Boofheads with deep voices: Sexual dimorphism in the Magpie Goose Anseranas semipalmata

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Magpie Geese use a unique polygynous mating system, involving apparently stable trios of one male and two females. Plumage shows little sexual differentiation, but there is considerable dimorphism in body size, with males being about 30% heavier. The males also develop an extraordinarily elongated and elaborately folded trachea early in life, whereas less than 8.5% of females show even minor tracheal elaboration. Head height, a measure of the size of a cranial bump of spongy bone increases with age in both sexes, but most markedly in males. Males found in association with nests have larger bumps and highly elaborated tracheal morphology. The deeper and louder calls associated with gross tracheal elongation, which probably compromises respiratory exchange, may influence female choice of mates by providing a reliable signal of male viability. Despite significant overlap in individual dimensions, especially among younger birds, more than 92% can be accurately sexed using a discriminant function based on three simple measures (head–bill length, head height, and tarsus length). Discrimination can be improved by checking birds assigned as females against an index of tracheal morphology. Simulations indicate that bias in estimates of sex ratios arising from application of the discriminant function, when combined with tracheal examination, is likely to be less than 2%.

Magpie Geese *Anseranas semipalmata* display a mating system that is unique among waterfowl. Most reproductive groups comprise trios of one male and two females, both of which lay approximately synchronously in a shared nest (Frith & Davies 1961). Equally unusually (Johnsgard 1978), while there is no obvious difference between the sexes in plumage, the species shows considerable sexual dimorphism in body size, with weights of adult males averaging about 30% more than females. In addition to greater general bulk, males also show much greater development of a distinctive, skin-covered cranial bump of spongy bone and an extraordinarily elongated trachea, lying in folds beneath the pectoral skin (Frith & Davies 1961).

Despite such an array of potentially quantifiable dimorphic characters, Frith and Davies (1961) concluded, from examination of a large sample (761 birds), that there was sufficient overlap in dimensions within populations (including birds of all post-fledging age classes) to prevent use of any single measurement to reliably determine sex. Perhaps as a result, there has been no systematic attempt to relate the species' unusually pronounced sexual dimorphism to its equally enigmatic mating system. This paper seeks to fill part of that gap.

Movever, the species is exploited for subsistence and recreation (eg Dexter 1988, Whitehead et al. 1988), and faces changes in habitat quality over parts of its already

Table 1. Summary of categories of tracheal loop length and configuration to which observations were assigned for analysis. Positions and configurations of loops were determined by palapating the skin at the base of the neck and overlying the breast.

Class	Number of loops	Length (cm) of longest loop	Location (relative to sternal crest)
0	0	-	-
1	1	<5	left side
2	1 or 2	<10	left side
3	2	<15	left side
4	2	<20	left side
5	2	>20	left side
6	3	>15	2 long loops on left, 1 shorter loop on right
7	4	>20	2 long loops on left, 2 shorter loops on right

drastically contracted contemporary range (Whitehead et al. 1992). Harvests and habitat deterioration will affect different elements of the life cycle in many interacting ways, and the dynamics of populations are too poorly understood (Frith & Davies 1961) for the cumulative effects of these changes to be predicted. Robust methods of sexing and assigning birds to age or other classes based on reproductive status will therefore be important for developing models of population dynamics as tools for management.

Accordingly, I also extend this re-examination of morphometric variation to provide:

(1) a method for sexing birds from a small number of simply- and non-invasively measured dimensions;

(2) measures of potential error in estimating sex ratios with this method; and,

(3) evidence of age-related variation in some dimensions that, with further study, might be employed to assign broad age classes or life cycle stages.

Methods

Study sites are located in the seasonal tropics of the Northern Territory, Australia. The region's climate is characterised by heavy rainfalls during a hot summer monsoon (November to April) when most of the annual rainfall of more than 1,600 mm occurs. For the remainder of the year (the cooler dry season) there is little or no rain. During the late dry season (early September to early December) Magpie Geese were captured in baited walk-in funnel traps or by cannon nets at Berrimah on the outskirts of Darwin, and at two sites on the western margin of the Mary River floodplain, about 60 km east of Darwin. During the breeding seasons (March/April) birds were also caught on nests by hand or using remotely-triggered clam traps in or near a breeding colony at Opium Creek, also on the Mary River floodplain. The Mary River sites are described in detail in Whitehead et al. 1990a.

All birds caught were released fitted with a stainless steel leg band and an aluminium (MacInnes et al. 1969) or laminated plastic neck

collar similar to that described by Johnson and Sibly (1989). As well, 26 birds of known age were hatched from artificially incubated eggs and raised in captivity for various periods. Data from live birds were supplemented by birds (i) killed by recreational hunters and (ii) taken for a genetic study while they were escorting goslings (Horn et al. 1996).

Head-bill length, head height and leg dimensions (tarsus) were measured with vernier calipers (±0.1 mm) as described by Whitehead et al. (1990b), and many birds were also weighed with a spring balance (±50g). The measurement of head height used here, from the top of the cranial bump to the bottom of the lower mandible, varies from that used by Frith & Davies (1961) - the distal corner of the eye to the top of the skull - to avoid the need to position calipers near the eye of live and struggling birds.

Live birds were sexed at the time of capture by cloacal examination (n=349) or subjectively by an experienced observer (n=428). Sex of dead birds was determined by dissection and gonadal examination. Only dissected birds or captive birds sexed by repeated cloacal examination were used in quantitative analyses used to discriminate sexes (below).

Many Magpie Geese show tracheal 'loops' of varying length and configuration originating at the base of the neck and overlying the pectoral muscle and wall of the abdominal cavity. The loops can be easily detected and their location determined by palpating the skin over the breast and abdomen (Frith & Davies 1961). Because of the time required to measure length of subcutaneous structures precisely, tracheal dimensions were estimated relative to conspicuous anatomical features such as the base of the sternum, and variation summarised by assigning observations to one of eight broad categories (**Table 1**).

Birds caught on nests were regarded as reproductively active, although it was not possible to demonstrate that captured birds had contributed genetically to the clutch. For all numerical analyses, only birds known to be less than one year old (ie captive bred) were assigned to the juvenile category.

Discriminant analysis (SAS procedure DISCRIM) was used to derive functions to assign individual observations to sex classes from a range of linear dimensions, using a group of 64 birds for which sex was unambiguously known (from dissection for wild birds (n=38) or repeated cloacal examination for birds of known age raised in captivity (n=26)). The sample of 26 captive birds was of known age (75 days) and was included to ensure that the discriminant function incorporated observations from the youngest birds likely to be encountered in free-flying populations.

A number of wild birds were recaptured and remeasured at intervals ranging from a few days to more than three years. Post-fledging variation in head and leg dimensions was modelled from re-measurements at intervals exceeding 30 d using the von Bertalannfy growth equation (which takes the form $y=a(1-be^{-kt})$, where y is the dimension of interest at time t, a is the asymptotic size, b and k are constants. As ages of birds were mostly unknown, methods summarised by Fabens (1965) were used. Models were derived iteratively using the SAS NLIN procedure (SAS Institute Inc. 1989), to fit values for the growth constant, k, and asymptote, a.

Analysis of covariance employed SAS procedure GLM. Frequency distributions were compared with the Kolmogorov-Smirnov test (SAS NPAR1WAY procedure). Means are given with the standard deviation unless otherwise indicated.

Results

Sex Differences

Head and Leg Dimensions and Body Weight

Mean dimensions for fledged wild Magpie Geese caught live or measured post-mortem are summarised in **Table 2**, and some patterns of association among these measures are illustrated in **Figures 1a-1c**. Males were typically larger than females in all dimensions.

Body weight was strongly correlated (P<0.0001) with all three linear dimensions in both sexes. The rate of increase in body weight with head-bill length (males, r=0.43; females,

Table 2. Mean (+SD) and range of measured dimensions of wild Magpie Geese (422 males and 420 females). Inter-sex variation was highly significant for all dimensions ($P<0.0001$). All birds were flying but varied widely in age.

Dimension	Male		Female	
	Mean±SD	Range	Mean±SD	Range
Weight (g)	2432±316	1480 to 3200	1858±232	1150 to 2420
Head-bill length (mm)	130.3±4.0	120.0 to 141.6	117.8±3.3	109.2 to 126.0
Head height (mm)	62.2±8.6	44.0 to 85.0	52.1±5.2	40.7 to 65.8
Tarsus length (mm)	103.8±4.9	87.7 to 117.7	92.3±4.2	80.6 to 104.3

$r=0.43$) was consistent between sexes (**Figure 1a**:ANCOVA, sex by head-bill interaction term, $F_{1,715}=0.7$, $P=0.40$) but males were significantly heavier than females with the same head-bill length (factor sex, $F_{1,715}=21.3$, $P<0.0001$). Fitting a power relationship between head-bill length and weight did not produce a significantly better fit. The relationship between weight and tarsus length (males, $r=0.40$; females, $r=0.36$) was similar to the head-bill/weight relationship.

Body weight was most strongly positively correlated with head height (males, $r=0.69$; females, $r=0.65$), a dimension that appears to vary with age in both sexes (Frith & Davies 1961; and below). Entry of head height into regressions already containing head-bill or tarsus length significantly increased explained variance in body weight in both sexes ($P<0.0001$).

Tarsus length was correlated with head-bill length in both sexes (**Figure 1b**). Slopes of simple regression lines were similar for each sex (ANCOVA: $F_{1,775}=0.41$, $P=0.52$), but intercepts varied significantly ($F_{1,775}=29.6$, $P<0.0001$). Males tend to have longer tarsi than females of the same head-bill length.

The relationship between head-bill length and head height was relatively weaker, probably due to post-fledging growth of the cranial bump in both sexes (**Figure 1c** and below). The great post-fledging increase in head height is illustrated in **Figure 1c** by inclusion of a regression line showing the relationship of head-bill length to head height in juvenile birds. There was no between-sex variation in this relationship for young birds ($F_{1,51}<0.24$, $P>0.62$). In contrast, the association between these head dimensions in the sample of wild birds of all ages varies significantly between sexes ($F_{1,774}=7.2$, $P=0.008$), with males developing relatively larger cranial bumps than females at equivalent head-bill lengths. If it is assumed that the age structure of the male and female samples are broadly similar, this variation in relationships implies more rapid growth in head height among males than in females.

Tracheal morphology

There was also marked between-sex variation in the length and configuration of the trachea. Most females (91.5%) lacked tracheal loops (**Figure 2**), or had small ones extending no more than a few centimetres from the left side of the neck.

Among birds with greater development of the trachea, there were invariably two loops on the left side of the sternum (classes 2 to 5 in **Figure 2**), one lying inside the other so that four closely-associated tracheal diameters could be felt beneath the skin. Many males also show a third, smaller loop on the right side of the neck (class 6), and one bird had a fourth right-side loop (class 7). The left-side loops are
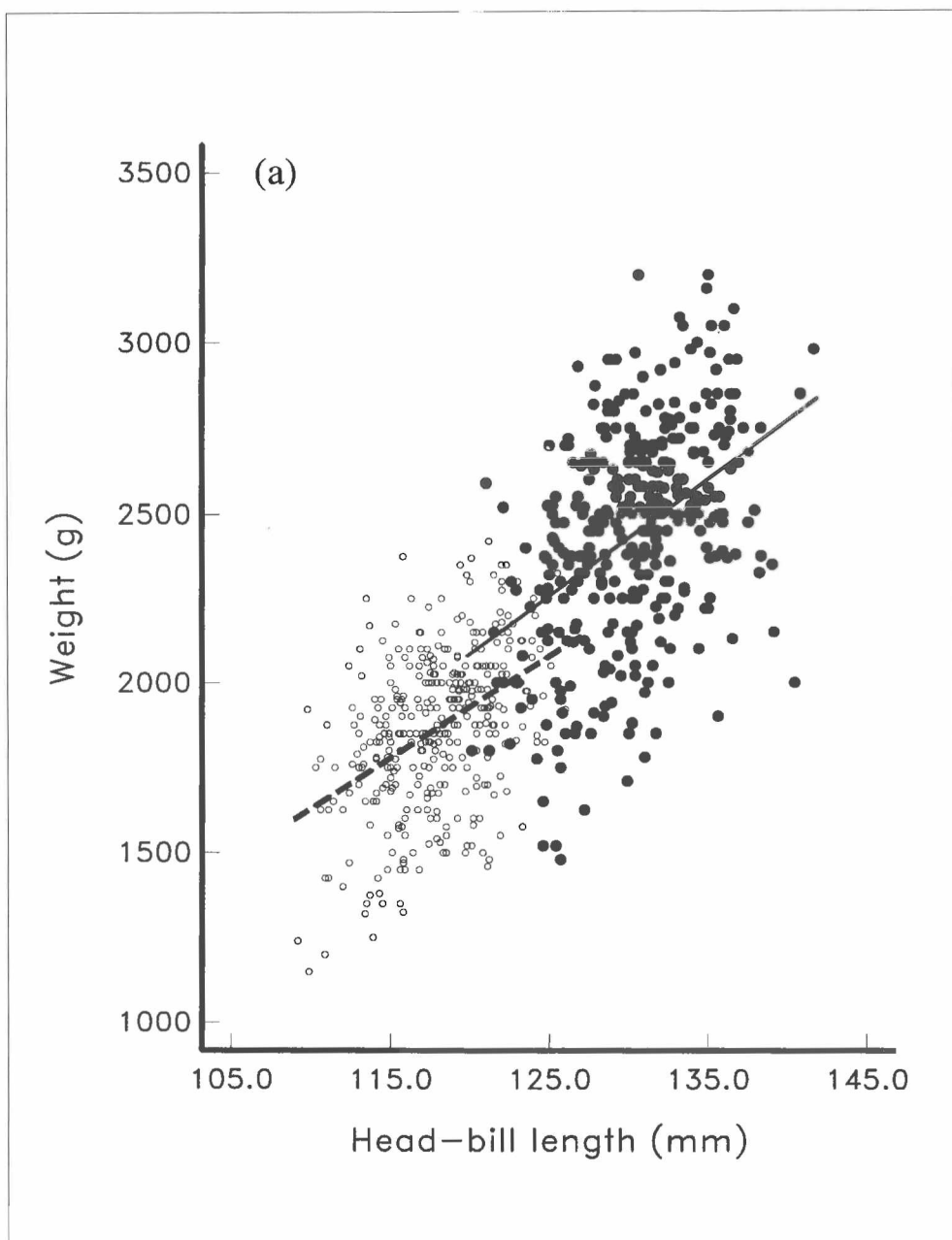
Figure 1a. Relationships between head-bill length and body weight for Magpie Geese. Males are shown with solid symbols and females with open symbols. Separate regression lines are shown for males (solid line) and females (dashed line). Much of the within- and between sex variation in body weight can be attributed to differences in general body size as reflected in head and leg measurements, although females are significantly lighter than males in the small region of overlap in head-bill length.
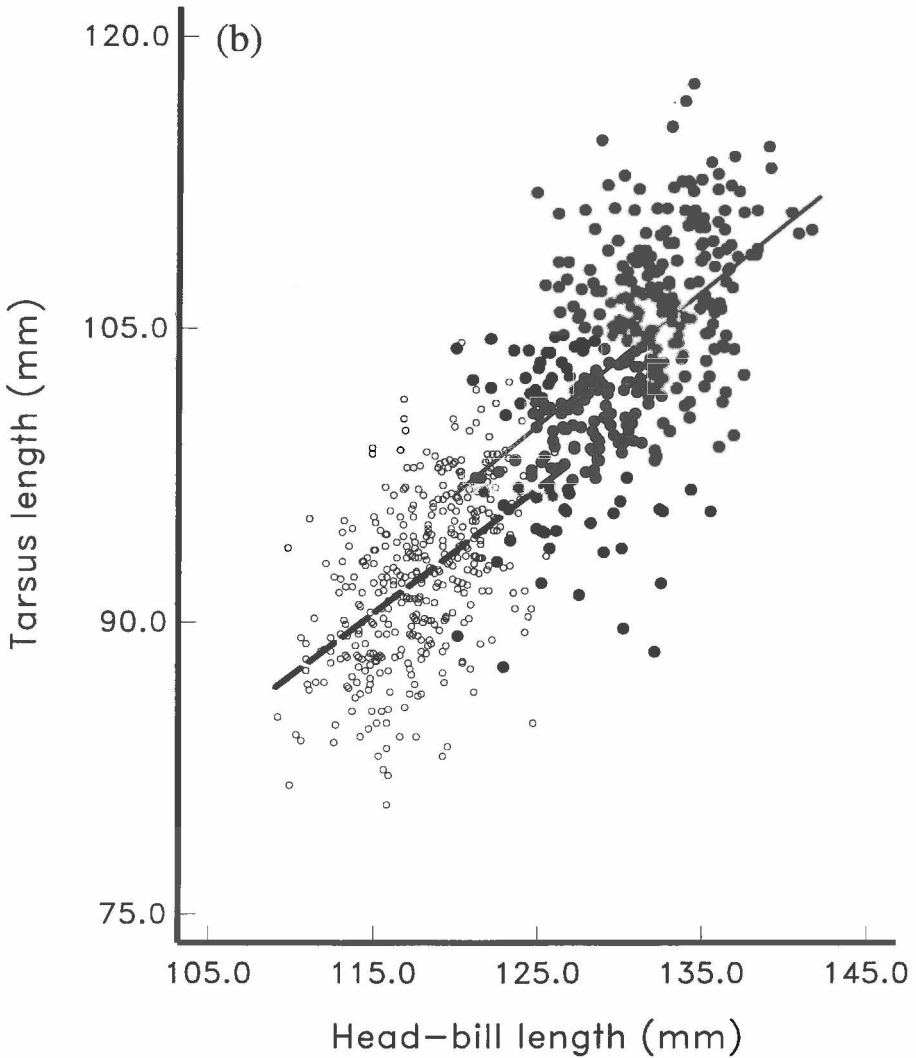
Figure 1b. Relationship between tarsus length and head-bill length in Magpie Geese. Symbols and lines are as in Figure 1a. The slope of the regession lines is similar for males and females, but there is a significant difference in intercepts. Males have longer tarsi at the same head-bill length.
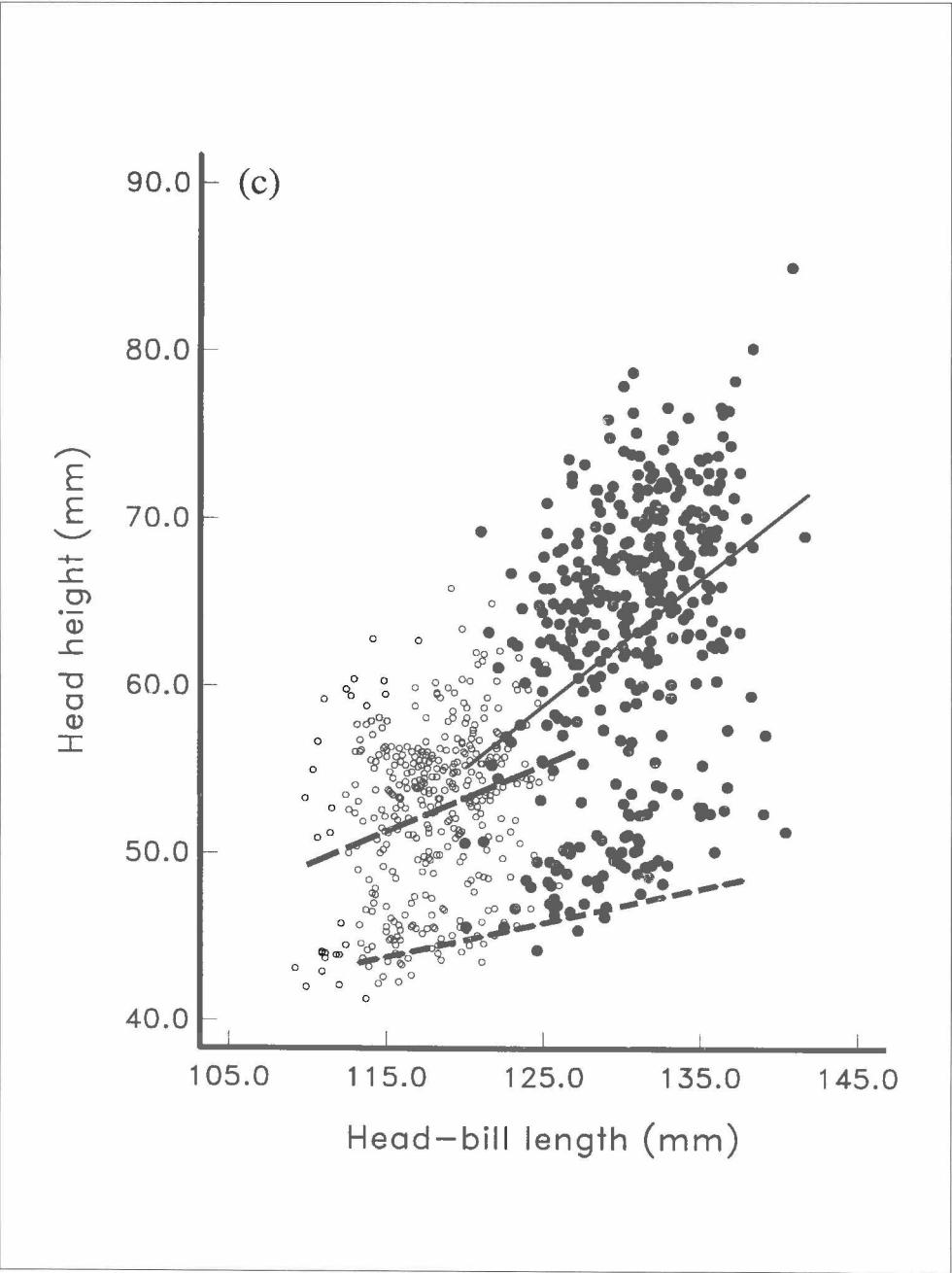
Figure 1c. Variation in head height of Magpie Geese with head-bill length. Symbols and lines are similar to Figure 1a, with the exception that the relationship is also shown separately for for recently fledged Magpie Geese raised in captivity, measured before substantial development of the cranial bump (lower dashed line). Much of the variation in head height is related to growth in the cranial bump, which appears to continue for many years (see text).

invariably the longest, often extending from the base of the neck to the bottom of the abdominal cavity near the cloaca.

Associations of tracheal morphology with body size

Within sexes, loop dimensions and configurations were strongly related to general variation in body size as indicated by measures of head and leg length (**Figure 2**). For example, in females neither head-bill length nor tarsus length varied significantly among loop configuration classes (head-bill; $F_{2,266}$=1.7, P=0.19: tarsus; $F_{2,266}$=2.0, P=0.14). Tarsus length did not vary significantly with loop class in males ($F_{7,301}$=2.0, P=0.055).

Variation in head-bill length with loop class was significant among males ($F_{7,301}$=2.5, P=0.018), but the proportion of variance explained was small (r^2=0.054). The only pairwise comparisons that showed significant variation were between class 0 and class 6 and class 0 and class 4 (Tukeys HSD, P<0.05). The class 0 sample was comprised entirely of birds regarded as less than one year old, as determined from similarities of plumage and soft tissue colouration to birds of known age reared in captivity.

In contrast, variation in head height among loop classes was considerable (**Figure 2**) and significant for both sexes (females; $F_{2,266}$=5.3, P=0.006: males ($F_{7,301}$)=95.1, P<0.0001). In both sexes, birds with loops have larger cranial bumps, and longer or more elaborate looping is associated with larger bumps. In males, 62.6% of variance in head height could be associated with tracheal loop class. Among males, head height in all individual loop classes up to and including three differed significantly from all individual classes at or above four. Within each of these groups (0 to 3 and 4 to 7) the only significant pairwise differences were between classes 0 and 3 and classes 4 and 6 (**Figure 2**). In pairwise comparisons for females, head heights varied between loop classes 0 and 1 (Tukey's HSD, P<0.05), but other contrasts were not significant.

Discriminant Analysis

All of the variables included in the discriminant function shown in **Table 3** varied significantly
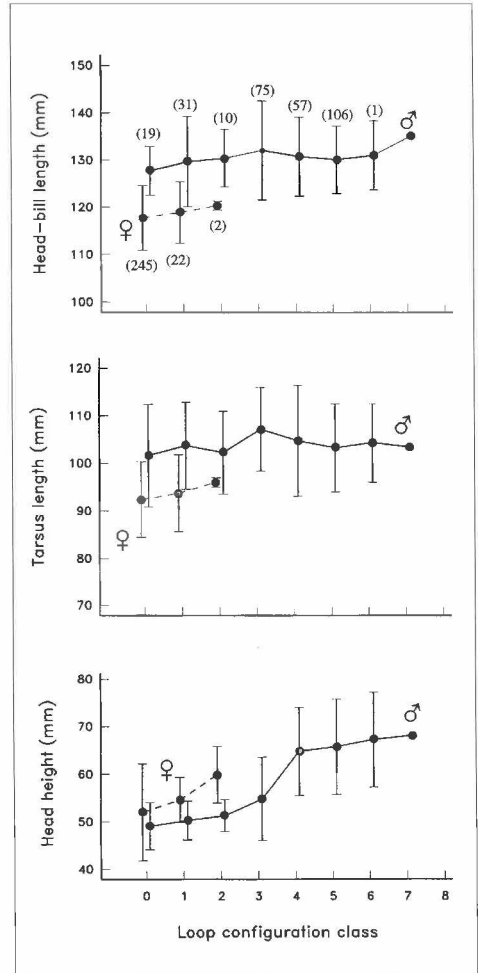

Figure 2. Variation in head-bill and tarsus lengths and head heights among tracheal loop classes. Dots are means, lines and bars delimit 2 standard deviations. Figures in parentheses are sample sizes. Plots are offset slightly on the horizontal axis for clarity. There are marked differences between sexes in the range of tracheal morphologies and their relative frequency. There is strong association between other measures of body size and tracheal morphology only in respect of head height. Birds of both sexes with longer and more complex tracheal configurations tend also to have larger cranial bumps.

Table 3. Details of a discriminant function derived from a sample of unambiguously sexed birds (n=64). The numbers are coefficients used to calculate a score from the sum of products of the relevant coefficient and measure of individual dimensions. An individual is assigned to the sex for which the discriminant function returns the highest value.

	Sex	
Variables	Female	Male
Constant	-757.2	-908.4
Head-bill length (mm)	12.573	13.680
Head height (mm)	0.601	0.674
Tarsus (mm)	-0.0356	0.0645

between sexes. Head-bill length showed the greatest between-sex differentiation, and head height the least. The function correctly classified 63 of 64 birds of unambiguously determined sex (**Table 4**).

The function also produced assignments of sex in a larger sample of live birds that were reasonably congruent with sex determined from cloacal examination, and a still larger combined sample that included the cloacally-sexed birds plus a number of adult birds sexed subjectively by an experienced observer. Birds sexed as females in the field were infrequently misclassified by the discriminant function. However, the trend for a substantial number of (smaller) males to be apparently misclassified as female was maintained in the larger samples (**Table 4**).

Some apparent misclassifications in the larger samples may result from actual errors of sexing or inaccurate data transcription. However, this is not a sufficient explanation for higher misclassification rates among males. Fourteen (61%) of 23 putative males classed as female by the discriminant function showed other distinctly male characteristics; in obviously older birds, tracheal lengths never recorded in females (Frith & Davies 1961), or in very young (first-year) birds with little development of the cranial bump, there was minor but distinct (class 1 or 2) elaboration of the trachea.

To explore potential bias in field studies, estimates of sex ratios were derived from 100 samples of 100 randomly-selected birds sexed

by the discriminant function, and the ratio so derived compared with estimates based on sexes assigned to the same birds by other criteria. Calculated ratios were re-examined following application of the additional tracheal criterion. Any bird classed as female by the discriminant function but possessing tracheal elaborations greater than ever measured in females (class 3 or above: Frith & Davies 1961) was reassigned to the male group. Similarly, birds with small head heights (<52 mm) classified as female showing significant tracheal development were reassigned as male. Results of applying the tracheal criteria are summarised in **Table 5.**

Growth rates - recaptured birds

Head-bill and tarsus lengths

There was no evidence of growth in head-bill length or tarsus length in the small sample of birds recaptured and remeasured at near annual or longer intervals (350 to 1,079 days). Fitting the von Bertalannfy growth model to paired measurements (Fabens 1965) generated estimates of growth constants k that did not differ significantly from zero (95% asymptotic confidence intervals straddled zero).

Head Height

Similarly, it was not possible to derive a model for growth of head heights of females. Given

Table 4. Performance of discriminant function for sexing Magpie Geese. Figures in parentheses are the percentage of the sample correctly classified. The validation sample is based on birds sexed by cloacal examination in the field.

Sample	Sexed by dissection		Validation sample (cloacal sexing)		Whole sample (cloacal & subjective)	
Classified from:			Classified to:			
	Female	Male	Female	Male	Female	Male
Female	32	0	197	4	385	6
	(100.0)	(0.0)	(98.0)	(2.0)	(98.5)	(1.5)
Male	1	31	11	137	23	373
	(3.1)	(96.9)	(7.4)	(92.6)	(5.8)	(94.2)

the small sample of remeasured birds (n=9), growth increments (the longest interval for a female was one year) may have been obscured by the error inherent in measurement on live birds under field conditions. In the slightly larger male sample (n=11) that also covered a longer period (up to 1,079 d), head height did increase significantly (k=0.196 ± 0.042(SE); a= 73.7 ± 2.3: **Figure 3**). The data are too few, particularly at larger head heights, and the asymptotic standard errors of parameter estimates too wide for interpretation as a comprehensive summary of age-related change in head height. The model's limitations are illustrated by estimation of an asymptote lower than the maximum head height observed in the study (**Figure 3**). An alternative model based on a fixed asymptote (85 mm) similar to the largest head height measured is shown for comparison. These alternative models diverge little within the range for which repeat measures are available (≤75.3 mm), and suggest that males may achieve head heights above the minimum observed among reproductively active birds about 4-5 years after fledging. A datum from one male reared in captivity from hatching for nearly three years is also consistent with this interpretation (**Figure 3**).

Tracheal Morphology

The manner in which tracheal loops were described inhibits detailed quantitative treatment of patterns of growth in tracheal length. However, some inferences can be drawn from patterns of within-sample variation in male tracheal morphology. In particular, the low relative frequencies (**Figure 4d**) of classes 0 to 3 (loops less than 15 cm in length), suggest that male tracheal elaboration begins early in life and tracheae rapidly attain substantial dimensions. Males caught during the period September to December and classed subjectively as first year birds - on bill colouration (large black areas on the bill and especially the nail), dull leg colouration (adults are bright yellow/orange), and generally darker plumage (Marchant & Higgins 1990) - sometimes showed significant tracheal elaboration (20 of 52). Exact ages of these birds are unknown but, given the typical time of nesting around the capture sites, is likely to range from 5 to 10 months (Whitehead 1998). Tracheal development ranged from a small 'kink' at the base of the neck, to doubled loops up to 7 cm long. One male caught initially when less than six months old with no loops apparent, had class two loops (doubled loops
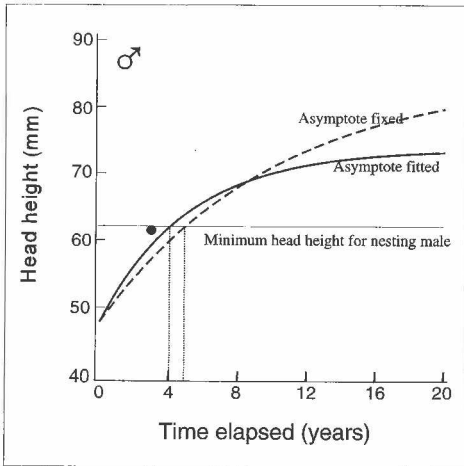
Figure 3. von Bertalannfy model of growth in male head heights from the mean at fledging (46.5 mm) estimated from non-linear regression on re-measurements of 11 wild birds. One model (solid line) fitted both asymptote and growth constant, and the second (dashed line) took the largest observed head height as asymptote. The horizontal line shows the minimum head height observed in a sample of birds captured on nests or escorting broods. The dot shows head height of a captive reared male of known age (2.8 years). Minimum head heights observed in breeding males appear likely to be reached in 4 or 5 years, although most of the breeding population appears to be substantially older (**Figure 4**).

extending between 5 and 10 cm from the base of the neck when re-caught a year later. A captive-reared male accidentally killed at a local wildlife park when aged 22 months (and hence well into its second post-fledging wet season, the time of breeding) had doubled loops reaching close to the base of the keel (class 4).

In contrast, patterns of variation in female tracheal morphology imply a much slower development, and the low frequency (8.5%) of substantially developed loops (classes 1 or 2) in birds with larger head heights implies that they develop predominantly in older birds (below). No evidence of tracheal elaboration was ever recorded in a first year female.

Morphology of Birds of Known Status

The total sample includes individuals of both sexes of known reproductive status. The first group comprises pre-reproductive birds hatched and raised in captivity for periods of up to seven months. The other group of known status comprises birds considered reproductive active because they were caught live on nests or taken while escorting broods. The position of these groups within the whole-population distribution of head and tracheal dimensions is shown in **Figures 4a-d**.

There was considerable overlap in head-bill and tarsus lengths between juveniles and reproductively active birds of both groups. Indeed the distribution of head-bill lengths of juveniles suggests that growth in this dimension is minor after the first year (**Figure 4a**). The situation is similar in regard to tarsus length (**Figure 4b**). In neither sex did frequency distributions of these dimensions vary significantly between juvenile and nesting birds, or nesting birds and the sample as a whole (Kolmogorov-Smirnov tests, $P>0.05$)

Head height showed greater divergence between juveniles and reproductive adults, especially among males (**Figure 4c**). There was no overlap in male head height between known juveniles (mean 47.8 ± 2.9, range 44.1 to 52.5, $n=14$) and breeding birds (mean 69.6 ± 3.7; range 61.9 to 76.6, $n=42$). The distribution of head heights among breeding males differed significantly from the sample population as a whole ($P<0.0001$). Even when comparisons are confined to that portion of the sample with head heights exceeding the minimum (61.9 mm) found in birds at nests, the distribution of head heights in the known reproductives was significantly skewed ($P=0.0007$) towards larger head heights (**Figure 4c**).

Among females, overlap was minor (juveniles; mean 45.0 ± 2.7, range 40.9 to 49.9, $n=15$: adults; mean 56.3 ± 3.3, range 49.9 to 62.7, $n=24$) and the distibution of head heights differed significantly between these classes. There was some suggestion of a skew towards larger bumps in the sample of known reproductives (**Figure 4c**) but when comparisons are confined to the birds with head
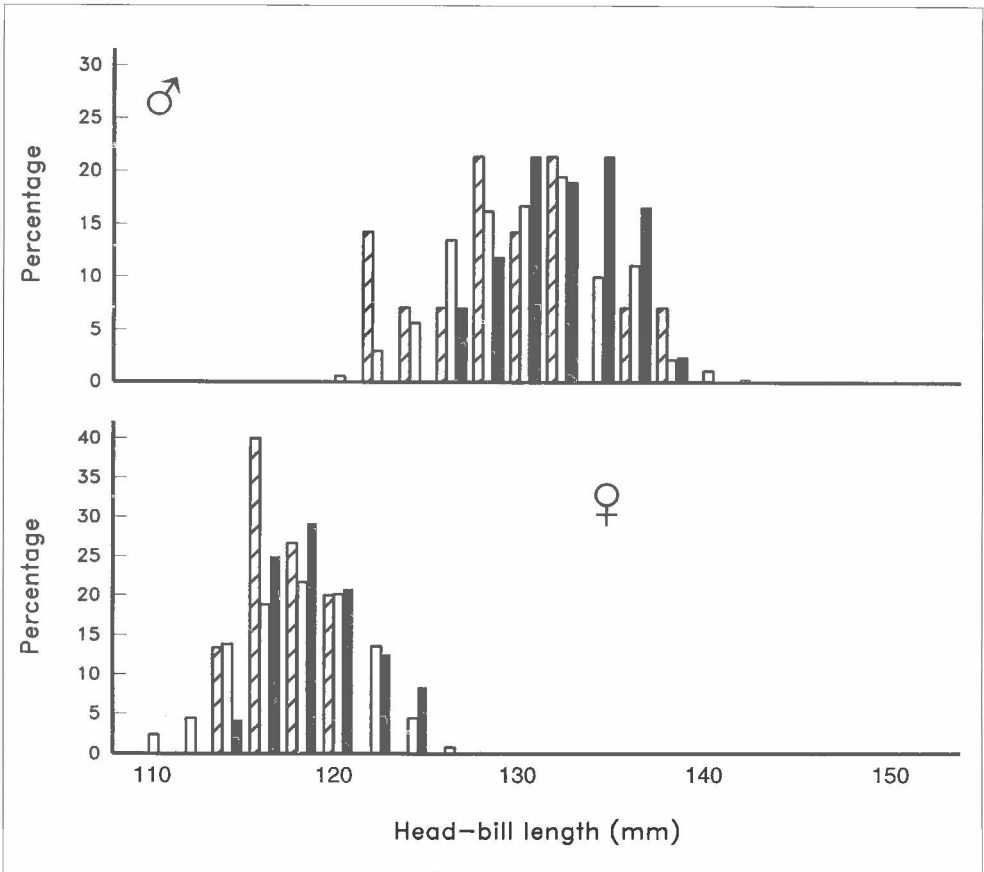
Figure 4a. Variation in the relative distribution of head-bill lengths in different components of the sample population of fledged birds. The wild-caught sample population of unknown reproductive status is shown by open bars, the juvenile sample of captive reared fledged birds by hatched bars, and the sample of birds taken in association with nests or broods by filled (black) bars. In both sexes there is considerable overlap in head-bill lengths between the sub-samples of juvenile (first-year) birds (hatched bars) and birds caught at nests or escorting broods (solid bars).

heights above the minimum found in a bird associated with a nest (49.9 mm), the variation in distribution was not significant ($P=0.16$).

Discussion

Sexual dimorphism and sexual selection

From the time of hatching, male Magpie Geese grow faster to greater asymptotic dimensions than females, so that at fledging there is a substantial difference in body size (Whitehead

et al. 1990b). This study shows that morphological divergence between the sexes continues to widen with post-fledging age in respect of two conspicuous characters: the length and configuration of the trachea and the size of a distinctive cranial 'bump'.

Among females, maximum tracheal development is confined to a single loop of a few centimeters near the base of the neck and is found in a small proportion of the population. In contrast, in all males the trachea grows rapidly to form an elaborately looped structure
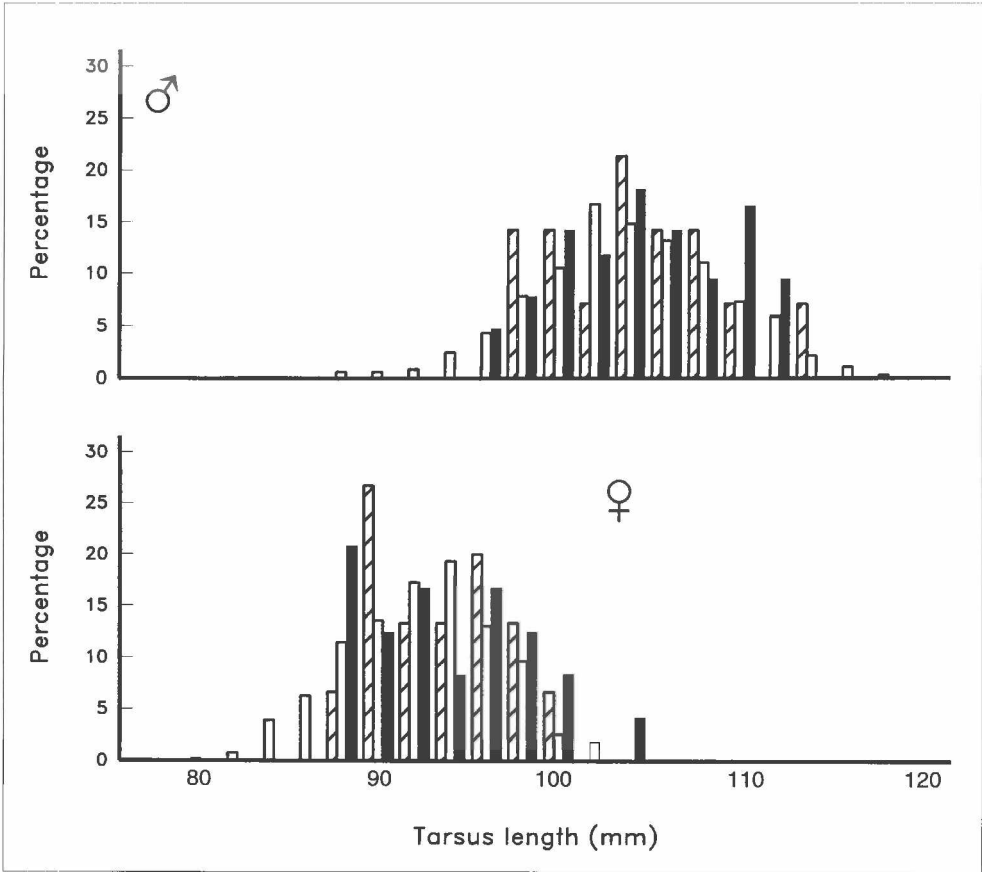
Figure 4b. Distribution of tarsus lengths in the sample population. Different bars relate to sample status in the same way as in Figure 4a. There is little evidence of age-related variation, with the samples of juvenile (first-year: hatched bars) birds and adults (nesting attending broods: solid bars) showing a similar distribution.

ultimately exceeding 125 cm in total length. Of the dimensions measured, tracheal development was the morphological feature most closely associated with male reproductive activity (**Figure 4**). All males on nests or with broods had greatly elongated paired tracheal loops, and most (84.2%) possessed a third loop.

Gross elongation of the trachea is likely to carry some physiological penalty, including the costs of growth and maintenance of additional tissue. More importantly, increased 'dead space' in an additional 80 cm or more of tracheal length is likely to compromise respiratory gas exchange (Hinds & Calder 1971). The length of the adult male trachea exceeds five times the

length (24.8 cm) calculated from allometric relationships between tracheal dimensions and body weight in birds, a ratio much greater than for the most elongated trachea described (3.3 for the Trumpeter Swan *Olor buccinator*) in the summary provided by Hinds & Calder (1971).

Such a feature, in a bird that frequently flies long distances (Whitehead 1998) and can be presumed to benefit from efficient respiratory function, implies important non-respiratory roles for tracheal structure in determining the fitness of male Magpie Geese. Males produce louder, lower pitched calls than females (Marchant & Higgins 1990). The functional significance of pitch and volume of calls has not
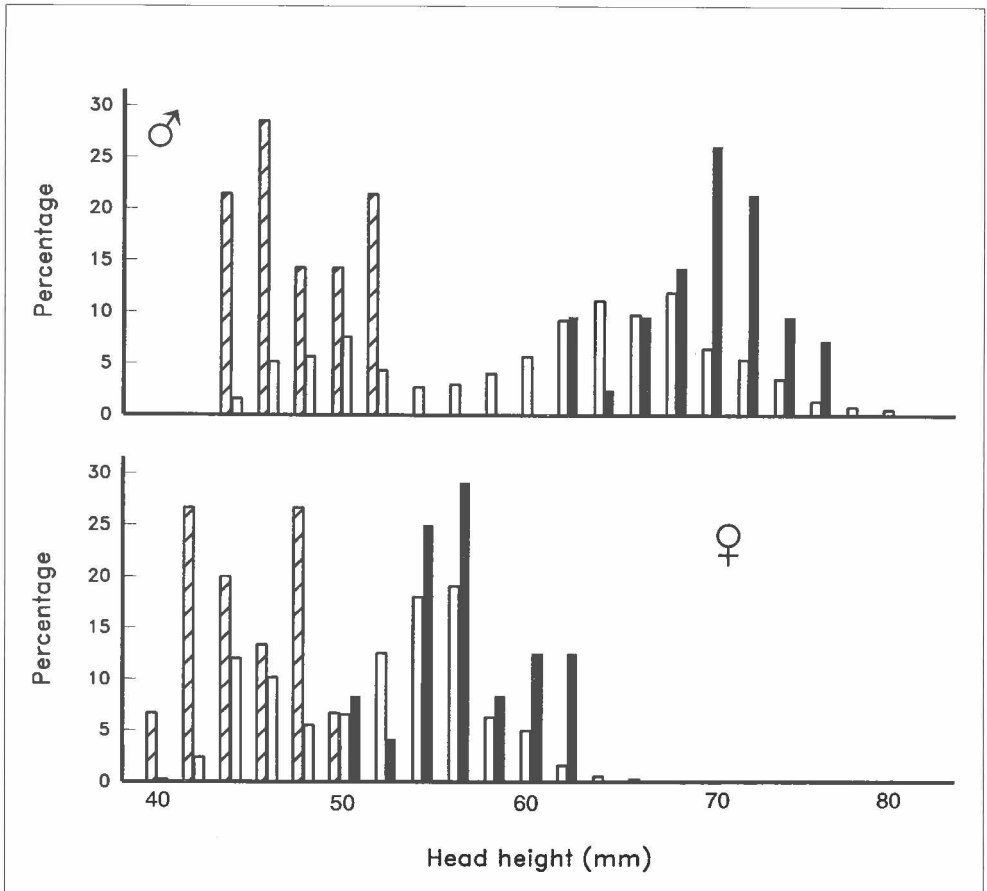
Figure 4c. Distribution of head height (and hence cranial bump) dimensions in the sample population. In contrast to other dimensions the juvenile (first year) age class is distinct (hatched bars) and contributes to a bimodal distribution in the population as a whole (open bars). Among males there is a large gap between juvenile (hatched bars) and reproductively active birds (solid bars). This trend is less clear in females, in which there is minor overlap.

been directly studied, but may involve enhanced contact among group members. However, Magpie Geese inhabit open swamps and mostly move in flocks. The lower rate of attenuation of lower-pitched calls with distance or in structurally complex environments often invoked as an important advantage of such calls (eg Endler 1992), appears an inadequate compensation for the likely physiological penalty. Rather, a conjunction of such extraordinary exaggeration of the trait in males and the equally unusual polygynous mating system

suggest an important role for sexual selection in its maintenance.

Exaggerated traits maintained by sexual selection are common in birds, including plumage dimorphism in some wildfowl, despite adverse impacts on male survival (Promislow et al. 1994, Andersson & Iwasa 1996). Sexual selection has previously been invoked to explain sex differences in some ecologically significant attributes of Magpie Goose biology. Whitehead et al. (1990b) argued that extended juvenile growth periods and consequent large body size in male Magpie Geese are maintained
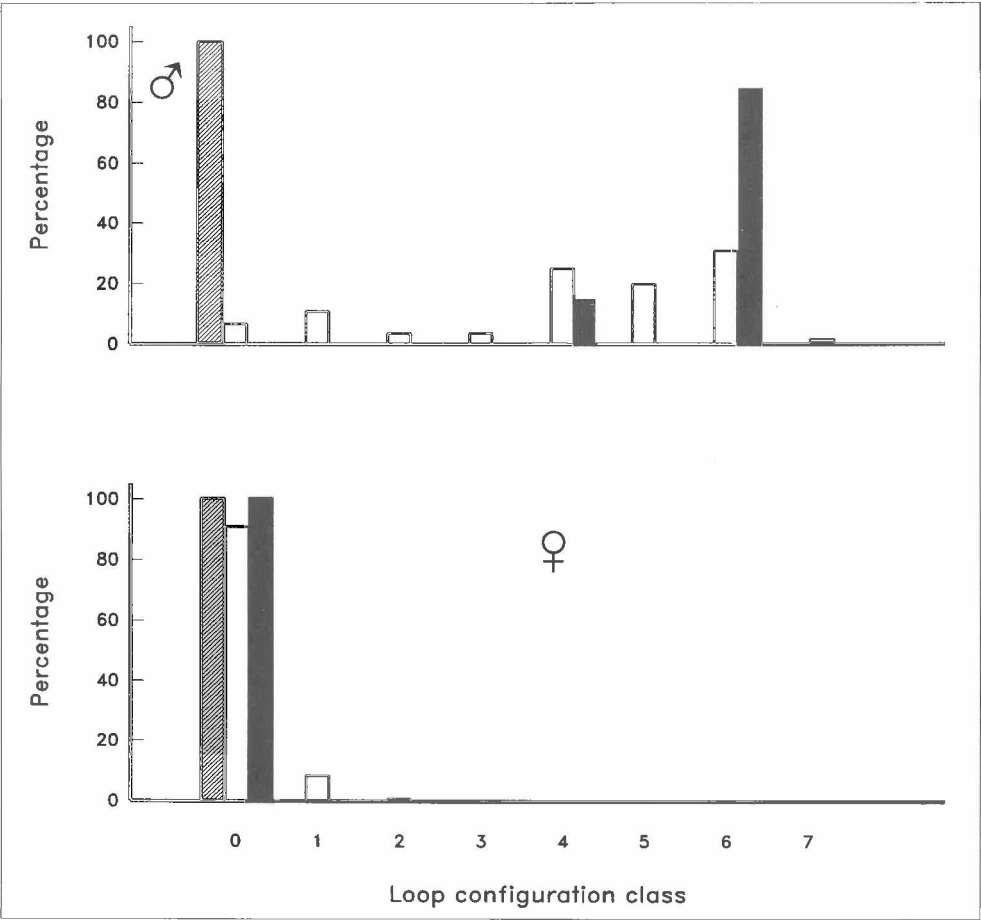
Figure 4d. Distribution of loop configuration classes among the sample population. Different bars relate to sample status in the same way as in Figure 4a. Most females show no development of loops, whether of reproductive age (filled bar) or not, while all males found in association with nests or broods had well-developed tracheal loops.

in populations by sexual selection, despite the potential for the survival of juvenile males to be compromised under some environmental conditions.

Male contests (intra-sexual selection) and mate choice (inter-sexual selection) may both be important in driving evolution of larger, louder male Magpie Geese. Large body size could play a role in both arenas, and also have a direct functional role in the capacity to defend a nest or family group against predators (Whitehead, in press). A role for the trachea in direct male-to-male competition cannot be

discounted (eg Kodric-Brown & Brown 1984, Zahavi 1987), for example in jamming the signals of competitors. However, the exercise of considerable female discrimination in choice of mates and maintenance of bonds is indicated by the stable polygynous mating system (Frith & Davies 1961). Magpie Geese are highly mobile and do not defend recognisable territories: foraging, nesting and brood-rearing sites vary daily, seasonally and from year-to-year (Frith & Davies 1961). It is unlikely that cohesion of reproductive groups could be maintained over long periods solely by male

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sequestration of females or territory.

In many vertebrates, females exercising choice of mates based on acoustic stimuli select stronger signals given at higher rates (Ryan & Keddy-Hector 1992). The greater volume and lower pitch of calls from males with exaggerated tracheal development may provide females with an honest signal of male viability (eg body condition: Genevois & Bretagnolle 1994), that is too expensive to be 'faked' by less robust birds (Zahavi 1975, Grafen 1991). In addition to this auditory signal, patterns of growth in the cranial bump and the greater frequency of larger bumps among males engaged in reproductive activity also suggest a role for mate choice based on this potential visual signal. No role unrelated to mate selection has been described or, so far as I am aware, suggested for the bump. Correlation of head height (and hence bump size) with body weight suggests that it may also signal body condition. However, the manner in which large cranial bumps might handicap males and so ensure the honesty of the signal is less obvious. It is possible that a bird depending on an ability to dig with its bill for food at depths considerably greater than the length of its head (Whitehead & Tschirner 1991) may be inconvenienced by a 3-4 cm protrusion perpendicular to the shortest route to those food items.

But even if bump size, in isolation, offered ambiguous signals to females regarding male condition, in combination with vocal attributes this age-related trait may offer a highly reliable measure of quality. Evidence from this study (below) and Johnsgard (1961) suggest that rates of increase in male tracheal lengths plateau after about two years, before males are commonly recorded in association with nests (**Figure 3**), whereas head height continues to increase much longer (below). If costs of assessing additional traits are low, female choice may select for multiple signals in the male population. Indeed, it has been suggested that in birds carrying multiple ornaments, one trait will often be an indicator of viability, while others are attractive 'Fisherian' traits, unconnected to wider variation in fitness, but maintained by self-reinforcing inheritance of the

female preference and of the preferred trait in her male offspring (Iwasa & Pomiankowski 1994). Older, big-bumped males with loud, low-pitched vocalisations demonstrate their viability by surviving long enough to develop large bumps (Buchholz 1991), despite their prominent tracheal handicap. More detailed studies of behavioural interactions between the sexes and, in particular, the initiation and maintenance of bonds among group members will be required to improve understanding of the separate or joint influence of these traits on female choice.

Growth patterns and estimating age

Patterns of variation in head-bill and tarsus lengths and remeasurements of recaptured adult birds suggest limited post-fledging change in these dimensions. Bimodal distributions of head heights, with the lesser peak dominated by cohorts of first year birds and the larger by adults, clearly demonstrates that the bump increases in size with age in both sexes (**Figure 4b**), although the increase is very much slower in females (Frith & Davies 1961). While I was unable to directly demonstrate growth of cranial bumps by remeasurements of recaptured females, this reflects the inadequacy of the sample rather than robustly demonstrating the absence of growth.

Birds with larger bumps tended to be heavier, even when other measures of body size were taken into account. This association could have many sources, including other morphological change directly associated with maturation, or older experienced birds being better able to exploit a capricious environment and hence maintain better condition than younger animals. I am currently unable to identify the most plausible link. However, it will be necessary to explore sources of variation in rates of bump growth and their association with other measures of condition if their size is ultimately to be employed as a tool for ageing birds (below).

Development of the male trachea begins during the first year and is substantially advanced during the second, with doubled loops reaching close to the distal end of the

sternum (classes 3 or 4). Subsequent rates of tracheal development, or at least their expression in terms of the development of a distinctive third loop on the right side of the sternum, appear to be somewhat variable. Head height was similar in birds with the third loop absent and in those with well-developed third loops, suggesting that this tracheal feature may not provide a reliable indicator of relative age. More precise measurements of total tracheal length rather than a series of somewhat arbitrary classes would probably be necessary to explore this question in detail.

Reproductive status, age and size

There is little evidence in these data that generally larger birds of either sex are more likely to be reproductively active. The span of head-bill and tarsus lengths in both males and females found in association with nests or broods was similar to that of the population as a whole (**Figures 4a** and **4b**). Tarsus and head bill lengths of 94.9% and 92.4% respectively of non-juvenile males exceeded the minimum dimensions of males found in association with nests or broods.

The range of bump sizes among reproductively-active males was somewhat narrower: about 71.0% of the non-juvenile sample had head heights exceeding the minimum measured in a nesting male. Perhaps more importantly, among nesting males there was a significant skew towards the upper end of the frequency distribution of head heights and a large gap in head heights between known-age juvenile males and nesting males. If it is assumed that all males caught at nests have a genetic stake in the clutch, the growth and frequency distribution data are consistent in suggesting that breeding in males is delayed to at least four years (**Figure 3**), with reproductive activity being significantly biased towards even older birds (**Figure 4c**). Delayed breeding in males is consistent with intense competition for mates and/or places within breeding colonies (Zack & Stutchbury 1992). Moreover, over-representation of larger-bumped, older, males in the breeding population may be stronger than suggested by these data.

Some nests may be attended by younger 'auxiliary' males, which may not have access to laying females (Marchant & Higgins 1990, Whitehead, in press). One or more of these 'auxiliaries' may have been included in our sample, and comprehensive genetic studies will be required to clarify association between male reproductive activity, bump size and age.

In contrast, head height of juvenile and nesting females overlapped slightly (**Figure 4**), and the frequency distribution of head heights of breeding females suggests little skew to larger bumps. These observation are consistent with suggestions by Frith & Davies (1961) that a large proportion of the female population is breeding within two years.

Discriminating sex using morphometrics

Despite marked differences in mean dimensions of male and female Magpie Geese, some overlap exists in all individual measurements, especially when first-year birds are included. Nonetheless, a simple linear discriminant function derived from a small suite of simply and non-invasively measured variables can be used to sex wild birds with accuracies exceeding 92%. The function is applicable to free-flying birds of all ages, as the sample used in its derivation includes a substantial number of recently fledged birds of both sexes. That this should be possible is unsurprising, given that Whitehead & Tschirner (1990) indicated that goslings as young as 20 days could be reliably sexed employing discriminant analyses based on a small number of morphometric characters, similar to those recorded by Frith & Davies (1961).

The discriminant function reported here was derived from samples taken over a relatively small part of the species' total range, and its applicability to distant and hence potentially distinct populations (eg New Guinea or Queensland) is uncertain. Studies of movement patterns in the Top End of the Northern Territory (Whitehead 1998) suggest that there is considerable mixing of populations, so it is likely to be applicable throughout the core populations along the northern coast from Darwin to Murgenella,

Table 5. Estimates of sex ratios derived from 100 samples of 100 birds randomly selected from the total sample population (n=787). Differences between the mean sex ratios calculated from the sex of the randomly-selected birds and sexes assigned by the discriminant function provide a measure of bias potentially arising from application in field studies. Bias is reduced if additional criteria for tracheal morphology are applied to birds assigned as females by the discriminant function.

Method	Sex ratio	
	Mean ratio+SD	Mean bias+SD
Nominal	1.024+0.215	-
Discriminant	0.941+0.188	-0.083+0.076 (8.1%)
Discriminant function plus tracheal morphology	1.008+0.209	-0.016+0.052 (1.6%)

north of Kakadu National Park.

However, there is potential for some systematic bias in sex ratios estimated from this discriminant function alone. Males show greater variance in all dimensions and hence are subject to a greater risk of misclassification. Monte Carlo simulations drawn from a sample population with a nominal sex ratio of about 1:1 ($\male : \female$) indicate a mean bias of -8.1% in sex ratio estimates based on the discriminant function (**Table 5**). Incidence of misclassifications can be reduced greatly by checking assignments as female against criteria relating to tracheal development. First, birds with two or more well-developed loops are invariably male (**Figure 4d**). Second, any bird with no or limited development of the cranial bump (head height less than 52 mm) but having distinct development of tracheal loops (class 2 and above) is almost certainly male (Frith & Davies 1961, Whitehead et al. 1990b, **Figure 2**) because no female with head height less than 55.3 mm was recorded with such loops. These attributes of tracheal morphology, used in conjunction with the discriminant function, reduce mean bias calculated from a similar series of simulations to -1.6%. Given the purposes for which sex ratio estimates are required and the sampling error inherent in any sample of achievable size (see, for example,

Brennan et al. 1991), I consider that this potential bias can effectively be ignored.

Management implications

Despite some limitations, particularly in regard to numerical models of patterns of growth, these data and the associated analyses demonstrate the potential to derive important demographic and other biological insights from more comprehensive studies of morphometric variation in the Magpie Goose. In particular, future studies should include capture-recapture programs to provide (i) information for robust models of growth in the cranial bump and subsequent estimates of population age structures and (ii) a substantial marked population to examine variation in male reproductive success and its morphological correlates. Such studies of marked birds will also help provide age-specific measures of variation in dispersal patterns, fecundity and survival rates, all of which are needed for informed management.

Taxonomic uniqueness, an extraordinary biology, and a particular sensitivity to habitat change, as evidenced by displacement from a large part of the species' previous Australian range, all justify special efforts to improve understanding of the factors influencing the

status of this icon of north Australia's tropical wetlands.

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