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Sexual Dimorphism in the Kea *Nestor notabilis*

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Summary: Morphological differences between the sexes in Keas *Nestor notabilis* were quantified from a sample of 86 sexed museum specimens, nine sexed zoo captives and 129 live, wild-caught birds. The results demonstrate that Kea are sexually dimorphic. Males are about 5% larger than females in linear measurements of body size and their upper bills are on average 12-14% longer, with a slightly larger radius of curvature. The dimorphism in bill size was statistically independent of the difference in

overall body size, suggesting the possibility of intersexual differences in niche utilisation. Culmen length appears to be a useful means for distinguishing sexes in the field: our data indicate an optimum separation criterion of 43.9 mm for wild-caught individuals. Culmen length measurements from specimens originating in captivity were more variable. There was no evidence that sexual dimorphism increases with sexual maturity in this species.

Introduction

Although Keas *Nestor notabilis* have been known since 1865, an awareness of the morphological differences between males and females of the species was slow to develop. Early writers felt that they could distinguish the sexes but were not clear about the criteria they used. Marriner (1908) claimed that the female Kea is 'more slightly built', with a bill that is 'neither so stout nor so powerful' as that of the male. Similarly vague criteria were invoked by Derscheid (1947), while Porter (1947) asserted that the sexes in Kea are distinguishable only by the 'aggressive demeanour' of the male.

Oliver (1955) was the first to settle on a specific di-agnostic feature, remarking that 'the upper mandible in the female is shorter than in the male and less curved'. This distinction has since become generally accepted (Soper 1965; Forshaw 1977; Falla *et al.* 1978), despite the lack of confirmatory quantitative studies. As an illustration of the problem, we note that the statement of the bill dimorphism in Forshaw (1977) is immediately followed with a summary description of morphological data from eight male and seven female Kea, in which the mean culmen lengths are statistically indistinguishable.

The question is not of negligible importance. Most parrot species are sexually monomorphic (Smith 1975; Forshaw 1977). Where dimorphism has been recorded, it is generally restricted to plumage colouration: Forshaw's (1977) comprehensive

review of the order cites only four other genera of parrots in which a sexual size dimorphism has been recorded. Since size dimorphism has commonly been associated with intersexual differences in feeding ecology (Selander 1966), social behaviour (Selander 1958; Verner & Willson 1969), or both (Snyder & Wiley 1976), its demonstrated presence in Keas would open up a number of features of their biology for further exploration. In addition, there are practical benefits for studies of ecology and social behaviour in being able to sex birds reliably in the field.

In this study, we have undertaken the first quantitative examination of sexual dimorphism in the Kea. The analysis focused on five issues: what were the morphological differences between sexes? Was there any evidence that the differences were independent of any overall difference in body size? How reliable a criterion is morphology for distinguishing sexes in the field? Could we substantiate Oliver's (1955) contention of a difference in the curvature of the bill? And finally, did the degree of dimorphism increase with age?

Methods

To analyse the nature of sexual dimorphism in Keas, we measured a total of 224 birds. The primary data source was a sample of 86 sexed study skins and museum mounts from museum collections and nine captive Keas that had been laparoscoped and measured under anaesthesia at the San Diego Zoo.

Together, these constituted a sample of 95 birds of known sex.

The second data set was obtained from 129 unsexed individuals trapped and banded in the field as part of a long-term study of population dynamics and feeding biology. These birds were captured between 1987 and 1988 in Arthur's Pass National Park, Mount Cook National Park, Westland National Park and Craigieburn Forest Park. Birds were captured at varying times of year, though more than 75% were taken between November and February. To avoid sampling biases, only the first set of measurements on any given individual was included in the analysis: recaptures were discarded.

Four measures of bill morphology were taken. Culmen length was measured as the chord between the tip of the bill and the anterior edge of the cere. Because of Oliver's (1955) suggestion that the bill may be more strongly curved in males than in females, the length of the culmen was also measured along its dorsal curvature. This variable, the 'curvature length', was taken using a flexible metal tape closely appressed to the surface.

Bill width was measured as the width of the maxilla at the anterior edge of the cere. In museum specimens, bill depth was also taken. We measured the vertical distance between the anterior edge of the cere and the posterior edge of the mandibular symphysis (the deepest point of the gonys) when the bill was fully closed. When specimens were mounted with their bills open, bill depth was approximated by measuring the maxillary and mandibular components separately and adding them. It was not feasible to measure bill depth on living birds.

Two foot and leg measures were taken. The length of the tarsometatarsus was measured along the anterior surface, between the articulation with the middle toe and the tibiotarsal joint. The customary measurement of the length of the middle toe, between the metatarsal joint and the base of the claw, proved to be difficult to obtain in living Keas, owing to their resistance to fully straightening the most distal phalangeal joint. Our toe measurement was, therefore, made between the meta-tarsal joint and the distal edge of the penultimate phalangeal scute. The wing chord was measured from the base of the pollex to the tip of the longest primary. The length of the tail was measured along the ventral side, from the base to the tip of the longest rectrix. Feather measurements were not recorded on live birds.

In addition to the linear measurements, the live birds were weighed with a 5 kg spring scale, accurate to the nearest 25 g. Juvenile Keas are characterised by yellow colouration in the cere,

mandible and eye ring (Schmidt 1971). On the basis of the presence, partial loss or absence of this yellow pigment, the live birds were classified into one of three age categories: juvenile, sub-adult or adult. Although museum specimens exhibited a range of pigmentation patterns in these areas, we had no way of determining whether this variation reflected differences in stage of maturity or simply post-mortem differences in the study skins. Therefore, we did not make any inferences about age class from the museum material.

Because of differences in technique and in the particular measurements taken, it was not feasible to combine the two data sets in a single analysis. Instead, the sexed specimen data set was used initially to determine whether Keas are, in fact, sexually dimorphic. Because accurate weight data were not available for most of the sexed specimen sample, we subsequently used the live, wild-caught sample to distinguish bill dimorphism from the effects of an overall difference in body size.

Results

The first concern in the analysis was to test for sexual dimorphism: Did males and females differ significantly in any regard? A comparison of the measures obtained from the 95 sexed specimens (63 males and 32 females) revealed that males were consistently larger on all eight variables (Table 1). Significant differences between sexes were observed for culmen length, curvature length, bill width, middle toe and wing chord (Table 1). The magnitude of the dimorphism was about 12% for the two culmen length measures; for most other variables, it was roughly 5%.

Such pervasive intersexual differences suggested an overall size dimorphism. This interpretation received additional support from an examination of the correlations among the eight measures. Of the 28 possible pairs of variables, 22 showed significant positive correlations. At the very least, therefore, overall size accounted for a significant portion of the variance in the data. The next step was to ask whether the dimorphic measures were distinctive. Specifically, was the difference in culmen length an independent phenomenon or was it simply one manifestation of an overall difference in body size?

To answer this question required the use of our second data set, obtained from live, wild-caught birds. The most reliable single measure of overall size is clearly weight but weight was recorded for only a handful of the sexed specimens. Weight was known for all of the live, wild-caught sample but they provided no independent confirmation of sex. To make sense of the relative contributions of

Table 1 Univariate comparisons of measures from 95 sexed specimens (SS) and 129 live, wild-caught specimens (LW). Sex for all LW specimens was assigned on the basis of cluster analysis. Where the estimated population variances differed between the sexes, an unpooled t-test was used, with an appropriate reduction in the degrees of freedom. Measures are in millimetres (mm) unless otherwise noted.

Measure	Sex	Mean	(s.e., n)	t(d.f.)	P	% Diff	
Culmen length	M	(SS)	49.5	(0.9, 63)	6.85 (93)	0.0001	11.7
		(LW)	48.2	(0.4, 91)	15.7 (53)	0.0001	14.3
	F	(SS)	43.7	(1.5, 32)			
		(LW)	41.3	(0.8, 37)			
Curvature length	M	(SS)	55.7	(1.2, 63)	6.70 (93)	0.0001	13.6
		(LW)	55.3	(0.6, 90)	15.8 (122)	0.0001	16.1
	F	(SS)	48.1	(2.1, 32)			
		(LW)	46.4	(0.9, 34)			
Bill depth	M	(SS)	28.4	(0.6, 62)	1.93 (48)	n.s.	4.2
		(LW)	no data				
	F	(SS)	27.2	(1.1, 32)			
		(LW)	no data				
Bill width	M	(SS)	13.1	(0.1, 62)	5.17 (92)	0.0001	5.3
		(LW)	13.2	(0.1, 90)	10.6 (84)	0.0001	8.3
	F	(SS)	12.4	(0.2, 32)			
		(LW)	12.1	(0.2, 34)			
Tarsometatarsus	M	(SS)	42.6	(0.7, 63)	1.77 (93)	n.s.	2.5
		(LW)	45.8	(0.5, 89)	2.14 (120)	0.03	2.2
	F	(SS)	41.5	(1.0, 32)			
		(LW)	44.8	(0.8, 33)			
Middle toe	M	(SS)	40	(0.5, 63)	5.87 (93)	0.0001	6.6
		(LW)	44.1	(0.4, 89)	6.15 (120)	0.0001	5.7
	F	(SS)	37.3	(0.8, 32)			
		(LW)	41.6	(0.5, 32)			
Wing chord	M	(SS)	307	(3.0, 63)	2.75 (93)	0.007	2.2
		(LW)	no data				
	F	(SS)	301	(4.0, 32)			
		(LW)	no data				
Tail length	M	(SS)	155	(3.0, 63)	0.68 (93)	n.s.	0.1
		(LW)	no data				
	F	(SS)	154	(4.0, 32)			
		(LW)	no data				
Weight (g)	M	(SS)	no data				
		(LW)	956	(18, 91)	10.9 (127)	0.0001	18.5
	F	(SS)	no data				
		(LW)	779	(22, 38)			
Cube root weight	M	(SS)	no data				
		(LW)	9.84	(0.06, 91)	11.2 (127)	0.0001	6.6
	F	(SS)	no data				
		(LW)	9.19	(0.09, 38)			

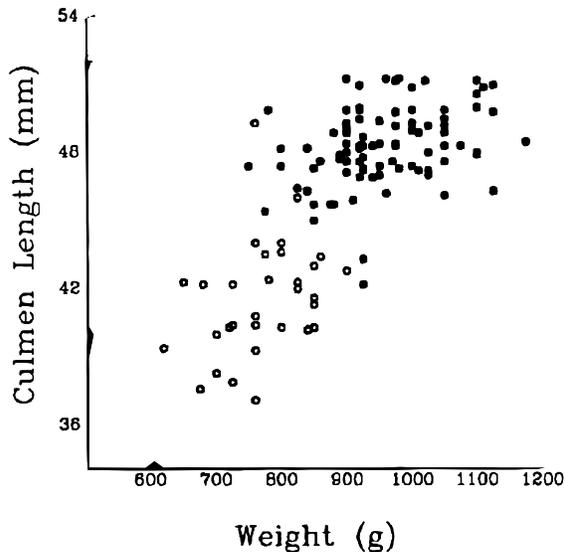


Figure 1 Scattergram of culmen length versus weight from live, wild-caught Keas. Open circles indicate observations that were classified as females on the basis of cluster analysis; closed circles indicate individuals classified as males.

weight and culmen length, we needed to obtain an objective estimate of sex for all of the live, wild-caught specimens.

Our approach was to use cluster analysis on the live, wild-caught data set to separate the observations into two consistent groups on morphological grounds alone. The mean values of the linear measures for these two groups were then compared with those taken from the sexed specimens to confirm that the clustering procedure had produced a satisfactory approximation to separating the sexes. Finally, we performed a discriminant analysis, using the sex assignments from the clustering procedure, to distinguish the contributions of weight and culmen length.

The set of measurements from 129 live, wild-caught birds, consisting of culmen length, curvature length, bill width, tarsometatarsus, middle toe and weight, was standardised prior to clustering to assure equal weighting in the procedure. Five clustering algorithms were applied to the observations, using the SAS programs CLUS and FASTCLUS (SAS 1985). The algorithms used included disjoint clustering by nearest centroids, two-stage density linkage, Ward's minimum variance method, hierarchical centroid method and average link-age.

The clustering procedure revealed two clear, homogeneous groupings: a set of 91 presumed males and a set of 38 presumed females. The structures generated by all of the algorithms, were very similar: only four individuals were placed in different

groups by one or another of the clustering techniques. In these few cases of disagreement, the observation was assigned to the group designated by four of the five algorithms. The results were dominated by the joint variation of weight and culmen length; it is in a scattergram of these two measures that the cluster structure is most clearly displayed (Fig. 1).

Univariate statistical comparisons were then performed on these groups for each of the six measures (Table 1). The degree of dimorphism in the linear variables from live specimens was generally comparable to what was observed in the sexed data set. Furthermore, when weight was converted to a linear measure, by taking the cube root, the degree of dimorphism exhibited was comparable to that shown by the middle toe or bill width, supporting the initial suggestion of a 5-6% difference in linear measures of body size.

To discover whether the dimorphism in bill size was simply a reflection of the body size difference, we used a stepwise discriminant analysis, in which a minimal set of distinguishing variables is obtained by adding or re-moving measures one at a time. The criterion for inclusion in the set is the added contribution that the given variable makes to our ability to discriminate sexes. This analysis thus partials out the common variance in the measures and considers only the unique, incremental contribution provided by each variable.

Discriminant analysis was performed on the live, wild-caught data set, using the SAS procedure STEPDISC (SAS 1985). The criterion for inclusion in the set of discriminating variables was chosen so as to generate a model that provided the best discrimination for the given sample size. To obtain a basis for comparison, we ran an initial analysis in which no variables were forced to be included in the set of discriminators. Under these circumstances, culmen length was the first variable to enter the discriminant set, followed by bill width, curvature length and weight. Presumed sex accounted for 70% of the variance in culmen length, 11-12% of the variance in bill width and curvature and 4% of the variance in weight.

Since the relationship between sex and culmen length necessarily included a component of body size, however, the influence of weight was greatly underestimated in this first analysis. To determine the actual influence of weight, it was necessary to run a second analysis, in which weight was forced to be the initial element of the discriminant set, thus eliminating any influence of overall size on the inclusion of subsequent variables. Under these conditions, presumed sex accounted for 48% of the weight variance but the same three bill measures —

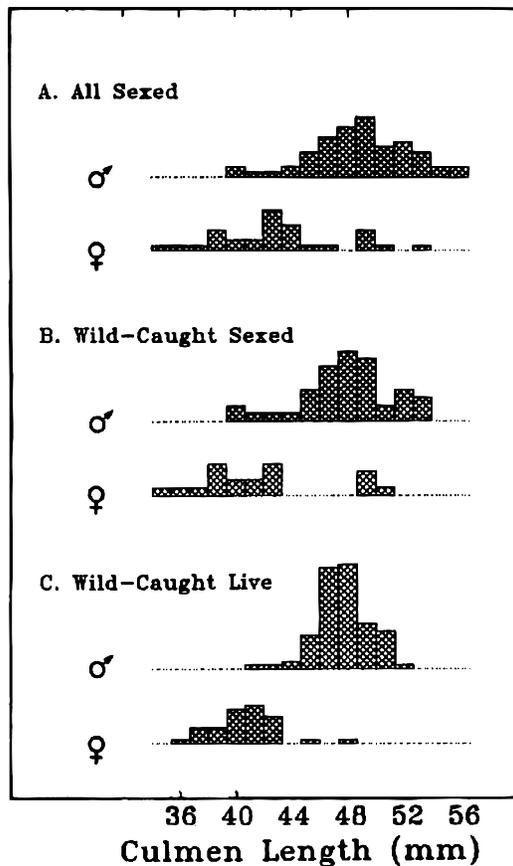


Figure 2 Histograms of culmen length, separated by sex, for each of three data sets: (A) Measurements from 95 sexed museum specimens; (B) Measurements from a sub-sample of 61 sexed museum specimens, including only birds obtained from the wild; (C) Measurements from 129 live, wild-caught birds, with sex inferred from cluster analysis. Histograms were normalised to equal areas; height of bar indicates proportion of given data set

culmen length, bill width, and curvature length — were again drawn into the discriminative set. With the influence of weight removed, presumed sex still accounted for 45% of the variance in culmen length, 8% of the variance in bill width and 12% of the variance in curvature.

These results suggest that bill size and body size are independently sexually dimorphic in the Kea. They also imply that the three dimensions of bill size make partially independent contributions to discriminating sex. That is, bills are wider, as well as longer, in males than they are in females and this is not entirely due to a tendency of longer bills to be wider at the base.

The degree of sexual dimorphism was greater for culmen length than for any other single morphological measure (Table 1). It was, therefore, reasonable to inquire whether culmen length could provide a reliable means of sexing Keas in the field. If we

assume that the sexes are equally probable, the optimum criterion for categorisation is the value of culmen length that minimises the difference between the cumulative percentiles for males and females. All animals with culmen lengths less than or equal to the optimum criterion would be classed as females; all those with lengths greater than the criterion would be considered males.

The data set based on the 95 sexed specimens shows an optimum criterion for culmen length of 45.7 mm: applying this criterion retrospectively would correctly classify 89% of the males and 78% of the females (Fig. 2a). To increase the usefulness of the classification criterion to the examination of Keas in the field, we selected a sub-sample of birds from the sexed specimen data set which excluded all specimens obtained from zoos or private aviaries. When specimens originating in captivity were removed from the sexed data, a number of outliers were eliminated (Fig. 2b) and the optimum criterion shifted to 43.9 mm, correctly classifying 90% of the males and 79% of the females. This criterion was identical to that derived from the live, wild-caught specimens, using the sex categories assigned on the basis of the cluster analysis (Fig. 2c)

Oliver (1955) asserted that the culmen in males is more highly curved than that in females, which is to say that the radius of curvature should be smaller in males than in females. To test this hypothesis, an independent estimate of the radius of curvature was obtained for each specimen. If the curvature of the bill is approximated by a segment of a circle, the culmen length constitutes a chord of the circle, C , while the curvature length measures the corresponding sector of the circumference, S . The relationship between these measures and the radius of curvature, R , is:

$$\sin[S / (2R)] = C / (2R) \quad (\text{Beyer 1987}).$$

Using this equation, an estimate of the radius of curvature was obtained for each of the sexed specimens. The mean radius for males was 34.2 mm, while that for females was 33.6 mm. This difference was not significant ($t_{93} = 0.84$, $P > 0.4$). The corresponding estimates obtained from the live data set were smaller: 31.6 mm for presumed males and 29.3 mm for presumed females. This difference proved to be significant, however ($t_{45} = 2.06$, $P < 0.05$). If anything, therefore, the bills of males were somewhat less curved than those of females.

To determine whether sexual dimorphism was greater in mature individuals than in juveniles, we conducted a two-way Analysis of Variance (age \times sex) on the measurements from live birds. Since the sample sizes were not constant across cells, we used

a general linear models procedure, SAS procedure GLM (SAS 1985), which takes unbalanced designs into account. If the degree of dimorphism increased with the onset of sexual maturity, a significant interaction of age and sex for dimorphic variables would be expected. The interaction term was, however, insignificant for all six of the variables tested ($F_{2,115} < 1.96$, $P > 0.14$). The main effects of age (Table 2) indicate that adults and sub-adults, irrespective of sex, were generally about 5% larger than juveniles. This difference was only significant for culmen length and tarsometatarsus, however.

Discussion

Our results demonstrate that Keas are sexually dimorphic. Males are about 5% larger than females in linear measurements of body size and their bills are roughly 12-14% longer. Oliver (1955) was, thus, correct in distinguishing the sexes by bill length but appears to have been mistaken in his belief that the bill of the male is more strongly curved. Where it was possible to find a difference in the radius of curvature between sexes, our results suggested that the male's bill may actually be less curved than the female's.

Measurement of culmen length appears to provide a useful criterion for distinguishing sexes in the field. On the basis of a subset of museum specimens, including only wild-caught birds, 79% of the specimens with culmen lengths of less than 43.9 mm were females, while 90% of those with culmen lengths of 43.9 mm or greater were males. Given the likelihood that at least some of these specimens

were incorrectly sexed, this probably represents a minimum estimate of the categorisation efficiency. Bill measurements from specimens of captive individuals, on the other hand, were often much larger than those observed in the field (Fig. 2). Identification of captive individuals through the use of culmen length should, therefore, be considered tentative and confirmatory laparoscopies should be performed before undertaking a captive breeding program.

The only previous quantitative study of Kea morphology was conducted by Campbell (1976), who measured curvature length on 132 specimens, mostly skeletal remains collected by sheep farmers. The histogram of these data shows a distinct bimodality, with a minimum at 51 mm (Campbell 1976). If we extract a critical value for curvature length (instead of culmen length) from our data set of live animals, the minimum for misclassification, and hence the highest value for females, occurs at 50 mm. Campbell's data thus appear to be entirely compatible with ours. If we apply the 50 mm criterion to Campbell's histogram, his sample divides into 45 presumed females and 86 presumed males, a ratio that is comparable to what we observed in both the museum and the live data sets. The lack of a sufficient sample of sexed museum specimens unfortunately misled Campbell into the belief that Kea are not sexually dimorphic, with the consequence that he did not differentiate males and females in his foraging study (Campbell 1976).

Among the Psittaciformes, Forshaw's (1977) compendium lists the shining parrots *Prosopieia*, the rosellas *Platycercus* and the Kakapo *Strigops* as

Table 2 Mean measurements for each age grouping (juveniles, sub-adults and adults) from live specimens and results of Analysis of Variance. Data are based on a sample of 129 live, wild-caught birds. Measurements are in millimetres (mm) unless otherwise noted.

Measure	Juvenile (n=48)	Sub-adult (n=17)	Adult (n = 59)	F	(di)	P
Culmen length	45.4	46.9	46.7	4.64	(2,115)	0.01
Curvature length	51.8	54.0	53.4	2.88	(2,115)	n.s.
Bill width	12.8	12.7	13.0	1.24	(2,115)	n.s.
Tarsometatarsus	45.1	46.7	45.6	3.53	(2,115)	0.03
Middle toe	43.4	44.1	43.3	0.4	(2,115)	n.s.
Weight (g)	876	927	922	1.65	(2,115)	n.s.

displaying sexual size dimorphism. However, only the Kea and the Palm Cockatoo *Probosciger aterrimus* appear to exhibit a bill dimorphism that is greater than any difference in overall body size (D'Ombra 1933; Forshaw 1977). In this regard Keas are apparently quite unusual for their order. Comparable degrees of bill dimorphism have been recorded for many other avian species, however, including Varied Sitellas *Daphoenositta chrysoptera* (11%; Noske 1986), Great Frigatebirds *Fregata minor* (11%; Schreiber & Schreiber 1988) and Gila Wood-peckers *Melanerpes uropygialis* (14%; Martindale & Lamm 1984).

Selander (1966) noted that many island species exhibit extensive sexual dimorphism in trophic structures. The bill dimorphism in the Maui Parrotbill *Pseudonestor xanthophrys*, for example, is 19% (Mountain-spring 1987); in the Cape Verde Island Lark *Alauda razae*, it is 21% (Burton 1971); and in species of *Centurus* and *Melanerpes* woodpeckers from Caribbean is-lands, it ranges from 15-21% (Selander 1966). In the most extreme case known, that of the extinct Huia *Heteralocha acutirostris* from the North Island of New Zealand, the female's bill was over 60% longer than that of the male (Burton 1974).

This observation led Selander (1966) to suggest that the development of dimorphism in these cases was the result of 'ecological release' due to the lower levels of interspecific competition on islands. He went on to argue that dimorphism in trophic structures is generally associated with differential niche utilisation (Selander 1966). Reduction of ecological competition between the sexes has since been cited as a factor in the evolution of dimorphism even in continental species, such as West-ern Grebes *Aechmophorus occidentalis* (Wallace 1978).

Differential selection for bill size could also, of course, result from effects on social behaviour if larger bill sizes were correlated with increased mating success in males. Our finding that dimorphism does not increase with sexual maturation in the Kea casts some doubt on this hypothesis. If the sexual difference were instrumental in obtaining mates, it would be unusual for it to be fully developed in immature animals. The results of the current study are clearly insufficient, however, to re-solve the issue. A thorough understanding of the adaptive significance of bill dimorphism in the Kea will require quantitative field studies of the differences between males and females in foraging behaviour, as well as an investigation of the relationship between morphology and mating success.

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