill length should be larger than variation in both female bill length and other male morphometric traits (Alatalo et al. 1988, Møller and Höglund 1991, Evans and Barnard 1995). Fourth, male bill length should be positively allometric with respect to body size (i.e. larger individuals should have relatively larger bills), rather than isometric (Alatalo et al. 1988; Petrie 1988, 1992; Green 1992, 2000). Moreover, the allometric slope of male bill length against body mass should be significantly more positive than that of females.

METHODS

We used measurements from individuals caught between 1981 and 2001 near Morgan's Bay (32°43'S, 28°19'E), Eastern Cape Province, South Africa. Birds were caught in nets placed over roost holes before dawn. Five measurements were taken from each bird: (1) mass (in grams) using a 100-g Pesola scale, (2) flattened wing chord (distance from the carpal joint to the tip of the longest primary), (3) tarsus length (along the anterior surface between the articulation with the middle toe and the tibiotarsal joint), (4) bill length (chord between the tip of the bill and the anterior edge of the cere), and (5) tail length. Wing and tail lengths were measured to the nearest millimeter with a stopped ruler. Bill and tarsus lengths were determined to the nearest 0.1 mm with dial calipers. To test the repeatability of measurements, 10 males were each measured three times on the same capture occasion. Each bird was marked with an individual combination of color bands and a uniquely numbered aluminum band. To avoid sampling biases, only the first set of measurements from any given individual was included in a particular analysis; subsequent recaptures were discarded.

Number of young fledged from the sole breeding attempt per season was determined by regular nest and group watches during the breeding period. Because of the strict queuing system that operates in this species, breeders tend to be those individuals of each sex that have been in the group the longest (A. N. Radford and M. A. du Plessis unpubl. data). When that information was unknown, breeding status was established by watching copulation attempts (preliminary paternity analysis has confirmed that only the dominant pair breed; A. N. Radford and M. A. du Plessis unpubl. data) and displacement activity during group foraging (when breeding individuals dominate nonbreeding helpers; Radford and du Plessis 2003).

To normalize data, all morphometric variables were natural-log transformed before analysis. Repeatabilities were calculated according to Lessells and Boag (1987). Relationship between bill length and RS (defined as the number of successfully fledged young in the season in which the breeding adult was caught) was investigated using an ANOVA, controlling for group size. Allometric slopes of bill and wing length in relation to body mass were calculated using reduced major axis (RMA) models to place the line of best fit in bivariate plots of natural-log transformed data. Theoretically, RMA regression provides a better estimate of the allometric relationship than ordinary least-squares regression (Lande 1979, Green 2000) but assumes that the ratio of the error variances equals the ratio of the two actual variances in the raw data (Pagel and Harvey 1988). See McArdle (1988) for the methods used to calculate the statistical significance of the deviation between observed RMA slopes and those expected under the null hypothesis of isometry, and to test the equality of slopes of distinct RMA regressions. Linear measures were considered to be isometric where they scaled with a slope of one-third against body mass in log–log bivariate plots.

RESULTS

Both breeding males and females were significantly older (males: $t = 2.86$, df = 62, $P = 0.006$; females: $t = 2.67$, df = 37, $P = 0.011$) and heavier (males: $t = 2.70$, df = 116, $P = 0.008$; females: $t = 2.25$, df = 88, $P = 0.028$) than nonbreeding adults of the same sex. There was no significant difference in bill length between breeding and nonbreeding individuals when controlling for these age and body-mass differences (males: $F = 3.25$, df = 1 and 57, $P = 0.079$; females: $F = 0.27$, df = 1 and 36, $P = 0.606$). There was also no significant relationship between bill length and fledging success for either breeding males ($F = 1.16$, df = 1 and 59, $P = 0.285$) or breeding females ($F = 0.97$, df = 1 and 53, $P = 0.365$).

Repeatability measures were high for bill, tail, and wing lengths (all $F > 16.32$, df = 9 and 20, $r > 0.82$), but not so for tarsus length ($F = 2.38$, df = 9 and 20, $r = 0.32$). Because measurement error may influence the coefficient of variation (CV), tarsus length was excluded from all subsequent comparisons. There was significantly greater variation in male bill length than in female bill length (CV: males = 5.3%, females = 4.3%; F-test: $F = 2.28$, df = 1 and 194, $P < 0.001$). This was not due to seasonal changes in male bill length in relation to food availability: there was no significant difference in the bill lengths of males caught in the breeding period (November to February) and those captured during the winter months of May to August ($t = 0.70$, df = 94, $P = 0.490$). There was no significant difference between males and females in the variation of their wing length (males = 2.4%, females = 2.6%; $F = 1.05$, df = 1 and 196, $P = 0.825$) or tail length (males = 5.0%, females = 5.9%; $F = 1.46$, df = 1 and 157, $P = 0.100$). Although there was significantly greater variation in male bill length compared to male wing length ($F = 6.55$, df = 1 and 195, $P < 0.001$), there was no significant difference in the variation of male bill length and male tail length ($F = 1.29$, df = 1 and 175, $P = 0.146$). Variation in female bill length was significantly greater than that in female wing length ($F = 3.14$, df = 1 and 197, $P < 0.001$), but significantly less than that in female tail length ($F = 2.14$, df = 1 and 173, $P < 0.001$).

When related to body mass, wing length did not deviate significantly from isometry in either sex (males: RMA slope = 0.438, $t = 1.18$, df = 97, $P > 0.05$; females: RMA slope = 0.392, $t = 0.69$, df = 97, $P > 0.05$; Fig. 1A). Bill length was positively allometric in both sexes (males: RMA slope = 0.980, $t = 4.69$, df = 96, $P < 0.01$; females: RMA slope = 0.643, $t = 2.82$, df = 94, $P < 0.01$; Fig. 1B). The allometric slope was more positive in males than in females for both bill and wing length, but the difference in slopes between sexes was not significant in either case (wing: $t = 0.342$, df = 97, $P > 0.50$; bill: $t = 1.30$, df = 94, $P > 0.10$).

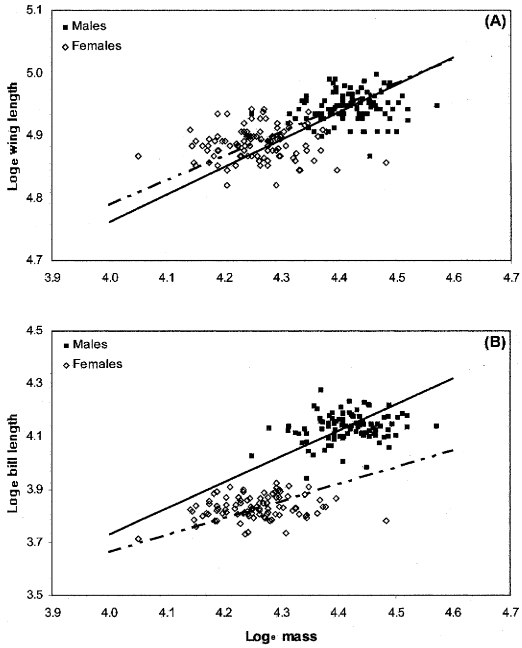

FIG. 1. Scaling of (A) wing length and (B) bill length against body mass in adult Green Woodhoopoes. Lines are plotted by reduced major axis: (A) males ($n = 99$), solid line: $y = 0.44x + 3.01$; females ($n = 101$), dotted line: $y = 0.39x + 3.22$; (B) males ($n = 98$), solid line: $y = 0.98x - 0.19$; females ($n = 98$), dotted line: $y = 0.64x + 1.09$.

DISCUSSION

The extreme bill dimorphism found in the Green Woodhoopoe could have arisen from one, or a combination, of three main mechanisms: sexual selection, reproductive role division, and ecological separation. Our study has supplied only limited evidence that sexual selection currently plays an important role. First, there was no significant difference in bill lengths of breeding and nonbreeding adult males, after controlling for overall body size and age. The mating system of the Green Woodhoopoe actually provides little opportunity for either female choice or male–male competition. Breeding vacancies are most frequently attained through inheritance, even when that results in incest, with males queuing in line for access to a mate (A. N. Radford and M. A. du Plessis unpubl. data). Queuing appears to follow a strict convention: access to mates is determined by the sequence in which males join queues, hence explaining the older age of breeding males. Thus, queuing males that survive for a sufficiently long period can expect eventually to gain access to a mate, irrespective of their bill length. Fighting between males is also rarely seen and, when apparent, does not rely on the use of bills (A. N. Radford and M. A. du Plessis pers.

obs.). If females accepted matings from males other than the dominant individual within their group, they might use bill length as an indicator of male quality. However, early paternity results suggest that only the dominant pair breed (A. N. Radford and M. A. du Plessis unpubl. data).

Second, there was no significant relationship between bill length and RS among breeding males. Other factors, such as food availability and predation, may explain more of the variance in RS in that species. Third, variation in male bill length (5.3%) fell within the range of variation in other body size characteristics (2.3–5.9%). Studies in many other species have found the CV of ornaments to be 3 to 5× greater than that of naturally selected traits (e.g. Alatalo et al. 1988, Jones and Montgomerie 1992, Evans and Barnard 1995). Moreover, although woodhoopoes pass lichen, flowers, or bark between one another during vocal rallying displays (Ligon and Ligon 1978), the use of flags does not form part of the courtship routine (A. N. Radford and M. A. du Plessis pers. obs.). Thus, males do not seem to draw attention to their bills while courting females.

The intersexual difference in bill-length variability could, theoretically, be due to seasonal changes in male bill morphology in relation to food availability (Gosler 1987). However, 72% of measurements were taken during the same four months each year. Furthermore, there was no significant difference in bill length of males caught during the breeding period, when food was likely to be abundant (see van Noordwijk et al. 1995), and those caught in the winter, when food may have been scarcer. Instead, the intersexual difference in bill-length variation might be a consequence of the different foraging techniques used by males and females (Radford and du Plessis 2003). For example, there may be tighter structural constraints on bill length in females, which spend more time hammering at bark, compared to males, which prefer to probe existing holes. Alternatively, if different foraging techniques result in differential bill wear, there could be more variation in male bill length as a result of greater variation in male technique use.

Finally, although there was a positive allometric relationship between male bill length and body mass, as expected for a sexually selected character (Green 1992, 2000; Petrie 1992), bill length was also positively allometric in females. Furthermore, there was no significant intersexual difference in the allometric slopes. Wing length was sexually dimorphic, but isometric in both sexes, as expected for a trait under natural selection. Petrie (1988) argued that structures important in displaying competitive ability between individuals should develop in a positively allometric manner in species where large animals usually win fights, but positive allometry has also been predicted for ornaments important in female choice (Alatalo et al. 1988, Green 1992). Green (2000) suggested that if sexual selection on a character acts more strongly on one sex, leading to dimorphism, then allometry should be more positive in that sex. Because Green Woodhoopoe groups may contain several members of each sex, sexual selection could theoretically operate in both males and females (see Jones and Hunter 1993). However, breeding females did not have significantly longer bills than nonbreeding females, variability in female bill length fell within the range seen in other morphometric characters, and there was no significant relationship between female bill length and RS. Hence, mutual sexual selection for bill length seems unlikely in that species. Positive allometry may therefore have arisen under circumstances other than sexual selection (Green 1992). For example, both sexes are involved in inter-group conflicts that, though usually resolved by vocal rallying displays (Radford 2002, 2004), do sometimes escalate to physical fighting. An individual of either sex with a bill that was disproportionately large might therefore present a greater threat to opponents.

Positive allometry implies relatively greater benefits for a larger individual in making a given investment in a character (Green 1992, Petrie 1992). Any finding of positive allometry should therefore include some differential cost or benefit with respect to body size, either during the development or the wearing of the structure (Petrie 1992). Longer bills may be costly in terms of growth and maintenance, reduced strength or increased fragility, and the slight gain in mass might increase energetic costs. The only individuals in the population seen with broken bills have been males (A. N. Radford and M. A. du Plessis pers. obs.).

Although the evidence is slightly equivocal, there is only a weak indication, at most, that sexual selection is currently operating on Green

Woodhoopoe bill length. Sexual dimorphism in bill length is also unlikely to be maintained by sex-specific functions, such as parental care or nest building. Green Woodhoopoes nest in natural cavities or holes created by woodpeckers and barbets. Hence, breeders do not need to excavate nest cavities. Because both sexes provision nestlings (du Plessis 1991) and helpers are often present (Ligon and Ligon 1978), no specialization is needed by males to provide for the young (cf. Jönsson and Alerstam 1990). Consequently, ecological separation appears to be the major process maintaining the extreme bill dimorphism: Green Woodhoopoes spend most of their time foraging as close-knit units, which may result in intensified foraging competition and an increased pressure for niche partitioning (Radford and du Plessis 2003). Further support for this hypothesis comes from two sources. First, Green Woodhoopoes only become physiologically capable of reproducing after one year (A. N. Radford and M. A. du Plessis unpubl. data), but the bill dimorphism is already apparent four months after fledging (Radford 2002). Second, the four Phoeniculidae species that live in cooperative groups, and thus experience greater foraging competition, tend to exhibit a larger degree of bill dimorphism (24.0 ± 4.0%) than the three species that form pairs (16.9 ± 1.7%; Radford 2002).

Finally, it is important to remember that the selective forces giving rise to morphological traits may not be the same as those maintaining them (Lande 1980). Even seemingly clear-cut cases of ecological causation may have originally resulted from sexual selection (see e.g. Simmons and Scheepers 1996). Hence, although the extreme bill dimorphism of the Green Woodhoopoe now appears to be maintained and shaped by ecological separation, we cannot rule out the possibility that sexual selection previously played a role.

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