

A basic statistical approach to determining adult sex ratios of moa (Aves: Dinornithiformes) from sample series, with potential regional and depositional biases

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Abstract: Adult sex ratio is a basic component of breeding systems. Estimates of sex ratios of moa (Aves: Dinornithiformes) have ranged from near balanced to significantly female-biased. However, ratios have usually been estimated by simple ratios of females to males identified by some level of sexual size dimorphism or, at most, tested against a balanced ratio by χ^2 test. Application of binomial tests confirmed a great heterogeneity, and high levels of uncertainty in estimates of moa sex ratios from different areas and from different kinds of fossil deposits. Large samples gave more constrained estimates than small, but even for some of the larger, binomial analysis often revealed a range of possible ratios, including one with a bias to males. Some causes of extreme values for swamp and lake bed deposits, including sexual differences in territorial behaviour, have been suggested before. However, a new issue – significant and sometimes abrupt changes in female and perhaps male body size through time – was identified here from series of genetically identified and radiocarbon dated moa from North Canterbury, New Zealand. The size changes compromise allocation of individuals to sex by morphometrics of limb bones, especially in undated samples. Intensive radiocarbon dating of series of genetically sexed moa of different taxa from a range of areas will be required to identify potential regional and temporal differences in their sex ratios before any interpretation of the evolution of size dimorphism and breeding systems based on moa sex ratios will be possible.

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INTRODUCTION

Adult sex ratio is fundamental to a species' breeding system (West *et al.* 2002; Liker *et al.* 2013; Székely *et al.* 2014). Ratios are not always straightforward to measure or identify even in living taxa which complicates interpretation of the role of sex ratio in breeding systems and of drivers of variation in sex ratios (West & Sheldon 2002; Postma *et al.* 2011; Bell *et al.* 2014). Sex ratios are especially difficult to measure in extinct taxa. Many assumptions have

to be made in assigning a sex to an individual.

Of the 65% of bird species whose published sex ratios suggest male or female bias, most are biased towards males (Donald 2007). As noted by Allentoft *et al.* (2010), the three families of extinct moa (Dinornithiformes) may be an exception. Based on the generally employed methods of estimating moa sex ratios from raw numbers of birds sexed by size (or, for some, by genetic analysis), and by χ^2 Goodness of Fit tests against a balanced ratio as in Bunce *et al.* (2003), Allentoft *et al.* (2010) suggested that sex ratios in giant moa populations rarely deviated from the balanced.

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Table 1. Sex ratios for moa published in and after 2003. Abbreviations: DINO, *Dinornis novaeseelandiae*; DIRO, *D. robustus*; EUCU, *Euryapteryx curtus sensu lato*; PAEL, *Pachyornis elephantopus*; PAGE, *P. geranoides*. Different values for each taxon within a reference are for different areas or sites, as in Figure 6.

Reference	Taxon – Sex ratio (♀/♂)					
	DINO	DIRO	EMCR	EUCU	PAEL	PAGE
Bunce <i>et al.</i> (2003)	1.2:1	1:1.2				
	1.6:1	1.6:1				
	1:1.6	1.2:1				
	2.2:1	1:1				
		1.6:1				
		1:1				
		1.4:1				
Huynen <i>et al.</i> (2003)						6.25:1
						1.67:1
Allentoft <i>et al.</i> (2010) [adults only]		19:1	7.2:1	2.5:1	2.5:1	
		1:1.5	5.5:1			
Allentoft <i>et al.</i> (2014)	“No differential reproductive success between the sexes”					
Holdaway (2022)				3.29:1		
				3:1		
				2.33:1		
				1.23:1		
				1.05		
			1.16			

In support, they cited values of 1:1 to (female-biased) 1.6:1 (reported in error as 1:6.1) for the different sites and areas reported in Bunce *et al.* (2003). Huynen *et al.* (2003) offered 1.7:1 based on genetic sex determinations of all moa taxa examined. Previous estimates of sex ratio are summarised in Table 1. Allentoft *et al.* (2010) echoed Bunce *et al.* (2003) in suggesting that the ratios in any one site (especially swamps and lake beds) could differ from that in the source population because of sexual differences in spacing and other behaviours. Wide variation in moa species compositions in five North Canterbury sites (Allentoft *et al.* 2012) supports a site-specific explanation.

While Huynen *et al.* (2003), Allentoft *et al.* (2010), and Bunce *et al.* (2003) all based at least some of their ratios on genetics, most moa sex ratios have been estimated from the morphometrics of the sexual size dimorphism first mooted by Cracraft (1976a, 1976b, 1976c). The presence of an egg with the skeleton of a large individual of *Emeus crassus* from Pyramid Valley (Holdaway & Worthy 1997; Worthy & Holdaway 2002) suggested that the females were the larger sex. Females were confirmed to be larger by ancient DNA analyses (Bunce *et al.* 2003; Huynen *et al.* 2003; Allentoft *et al.* 2010; Rawlence *et al.* 2012; Allentoft *et al.* 2014, 2015).

Samples from many sites and areas supported a balanced sex ratio for giant moa (Dinornithidae). Others – including many for moa in the Family Emeidae, especially *Euryapteryx* – suggested

female-biased ratios. Within *Euryapteryx*, however, evidence was equivocal. One sample (from dunes at Tokerau Beach in the far north of the North Island) had a balanced sex ratio (Worthy 1987), whereas others had ratios of 2–2.5♀/1♂ (Worthy 1987; Holdaway 2022).

Among the factors associated with avian reproductive systems, if there is sexual size dimorphism in birds it is usually biased, as with sex ratio, towards larger males. Females are, however, larger than males in raptors (Falconidae; Accipitridae) and owls (Strigidae) (Krüger 2005), in shorebirds (Calidrifformes) (Lindenfors *et al.* 2003), including skua (*Stercorarius*) (Cтры *et al.* 1999), and in button quail (Turnicidae) (Leitner *et al.* 2021), and tinamous (Tinamidae) (Tubaro & Bertelli 2003). Most if not all moa taxa have extreme sexual size dimorphism biased towards larger females (Worthy 1987; Huynen *et al.* 2003; Bunce *et al.* 2003; Olson & Turvey 2013; Holdaway 2022): the size differences are assumed to be constant. Slight overlap between the smallest females and largest males introduces only negligible error in the allocation of individuals to sex. However, temporal stability in body size of one or both sexes in moa has been a working hypothesis. If female or male body size changed through time, it could lead to more errors in allocating sex within (particularly undated) samples. Fortunately, the hypothesis can be tested using the long series of high precision radiocarbon ages available for

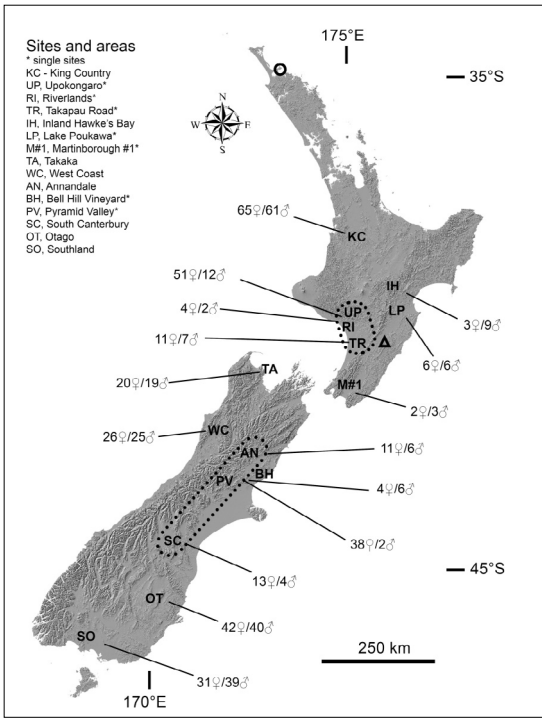


Figure 1. Sex ratios of the species now known as *Dinornis novaezealandiae* (North Island) and *D. robustus* (South Island) based on identifications of morphometric species of *Dinornis* now recognised as females (*D. giganteus*; *D. novaezealandiae*) and males (*D. struthoides*), for sites and regions from identifications by T. H. Worthy (references in text). Circle, Tokerau Beach; triangle, Tangatupura

four species in a small area in the late Holocene (Holdaway *et al.* 2014; Allentoft *et al.* 2014).

The adult sex ratio has to be known with reasonable certainty before the breeding system in any species of moa can be understood. To better resolve the sex ratios in dinornithid and some emeid moa, we revisited the data sets of Worthy (1987) and Bunce *et al.* (2003), applying χ^2 Goodness of Fit tests against other possible integer sex ratios, and then extended the analysis to new data sets for giant moa and *Euryapteryx* in the South Island (Fig. 1 and Holdaway [2022]). We then generated binomial probability distributions for each sample for a range of potential sex ratios to better define the ranges of possible values for the sex ratios represented by the samples.

MATERIALS AND METHODS

Data sources

Samples were gathered from lists in Worthy (1989, 1997, 1998c, 1998b, 2000), Holdaway & Worthy (1997), Worthy & Holdaway (1993, 1994, 1995,

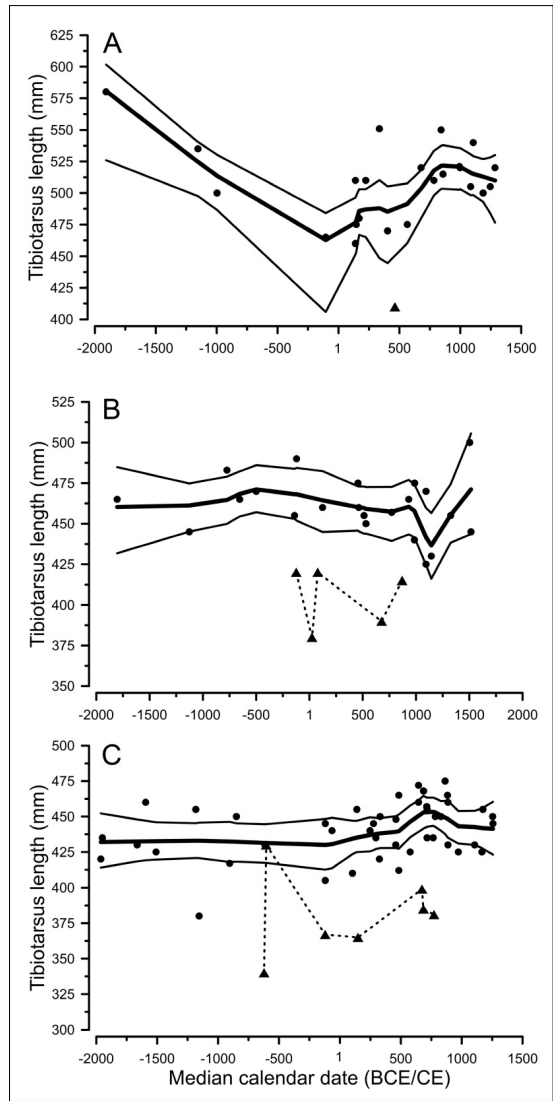


Figure 2. Body size in (A) *Pachyornis elephantopus*, (B) *Euryapteryx curtus*, and (C) *Emeus crassus*, all Emeidae (Dinornithiformes), as indicated by length of the tibiotarsus, for genetically sexed, morphologically adult birds. Filled circles, females, with trends indicated by 0.35 Smoothing Factor Local Regression (LOESS, heavy line, with 2.5 and 97.5 percentiles) for the adult females. Filled triangles, males. Median calibrated dates adjusted for 2% old carbon contamination.

1996, 2000, 2002), Bunce *et al.* (2003), Huynen *et al.* (2003), Allentoft *et al.* (2010), and Allentoft *et al.* (2014). Sex ratios for giant moa were assigned as in Bunce *et al.* (2003) from the three formerly recognised morphometrically-based species (sensu Worthy [1994]), with *D. struthoides* becoming the males, and *D. novaezealandiae* and *D. giganteus*

together, the females, of *D. robustus* (in the South Island) and *D. novaezealandiae* (in the North Island). Site and regional totals for adult giant moa were assembled from Worthy (1997, 1998c, 1998b), and Worthy & Holdaway (1993, 1994, 1995, 1996, 2000). Samples for *Euryapteryx* and *Pachyornis germanoides* were assembled from lists in Worthy (1987) and Holdaway (2022).

Moa body size

Lengths of moa tibiotarsi were measured by MEA for genetically identified and sexed individuals (Allentoft *et al.* 2010; Holdaway *et al.* 2014; Allentoft *et al.* 2014). Body size series for the genetically sexed and radiocarbon dated – using median calibrated dates according to the SHCal20 curve (Hogg *et al.* 2020), applied in the OxCal 4.4 software (Bronk Ramsey 2009) – were smoothed using the LOESS (Local Regression) option in PAST© (Hammer *et al.* 2001). A smoothing factor of 0.35 was chosen as giving the best compromise between detail and excessive smoothing: 2.5 and 97.5 percentiles were plotted to compare potential ranges of body sizes at different times.

Statistical analyses of sex ratios

Only the *Euryapteryx* samples from Tokerau Beach (Fig. 1) and Tangatupura (Fig. 1) (Worthy 1987) and the giant moa data presented here were subjected to χ^2 Goodness of Fit analysis. Binomial Distribution analyses were conducted on all samples.

χ^2 Goodness of Fit

χ^2 Goodness of Fit probabilities were calculated against assumed ratios of 1, 2, and 3♀/1♂ for data on giant moa (Bunce *et al.* 2003) and those accumulated for this study (Fig. 1), North and South Island *Euryapteryx* (Worthy 1987; Holdaway 2022) and *Pachyornis germanoides* (Worthy 1987).

Binomial probabilities

We assumed that the probability for each moa being incorporated in a fossil deposit reflected the sex ratio in the local population, at geographic scales down to the area around a site. For each “interment” from a population with a balanced ratio, the binomial probability for the “interment” being of a female was 0.5. Similarly, for a 2♀/1♂ ratio, $P(\text{♀}) = 0.667$, for 3♀/1♂, $P(\text{♀}) = 0.75$, and so on. Ratios of 1.1♀/1♂ and 1.4♀/1♂ were included to cover the range favoured by earlier studies. The probability of X females in a deposit containing Y members of the species is therefore the binomial probability for X on Y for a given postulated sex ratio. Binomial Distribution analyses were performed in R (R-Core-Team 2017), using the scripts in Appendix 1.

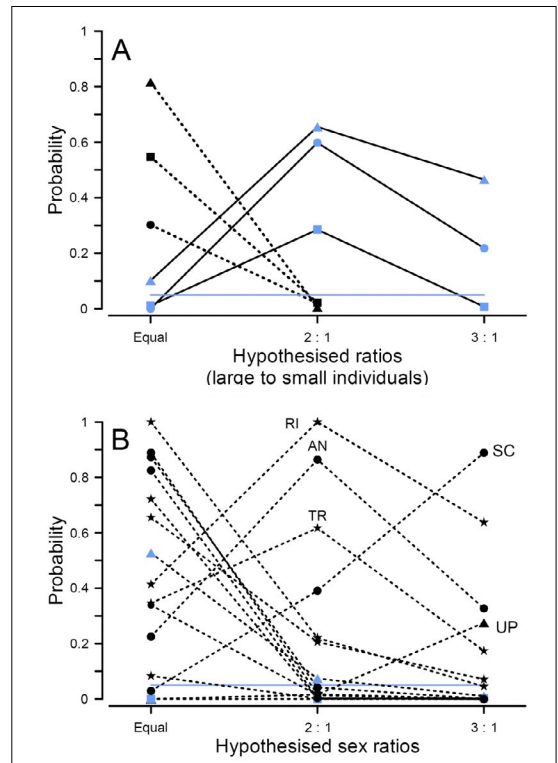


Figure 3. χ^2 Goodness of Fit probabilities for samples of femora (circles), tibiotarsi (triangles) and tarsometatarsi (squares) in relation to three hypotheses of sex ratio (assuming females larger) for (A), two North Island populations of *Euryapteryx*. Filled symbols, dotted lines, Tokerau Beach dunes Holocene; blue symbols, solid lines, late glacial Tangatupura swamp, and (B) samples of *Dinornis* spp. from areas and sites shown in Fig. 1. Data from Worthy (1987). Blue line: critical $\alpha = 0.05$.

RESULTS

Body size fluctuations in moa

Tibiotarsus length, and hence body size, of genetically-sexed individuals (Allentoft *et al.* 2010; Allentoft *et al.* 2014) changed at different times in the three emeids during the late Holocene of North Canterbury (Fig. 2). Females of *P. elephantopus* and *E. crassus* were largest at slightly different times in the first millennium CE (Fig. 2A, C), whereas female *E. curtus* were suddenly smaller c. 1000 CE.

There were too few adult males in the samples to identify any potential trends in size (Fig. 2), but the only male *P. elephantopus* was within the 2.5 percentile range for females about 2,000 years ago (Fig. 2A). The smallest female *E. curtus* was indistinguishable from the largest males just after c. 1000 CE (Fig. 2B). At times, the sexes of *E. crassus* were the same size (Fig. 2C).

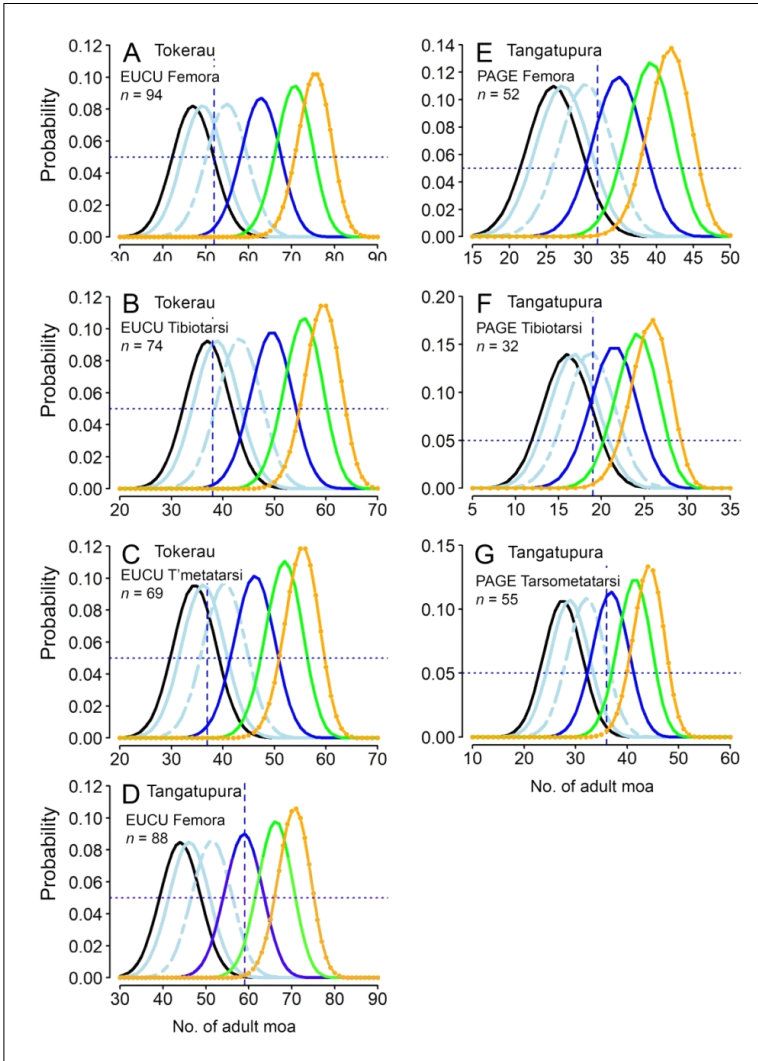


Figure 4. Binomial distributions for sex ratios of *Euryapteryx curtus* and *Pachyornis geranoides* from Tangatupura Swamp, by numbers of leg elements assigned by Worthy (1987) to sex by length. **A**, *E. curtus* femora; **B–D**, *P. geranoides* (**B**) femora; (**C**) tibiotarsi; (**D**) tarsometatarsi. Black, 1♀/1♂; light blue 1.1♀/1♂; light blue dashed 1.4♀/1♂; blue, 2♀/1♂; green, 3♀/1♂; orange, with symbols, 4♀/1♂. Vertical blue dotted line, number of females in sample; horizontal blue dotted line, critical value $\alpha = 0.05$.

χ^2 Goodness of Fit

Euryapteryx curtus at Tokerau and Tangatupura

The Tokerau Beach (dune deposit) samples of all three major leg bones yielded best fits to a balanced ratio (Fig. 3A). The femora from Tangatupura (swamp deposit) suggested a sex ratio of 2♀/1♂, but the proportions were also consistent, at very low significance, with a 1♀/1♂ ratio too. Numbers of large and small tibiotarsi and tarsometatarsi fit best to a 2♀/1♂ ratio (Fig. 3A), and the numbers of tibiotarsi could also represent a 3♀/1♂ ratio. Only the tarsometatarsi yielded an unequivocal 2♀/1♂ ratio (Fig. 3A).

Dinornis novaezealandiae and *D. robustus* from sites and areas in Fig. 1.

Two thirds of the sex ratios derived by attribution

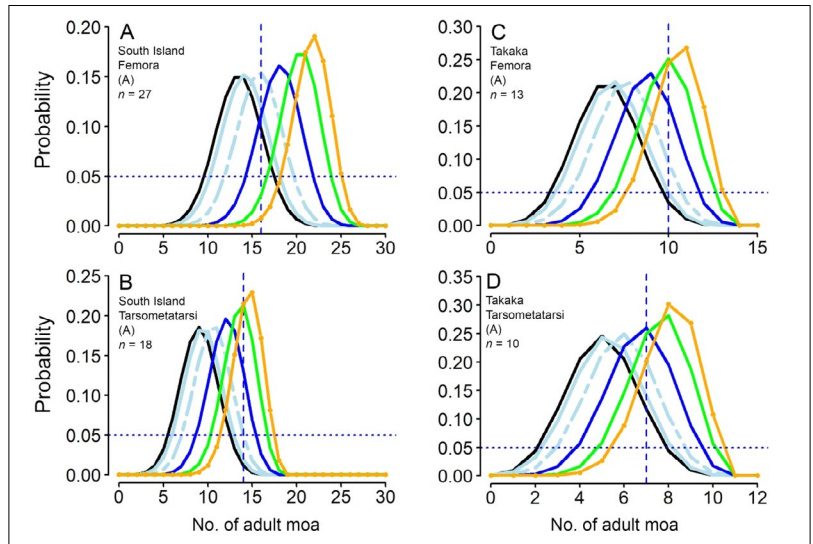
by previous species identifications had best fits near a ratio of 1♀/1♂ (Fig. 3B). Only those from Upokongaro (lower Whanganui River), Pyramid Valley (North Canterbury), and South Canterbury and Upokongaro samples had best fits at 3♀/1♂ (Fig. 3B), whereas at Pyramid Valley the best fit was “off the scale” at c. 19♀/1♂. The two lowland, southwestern North Island swamp sites best represented a 2♀/1♂ ratio, but neither 1♀/1♂ nor 3♀/1♂ could be rejected on the small samples (Fig. 3B).

Binomial distributions

Tokerau and Tangatupura - Euryapteryx and Pachyornis

Although χ^2 analysis supported balanced sex ratios

Figure 5. Binomial distributions for sex ratios of *Euryapteryx curtus* in (A, B) the South Island, and (C, D) the Takaka area, according to size distributions of (A, C) femora, and (B, D) tarsometatarsi, in relation to number of females posited in samples. Conventions as in Fig. 4. Data from Holdaway (2022).



the three major leg bones of *E. curtus* from Tokerau Beach, binomial distributions gave less consistent results, with ratios $>1♀/1♂$ being better supported for the femora and tarsometatarsi (Fig. 4A, C). If only tibiotarsi had been available, however, a balanced ratio would be solidly supported, with no likelihood of ratios of $1.4♀/1♂$ or above (Fig. 4B).

Binomial analysis of the *Euryapteryx* femora from Tangatupura supported the $2♀/1♂$ ratio favoured in the χ^2 results (Fig. 4D). In the same site, numbers of large and small sizes of all three major leg bones of *P. geranoides* (formerly *P. mappini*) all fit with a range of ratios of $1.4-2♀/1♂$. The tarsometatarsus sample was closest to an unequivocal $2♀/1♂$ (Fig. 4E–G).

South Island - *Euryapteryx*

Femora and tarsometatarsi of *Euryapteryx* from the South Island (except North Canterbury), and from the “pit-trapped” sample from the Takaka area, all sexed by size (Holdaway 2022), yielded different sex ratios (Fig. 5). There were too few complete, measurable, tibiotarsi for analysis (Holdaway 2022). A $1.4♀/1♂$ ratio was favoured for the South Island apart from Takaka and North Canterbury, but ratios between 1 and $2♀/1♂$ were also possible (Fig. 5A). However, in the general South Island sample of tarsometatarsi, a $3♀/1♂$ ratio had a highest probability, but any ratio between $2♀/1♂$ and $4♀/1♂$ in the living population was also possible (Fig. 5B).

Counts of femora and tarsometatarsi in the relatively small samples from the Takaka caves were consistent with female-biased ratios. These were centred on $3♀/1♂$ for the femora, but again ratios of $2-4♀/1♂$ were possible. There was only a marginal probability for $1.4♀/1♂$ and none for any ratio closer to equality (Fig. 5C). Although the

highest probability for the sex ratio represented by the 10 tarsometatarsi was $2♀/1♂$, the other ratios tested all had some level of support (Fig. 5D).

Dinornis spp.

Sex ratios in the samples of *Dinornis* presented by Bunce *et al.* (2003), varied in relation to the kind of sites (e.g. arrays of caves or of swamps) (Fig. 6). The large sample (87) from the Waitomo karst caves suggested a population ratio of $1.1-1.2♀/1♂$ (Fig. 6A), with low but still significant probabilities for the range $1-1.4♀/1♂$. In the eastern hills of the North Island, the sex ratio was somewhere between 1.4 and $2♀/1♂$ (Fig. 6B), but there was a surplus of males from lowland North Island sites (Fig. 6C).

Swamps in the rain forest of the western North Island, yielded samples with sex ratios of $>2♀/1♂$ (Fig. 6D). In contrast, the number of females in the very large (316) sample from swamps in the dry eastern South Island suggested a ratio between $1.4♀/1♂$ and $2♀/1♂$, but neither was significant ($P > 0.05$). Only the unrecorded ratios of $3♀/1♂$ and $4♀/1♂$ were significantly supported (Fig. 6E).

Sex ratios in samples from caves on Takaka Hill (Fig. 6F), in Takaka Valley (Fig. 6G), in northwest Nelson (Fig. 6H), and in the Punakaiki karst (Fig. 6I) closer to equality ($1 < 1.4♀/1♂$, $1.4-2♀/1♂$, $1.1-1.4♀/1♂$, $1-1.1♀/1♂$, respectively). The small Takaka Valley sample could have come from a population whose sex ratio was anywhere between 1 and 4 females to 1 male (Fig. 6G).

Anomalously, perhaps, for a wetland site, the sex ratio in the sample of 18 from Bell Hill Vineyard was near balanced (Fig. 6J). Bell Hill Vineyard is <6 km from Pyramid Valley where females far outnumbered males (Fig. 1).

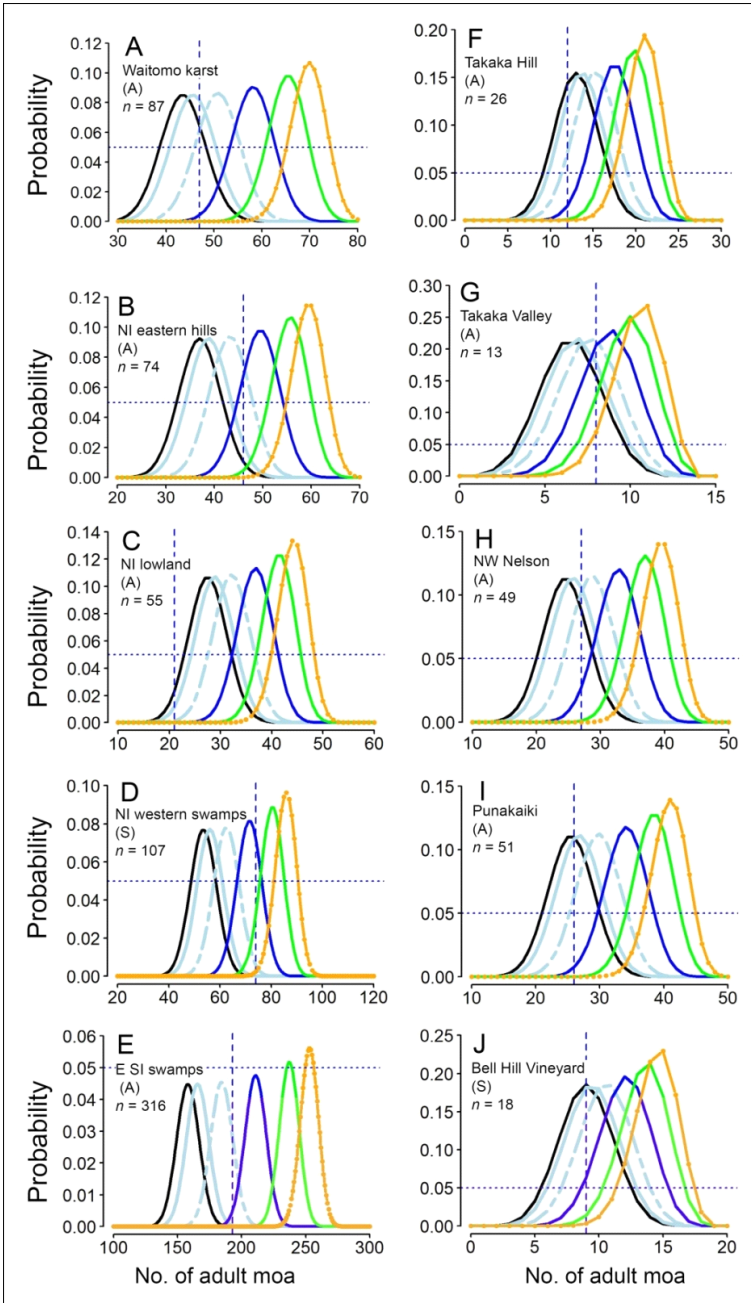


Figure 6. Binomial distributions for sex ratios of *Dinornis* spp. in areas and sites (A–D) the North Island (*D. novaeseelandiae*), and (E–J) the South Island (*D. robustus*), according to sex allocations from “morphometric species”, in relation to number of females posited in samples. Conventions as in Fig. 4. Data from Bunce *et al.* (2003).

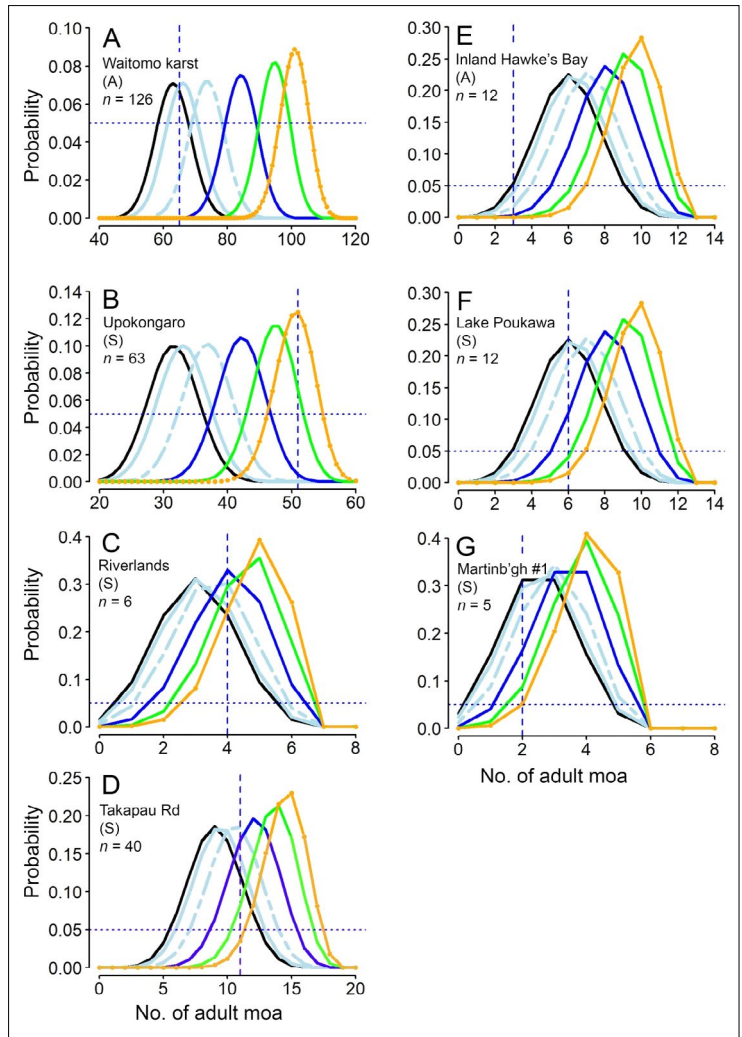
***Dinornis* - Present samples**

Of the sites and areas in Fig. 1, only a few – Waitomo karst, Takaka (Hill and Valley combined), West Coast, and Bell Hill Vineyard – were more or less directly comparable in location and extent to those in Bunce *et al.* (2003).

North Island (Fig. 7)

The much larger sample (126 cf. 87) for the caves in the dense Holocene rain forest in the Waitomo karst yielded a sex ratio in the range 1–1.1♀/1♂; ratios at or above 1.4♀/1♂ were excluded (Fig. 7A). The samples from Upokongaro (Makirikiri in

Figure 7. Binomial probability distributions for sex ratios of *Dinornis novaezealandiae* in North Island areas and sites as shown in Fig. 1, in relation to the number of females posited in the samples.



Worthy [1989]), Riverlands, and Takapau Road (Fig. 7 B, C, D, respectively) had ratios of $>1\text{♀}/1\text{♂}$. At Upokongaro, the spring bog upstream from the mouth of the Whanganui River, which was within rain forest until the 19th century, the sex ratio in the large (63) sample was $4\text{♀}/1\text{♂}$ (Fig. 7B). The sex ratio in the tiny (6) sample from Riverlands, nearer the river mouth, was centred on $2\text{♀}/1\text{♂}$ but again could have represented a population with ratios in the range $1\text{--}4\text{♀}/1\text{♂}$ (Fig. 7C). The population sex ratio reflected in the larger (40) sample from Takapau Road (Fig. 7D) was almost as ambiguous: all tested ratios between $1\text{♀}/1\text{♂}$ and $3\text{♀}/1\text{♂}$ were possible around an apparently favoured value of $1.4\text{--}1.5\text{♀}/1$.

The small samples (12, 12, and 5) from the hill country and a lowland lake bed in the south-eastern North Island (Fig. 7E–G) also yielded contradictory results. Sex ratios in the (mostly) rock shelter sites

in inland Hawke's Bay were biased toward males. Equality was barely supported (Fig. 7E). To the south, lowland Lake Poukawa had a balanced ratio on raw numbers (6:6), but ratios of $1.1\text{--}1.4\text{♀}/1\text{♂}$ were well supported and $2\text{♀}/1\text{♂}$ was possible. Only ratios of $\geq 3\text{♀}/1\text{♂}$ were excluded (Fig. 7F). The tiny (5) sample from Martinborough #1 pitfall cave had a similar pattern.

South Island (Fig. 8)

The relatively large (39, 51, respectively) samples from caves in the Takaka and West Coast karst yielded sex ratios very close to $1\text{♀}/1\text{♂}$. Ratios as high as $1.5\text{♀}/1\text{♂}$ were possible, but very unlikely (Fig. 8A, B). East of the Main Divide, the pothole samples from the Annandale plateau (Worthy & Holdaway 1995) may represent a $2\text{♀}/1\text{♂}$ ratio in the resident

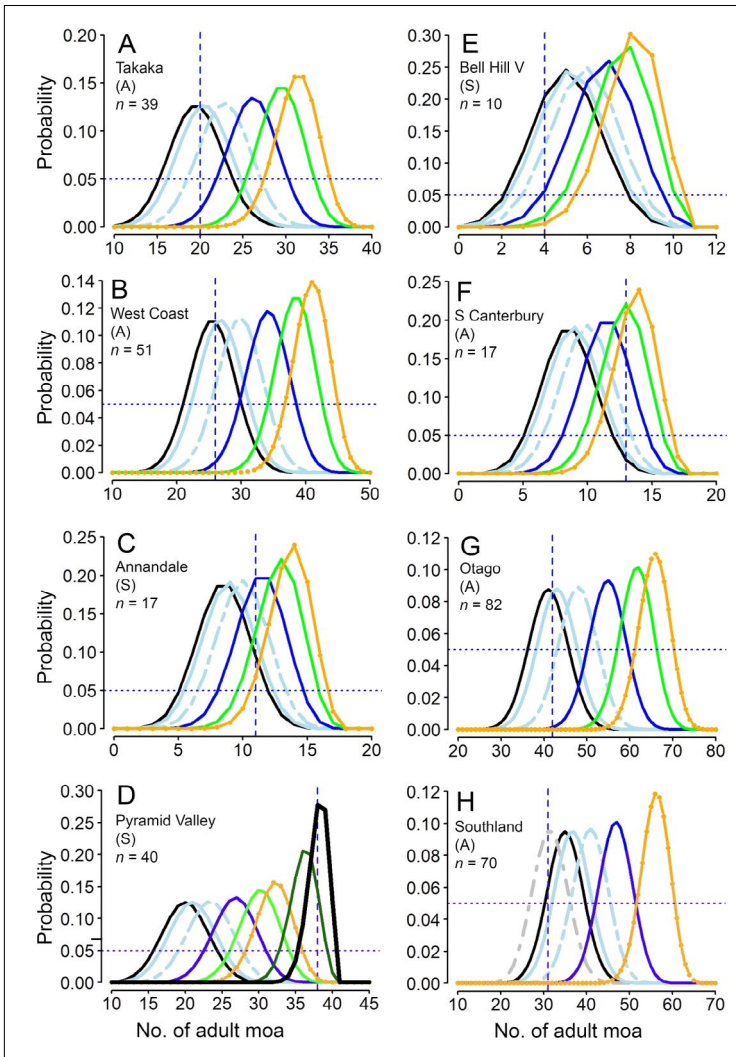


Figure 8. Binomial probability distributions for sex ratios of *Dinornis robustus* in South Island areas (A) and sites (S) as shown in Fig. 1, in relation to the number of females posited in the samples. Conventions as in Fig. 4, plus dark green for 9:1 and wide black for 9.5:1 ratios, and dashed grey (in H) for 1:1.22 male-dominated ratio.

population, but the sample of only 17 meant that ratios of 1–4♀/1♂ were also possible (Fig. 8C).

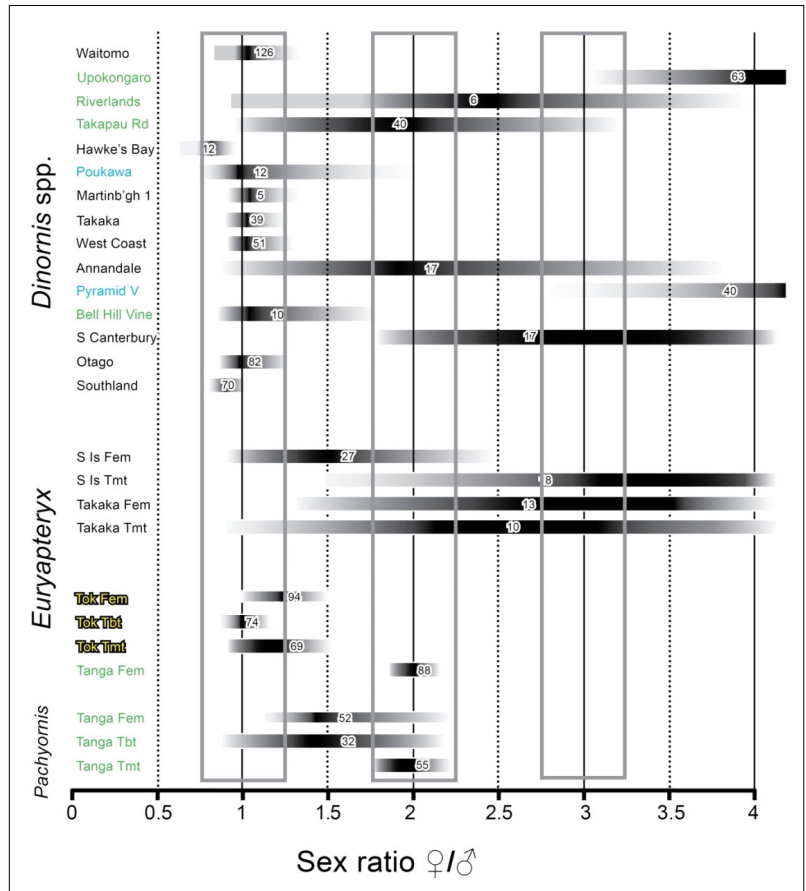
The classic (Eyles 1955; Gregg 1972; Burrows 1989; Holdaway & Worthy 1997; Allentoft *et al.* 2009; Allentoft *et al.* 2010; Johnston 2014; Allentoft *et al.* 2014; Holdaway 2015, 2021a, 2021b; Johnston *et al.* 2022) lake bed site of Pyramid Valley had the most extreme raw sex ratio – 19♀/1♂ – for *Dinornis* of any site or area, (Fig. 8D). Less than 6 km away, the ratio in the small (10) sample from the stream bed/lake shore deposit at Bell Hill Vineyard was near 1♀/1♂ and ratios above 1.4♀/1♂ were not supported (Fig. 8E).

The ratio for the 17 individuals from sites (including caves and a swamp, (Worthy 1997) in South Canterbury was centred on 3♀/1♂. The sample

size was too small to exclude ratios of anywhere between 2 and 4♀/1♂ (Fig. 8F). The large (82) sample from a range of site types in Otago (Worthy 1998c) represented a population sex ratio of 1–1.1♀/1♂ (Fig. 8G). Immediately to the south, the sample from dunes, swamps, and caves in Southland (Worthy 1998b) may represent a balanced sex ratio, but there was a significant surplus of males in both χ^2 and binomial analyses (1♀/1.21♂, $\chi^2 = 0.0144$, $P = 0.904$) (Fig. 8H).

The ranges of possible sex ratios represented by the samples of *Euryapteryx* from the South Island, Tangatupura, and Tokerau Beach, of *Pachyornis geranoides* from Tangatupura, and of *Dinornis* species in both islands are summarised graphically in Figure 9.

Figure 9. Summary of approximate probability density distributions for binomial probabilities of sex ratios in dinornithid and emeid moa from different areas and sites, summarised from Fig. 4, 5, 7, 8. Darkest, ratios with highest probability. *Dinornis* spp., *D. novaezealandiae* (North Island), *D. robustus* (South Island); *Euryapteryx curtus* sensu lato, both islands; *Pachyornis geranoides*, North Island. Green, swamp; blue, lake bed; yellow outline, dunes; black, caves or mixture of sites in sample. Sample sizes on bars. Pyramid V, Pyramid Valley; Bell Hill Vine, Bell Hill Vineyard; S Canterbury, South Canterbury; Tok, Tokerau Beach; Tanga, Tangatapura; Fem, femora; Tbt, tibiotarsus; Tmt, tarsometatarsus.



DISCUSSION

General

RNH suggested recently (Holdaway 2022) that “A female-biased sex ratio in giant moa (*Dinornis* spp.) was confirmed by early ancient genetics studies (Bunce *et al.* 2003; Huynen *et al.* 2003).” The basic statistical analyses reported here suggest that that confidence was misplaced. Indeed, unfortunately, it is probably true to say that at present we do not have a good understanding of moa sex ratios. The vagaries of deposition and preservation, potentially different social organisations in moa (taxonomic) families and species, and uncertainty in non-genetic sexing of individuals combine to generate wide variation in estimates of sex ratio. While some of the variation results from the nature of the deposition and preservation of the samples, a substantial proportion is, as Bunce *et al.* (2003) and Allentoft *et al.* (2010) proposed, a potential source of information on moa biology.

That social and ecological spacing could drive the (sometimes extremely) biased sex ratios of birds preserved in swamps and lake beds, is supported,

at least for Pyramid Valley, by the presence of four sets (dyads) of closely related, perhaps dominant, adult females (Allentoft *et al.* 2015). The birds were all adults and members of each dyad died at about the same time, which suggests that the lake may have been within the territory of “dynasties” of dominant females. Males may have been excluded, except for brief periods for mating.

Potential sources of bias of sex ratio in samples

Low sample size was responsible for by far the greatest uncertainty in the estimation of population ratios from the raw proportions of sexes. After that came issues of allocation of individuals to sex in non-genetic studies, and biological spacing effects on availability of each sex for incorporation in a fossil site.

Adult body size and sex determination by size dimorphism

Trends in body size and episodes of sudden,

reversible, size change have not been reported in moa before. This study shows that body size in female moa could change. Male body size may also have changed but the samples are too small at present. Dwarfing of females and the presence of an occasional unusually large male (e.g. in *Emeus*) provide a source for the apparent overlap in sizes in many populations (Worthy 1987, 1994). The occasional overlap in size in undated samples raises the possibility of substantial error in the morphometric allocation of individuals to sex, in the absence of genetic data.

Genetically-sexed, time-stamped samples (Fig. 2), confirmed the extreme sexual size dimorphism proposed for *Euryapteryx* (Holdaway 2022), and in *P. elephantopus* and *E. crassus*, in North Canterbury. The lack of continuous series of genetically sexed males from the deposits probably reflects behavioural or ecological factors that rarely brought the males to the sites (Allentoft *et al.* 2010). The paucity of males precludes estimates of sex ratios from these genetically identified series, except perhaps for adult *Euryapteryx* in the 500 years after 250 BCE (Fig. 2). The samples from that period suggest a balanced sex ratio, in contrast to the significantly female-biased ratio in Bell Hill Vineyard. The juvenile sex ratio at Bell Hill Vineyard was apparently balanced (Allentoft *et al.* 2010) but the sample is too small to exclude other ratios. The effects of different combinations of males and females added to the juvenile sample from the site are shown in Appendix 2.

Differential mixing from sexual differences in size

Worthy in Worthy & Holdaway (2002) asserted that the apparently balanced sex ratio in *Pachyornis geranoides* (then *P. mappini*) in Tangatupura resulted from a higher likelihood of the heavier females being mired in the swamp deposit. He concluded that the sex ratios of both species at the site were “about equal” Worthy, in Worthy & Holdaway (2002: 175).

“In the dunes at Tokerau Beach, where entrapment is not relevant, the smaller and larger sexes of *Euryapteryx curtus* are roughly in equal proportions, whereas in the swamp miring site of Tangatupura, the larger sex is more numerous (Fig. 5.24). In the same deposit, the proportions of *Pachyornis mappini* seem to be about equal. Assuming the lighter sex of *E. curtus* was less likely to be mired, we can infer that in both these species, the sex ratios were about equal.”

The contention that larger moa (females) were more likely than smaller (males) to be included

in swamps or lake beds is not supported by, for example, the presence of almost equal numbers of the smallest emeid (*Emeus crassus*) – which were smaller than male *D. robustus* – among the adult female *D. robustus* in Pyramid Valley (Allentoft *et al.* 2010).

The main factor in moa deposition in Pyramid Valley was probably predation by Haast’s eagle (*Hieraetus moorei*) (Holdaway 2015). The eagle was never present in the North Island (Holdaway 1992; Worthy & Holdaway 2002), but the near-golden eagle-sized extinct North Island harrier (*Circus teauteensis*) may have been a previously-unrecognised predator on smaller moa there. The harrier was present in the eastern North Island in the Holocene (Worthy & Holdaway 2000) and probably during the late glacial period at Tangatupura swamp as well. Evidence of raptor predation is, unfortunately, unlikely to be present as the moa material consisted largely of leg bones. Raptor predation is revealed by damage to pelvises and crania (Holdaway 2015).

“Ideal” sampling in ‘pitfall’ caves

An ideal sampling regime would permit deposition such that $P(\text{each sex in deposit}) \cong P(\text{each sex in local population})$. For large, flightless moa, pitfall trapping in caves is unlikely to have favoured either sex. An ideal arrangement would be sufficient numbers of traps spaced at intervals likely to include several home ranges and operating over time periods well above the individual life span. Cave systems, especially ‘pitfall’ sinkholes, in extensive areas of karst such as around Punakaiki, Takaka, and Waitomo are likely to have been closest to ideal. Many entrances were open for centuries, if not millennia (Worthy & Holdaway 1994). Preservation conditions within the caves ensured the survival of remains of most individuals up to the present. Similar sex ratios for giant moa were recorded in areas dominated by or exclusively involving cave deposits (Fig. 9). All these areas were covered in dense lowland rain forest during the Holocene.

Ecological and breeding system differences

The often-substantial differences between sex ratios of giant moa in wet and dry landscapes may indicate that something more than occupation of fixed home ranges by females (Allentoft *et al.* 2010) may be responsible for female dominance in deposits in drier areas. If breeding territory quality was important for moa, as suggested by the presence of related adult females in the same site (Allentoft *et al.* 2015), higher quality territories might have favoured deposition of females regardless of the adult sex ratio of the population.

If there was a real bias towards females in North Canterbury, for example, the equal reproductive output of the sexes (Allentoft *et al.* 2010) would have required competition for males. If the apparent bias to females was an artefact of the territorial behaviour of giant moa in a population with a balanced sex ratio, then the equal reproductive output would follow.

Moore (2007) reported studies that showed that both sexes of the southern cassowary (*Casuarius casuarius johnsonii*), a living forest large ratite, defended permanent home ranges, but that home ranges could vary in size and shape seasonally and between years. Males bonded with two or more females simultaneously in a season. Some females bred simultaneously or sequentially with several males. There was a male-dominated sex ratio of 1:1.47 in a sample of 47 adults (Fig. 10) (Moore 2007), a ratio approached by giant moa in Southland (Fig. 8H). The cassowary is a clear warning that even a well-established adult sex ratio can conceal significant heterogeneity within a species' reproductive system.

In modern birds, territory quality (in the sense of food supply for the young) can influence the effect of the quality of the parent on any sex ratio bias in the offspring (Bell *et al.* 2014). If that effect existed in moa, territory quality could have been a major driver of sexual size dimorphism in moa and potentially also in determining the natal sex ratio. Only one moa juvenile sex ratio is available, the apparently balanced ratio in *Euryapteryx* at Bell Hill Vineyard (Allentoft *et al.* 2010), but see Appendix 2. This contrasted with an adult sex ratio biased to females. If either sex "sought" to bias the sex ratio of its offspring, the effort ultimately failed. However, holding the "best" territories – with the best food resources – and preferentially producing female offspring would have contributed to any female bias in sex ratio as well as size dimorphism.

Habitat quality could affect growth rates and body size in giant moa, resulting in the smaller "wet forest" female individuals formerly recognised as a separate species. The best territories may well have been in drier, high productivity areas, but near swamps or lakes, where there was rarely a water deficit. It is in such sites, even in wet climates, that the female bias in sample sex ratio is greatest. Habitat quality may also have driven differences in the adult sex ratio, but any effect may be obscured by deposition biases.

Effects of habitat on sex ratio could be explored by following the sex ratio of resident populations of moa taxa with broad ecological requirements, such as the South Island giant (Worthy 1990a; Worthy & Holdaway 2002), through time. Changes in the sex ratio of such resident populations as climate and vegetation/habitat changed around them after

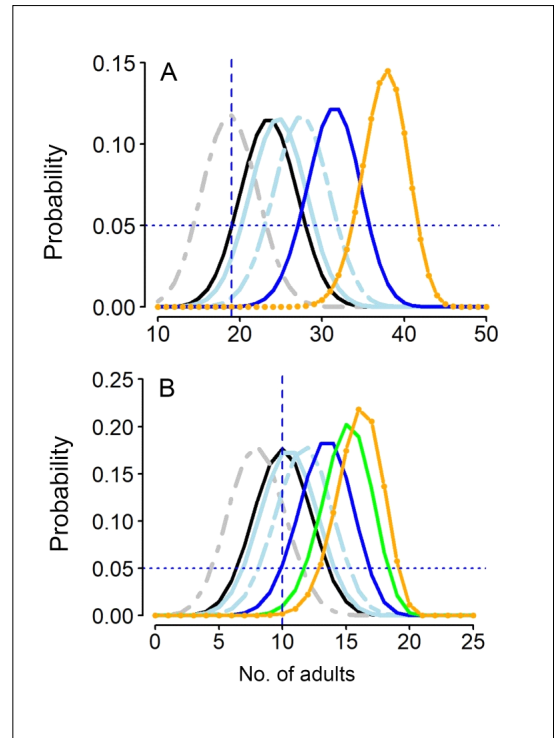


Figure 10. Sex ratios of (A) 19:1.47♂, southern cassowary (*Casuarius casuarius johnsonii*), from data in Moore (2007); (B) balanced juvenile *Euryapteryx curtus* in the Bell Hill Vineyard deposit.

the glaciation may show whether their sex ratio depended on habitat quality.

Samples of *D. robustus* are available from throughout the South Island (Fig. 2). The sex ratios could be followed by genetic sexing of radiocarbon-dated individuals. The advance of rain forest could be tracked by dating the southwards spread of the rain forest specialist moa *Anomalopteryx didiformis* (Worthy 1990b; Worthy & Holdaway 2002). *Anomalopteryx didiformis* was not present on Stewart Island (Worthy 1998a) so could not have reached Southland before Foveaux Strait was flooded 10,000 years ago. The giant moa was certainly resident in Southland before then as it did reach the island (Worthy 1998a).

A southward spread of *A. didiformis* would have had to circumvent the *Sophora microphylla* forest whose post-glacial expansion resulted in an extensive dry forest which dominated the central Otago landscape (Pole 2022). *Anomalopteryx didiformis* may have reached Southland well after rain forest developed there, but knowing when it arrived would provide a minimum date for changes in giant moa habitat.

Conclusions

The ambiguities in estimates of moa sex ratios identified here, and the possibility that sex ratios of some species may have differed between areas, suggest that attempts to model moa breeding systems and interpret evolution of sexual size dimorphism, e.g. Olson & Turvey (2013) are premature. Progress in understanding the reproductive biology of moa will be possible only when variables such as temporal variation in body size that affected sexual size dimorphism are better known. Genetic sexing of series of radiocarbon-dated individuals from a range of species through time and space is probably the only way forward.

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APPENDIX 1: R scripts used in the statistical analyses

A χ^2 Goodness of Fit

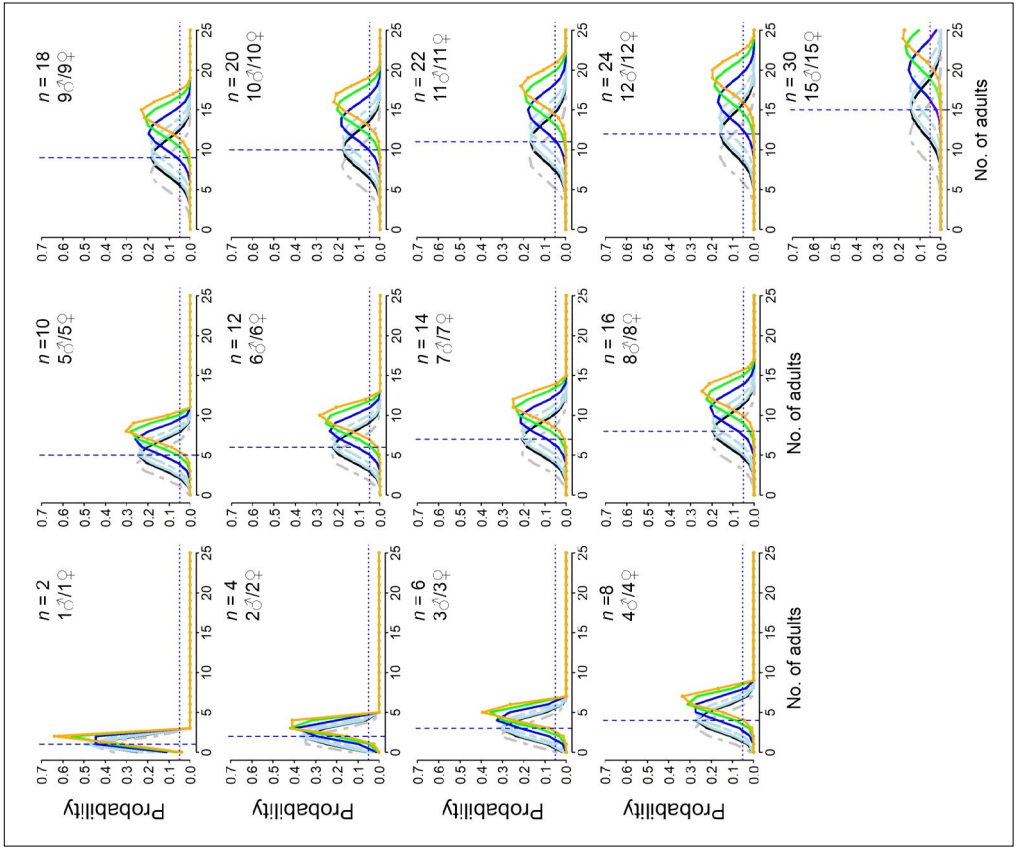
```
#Chi-square Goodness of Fit for sex ratios of 1: 1.26, 1:1,
2:1, 3:1, 4:1, 5:1
#Small sample sizes may give error messages for some
unlikely ratios
observed <- c(31, 39)
#Less than 1:1
expected <- c(.45, .55) #must add up to 1
chisq.test(x=observed, p=expected)
# 1:1
expected <- c(.5, .5) #must add up to 1
chisq.test(x=observed, p=expected)
# 2:1
expected <- c(.667, .333) #must add up to 1
chisq.test(x=observed, p=expected)
#3:1
expected <- c(.75, .25) #must add up to 1
chisq.test(x=observed, p=expected)
#4:1
expected <- c(.8, .2) #must add up to 1
chisq.test(x=observed, p=expected)
```

B Binomial probability distributions

```
#Binomial probabilities for sex ratios (female to male) in
moa given sample size and number of females
# Sample size
n <- 40
#Range of number of samples, e.g., from 10 to 45 as here
k <- seq(10,45, by = 1)
par(mar=c(5.1,6.1,4.1,2.1))
#Plot for ratios of 1:1, 1.1:1, 1.4:1, 2:1, 3:1, 4:1 and optional
19:1
#First 1:1
plot(k, dbinom(k, n, 0.5), type = "l", lwd =
8,xlim=c(10,45),xlab="",ylim=c(0,0.3),ylab="",col.
lab="black",
, cex.axis = 3.5,cex.lab=3,axes=F)
#Then 1.1:1
lines(k, dbinom(k, n, 0.5238), type = "l", lwd = 10,
col="light blue")
#Then 1.4:1
lines(k, dbinom(k, n, 0.5833), type = "l",lty=6,lwd = 10,
col="light blue")
# 2:1
lines(k, dbinom(k, n, 0.667), type = "l", lwd = 8,
col="blue")
#3:1
lines(k, dbinom(k, n, 0.75), type = "l", lwd = 8,
col="green")
#4:1
lines(k, dbinom(k,n,0.8, log=FALSE),type = "b",
col="orange", lwd = 8)
lines(k, dbinom(k,n,0.9, log=FALSE),type = "l",
col="dark green", lwd = 8)
#Optional 19:1 ratio
lines(k, dbinom(k,n,0.95, log=FALSE),type = "l",
col="black", lwd = 12)
#Plot number of females in sample = v
abline(v=38, col="blue", lty=2, lwd=4)
#Plot critical value = 0.05
abline(h=0.05, col="blue", lty=3, lwd=4)
axis(side = 1, lwd = 4,las=0,cex.axis=3,mgp=c(3,2,0))
axis(side = 2, lwd = 4,las=2,cex.axis=3)
```

This will generate a multi-curve plot. For the figures included here, "Export" was selected, then "Save as image" and "Height" reset to 750 pixels.

APPENDIX 2. Part 2. Effects of increasing sample sizes with balanced sex ratios in the raw data on binomial probabilities of other sex ratios represented by the data.



APPENDIX 2. Part 1. Effects on binomial probabilities of minor changes in sample size and sex of individuals additional to those in the present Bell Hill Vineyard sample of juvenile *Eurypteryx curtus*.

