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Sex-ratio bias across populations of a freshwater turtle (Testudines : Chelidae) with genotypic sex determination

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Abstract. Adult sex ratios vary considerably among populations of single species and across years, but the best evidence is drawn from species with temperature-dependent sex determination. It is difficult to disentangle the effects of bias in the production of the sexes and the effects of a range of other factors contributing to biased adult sex ratios. In this paper, we survey sex ratios across populations of a species constrained to produce 1 : 1 offspring sex ratios by genotypic sex determination and show considerable variation in adult sex ratios. Raw adult sex ratios of *Emydura macquarii emmottii* were significantly biased in nine of the 11 populations examined. In all but one case, the bias was strongly in favour of males. Part of the bias in sex ratio was attributed to the differing ages of maturity of males and females – males mature younger than females – which leads to more male cohorts being included in the calculations of sex ratio than female cohorts. However, correcting for this effect brought the sex ratios of the populations closer to parity, as expected, and accounted for an overall 62% of the male surplus evident in the adult sex ratio. Even so, it was insufficient to explain the strong male bias (1.2–2.9) in five of the nine populations initially showing such bias. This provides support to those who advise caution in interpreting adult sex ratio data for freshwater turtles in the context of demography, sex allocation or evaluating the impact of climate change.

Introduction

Fisher's model of frequency-dependent selection (Düsing 1884; Fisher 1930; Shaw and Mohler 1953) and Mendelian segregation of the sex chromosomes (Ohno 1967; Williams 1979) are compelling reasons for expecting a 1 : 1 primary sex ratio in vertebrates with genotypic sex determination (GSD), including many reptiles. However, many other reptiles have the sex of their offspring determined by the temperatures that prevail in the nest (Bull and Vogt 1979; Vogt and Bull 1984) or in the oviducts (Robert and Thompson 2001; Robert *et al*. 2003; Wapstra *et al*. 2004), a trait known as temperature-dependent sex determination (TSD). In these species, the constraint placed on offspring sex ratio by Mendelian segregation is removed. Add to this uncertainty over whether or not a 1 : 1 sex ratio is the equilibrium condition in species whose fitness, within each sex, may vary with and depend on the very factor responsible for determining sex (Bull 1981; Bull and Charnov 1988), and one might expect sex ratios to vary more widely in species with TSD than in those whose sex is constrained by a chromosomal mode of sex determination.

There have been several reviews of adult sex ratios for freshwater turtles (Bury 1979; Gibbons 1990; Ewert and Nelson 1991). Sex ratio data available to Bury (1979) ($n = 23$) suggested that, with some notable exceptions (e.g. *Sternotherus odoratus*: Risley 1933; *Pseudemys scripta*: Moll and Legler 1971), most freshwater turtles tend to have a 1 : 1 adult sex ratio. Sex bias, when it occurred, was in favour of males in 31 cases and in favour of females in 15 cases for turtle populations included in the review by Ewert and Nelson (1991). Extensive work on the slider turtle (*Trachemys scripta*) in South Carolina revealed variously no bias and bias in either direction among populations (Gibbons 1990). Most of the abovementioned species showing bias have TSD, and it is tempting to invoke TSD as the primary causal factor, but in fact it is not possible to disentangle biases arising from incubation effects from biases arising from a range of other confounding factors (Gibbons 1990).

In this paper, we consider sex ratio bias across populations of the Cooper Creek turtle (*Emydura macquarii emmottii*), a turtle that occupies isolated waterholes in central Australia. The Cooper Creek turtle has its sex ratios constrained by GSD (probably a cryptic XY system: Ezaz *et al*. 2006). We show that, even in the absence of TSD, sex ratio variation across populations of freshwater turtles is considerable, and that if we are to demonstrate an impact of climate change or habitat alteration on adult sex ratios in freshwater turtles with TSD, or to interpret biased production sex ratios in the context of adult sex ratios, we need to achieve much greater control over the many ecological and methodological factors that influence the measured sex ratio.

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Materials and methods

The study animal

The Cooper Creek turtle is a member of the southern *Emydura* complex (Georges and Adams 1996) and has been recognised at the level of subspecies (*Emydura macquarii emmottii*) (Cann *et al.* 2003). It is the only turtle to inhabit the arid Australian interior and is one of the largest chelids in Australia – specimens are known to reach up to 8 kg in mass and over 400 mm in carapace length. The species shows strong sexual size dimorphism, with females the larger sex. Further information on the natural history of the subspecies is provided by Cann (1998).

The study area

The Cooper drainage has its headwaters in tropical and subtropical Queensland, flows south-west through land of very low relief as a broad distributary system (Rust and Nanson 1986) before flowing into Lake Eyre. It is a dryland system, where flow is episodic, fed by rains in its headwaters under tropical monsoonal influence (Allan 1985). During the extended dry periods, water is restricted to permanent and semi-permanent waterholes scattered across the arid landscape.

Methods

We captured turtles in 11 waterholes from five isolated floodplain units of the Cooper Creek catchment (Table 1). Turtles were captured in traps (Legler 1960) baited with meat (usually ox/mutton, livers and hearts) on annual field trips between 2001 and 2004. Some of the traps were fitted with a breathing column to allow captured turtles access to the surface to breathe. This modification allowed us to extend trapping sessions by up to 36 h in what were otherwise remote locations.

Upon capture, each turtle was individually marked by cutting a unique combination of notches in the marginal scutes and underlying bone. Sex and maturity were determined either visually by examination of the tail using criteria established in the results, or internally via laparoscopy (Wood *et al.* 1983). We checked for gravidity by palpation and laparoscopy. None of the females were gravid at the time of sampling. Maximum straight-line carapace length, midline plastron length, and maximum head width was measured (±0.1 mm) for each turtle with vernier callipers.

To determine size at maturity, turtles were examined internally with a laparoscope (Olympus A7591) by visually examining the gonad and associated ducts (Wood *et al.* 1983). Turtles were examined on site, kept for a few hours, and then released. Animals recaptured a year later indicated full recovery from the procedure.

Growth was determined from mark–capture–recapture data and scute annuli. The rate of deposition of growth lines at one line per year was verified from mark–capture–recapture data. Growth ring data were mainly used for subadults and juveniles as rings became intermittent and undetectable in older individuals. Only rings representing the most recent full year of growth were used. Growth for older adults and some juveniles was determined only from mark–capture–recapture data. Von Bertalanffy growth models were fitted to the turtle growth data for each sex (Schoener and Schoener 1978). This approach estimates growth parameters, enabling age to be predicted from length, and so enabling matched cohort comparisons for our sex ratio analyses.

Sex ratios were tested for significant departure from 1 : 1 using Chi-square tests (with Yate's correction) applied at the 95% level of significance. Sex ratios for other *Emydura macquarii* populations were obtained from the published literature and unpublished records.

Results

Dimorphism, size and age at maturity

Adult male *Emydura* can be distinguished from females of the same size by the greatly enlarged tail, which accommodates the penis and is used to effect copulation. Herein, we describe new, more detailed criteria for determining the sex of an individual from external characteristics. In particular, the development of the tail can be used to determine sex well before maturity using the following criteria. We recognise

Table 1. Sex ratios of mature males to mature females and sex ratios of matched cohorts (>12 years old) for *Emydura macquarii emmottii* from the Cooper Creek of central Australia

Exchange between waterholes within floodplain units is possible during times of extensive flooding, but not between floodplain units. Correction for differing ages of maturity to yield matched cohorts of males and females yielded the reduction in the surplus of males compared to that of the raw adult sex ratios, as shown. The overall reduction (samples pooled) was 62%

Floodplain unit	Sex ratios of adults					Sex ratios of matched cohorts					
	Males	Females	M/F	χ^2	Significance	Males	Females	M/F	Reduction in male surplus (%)	χ^2	Significance
Lochern NP											
Broadwater	92	20	4.6	45	<0.0001	92	32	2.9	–16.7	28.1	<0.0005
Fish Hole	102	28	3.64	41	<0.0001	102	59	1.7	–41.9	11	<0.005
Waterloo	100	38	2.63	27	<0.0001	100	82	1.2	–71	1.6	n.s.
Windorah						0					
Currareeva	60	25	2.4	13.6	<0.0005	60	32	1.9	–20	7.9	<0.01
Murken	35	14	2.5	8.2	<0.005	35	22	1.6	–38.1	2.5	n.s.
Tanbar Station						0					
Eulbertie	504	312	1.62	44.7	<0.0001	504	427	1.2	–59.9	6.2	<0.01
Tanbar	29	16	1.81	3.2	n.s.	29	31	0.9	–115.4	0	n.s.
Welford NP						0					
Little Boomerang	62	23	2.7	17	<0.0005	62	55	1.1	–82.1	0.3	n.s.
Trafalgar	62	26	2.38	13.9	<0.0005	62	39	1.6	–36.1	4.8	<0.05
Woolshed	23	6	3.83	8.8	<0.005	23	15	1.5	–52.9	1.3	n.s.
Springfield Station						0					
Springfield	95	143	0.66	9.3	<0.005	95	173	0.5	62.5	22.1	<0.0005

that the categories of 'juvenile male' and 'subadult male', although defined as discrete, are part of a gradient from immature to mature.

Juvenile male. Anterior margin of the cloaca on or outside the posterior margin of the carapace when gently extended between finger and thumb; tail extends to cover a maximum of ~2.5 marginal scutes when folded around the upper thigh; anterior margin of the cloaca remains within the carapace margin in females throughout life. Under laparoscopy, the testes are small, compact, regressed and the epididymides is a simple uncoiled translucent tube.

Subadult male. Secondary sexual characters of tail partially developed; anterior margin of cloaca well clear of the posterior margin of the carapace when extended; tail extends to cover 3 marginal scutes when folded around the upper thigh. Penis does not extrude when the animal is held plastron up, rocked, and inward pressure is placed on the hind feet. Under laparoscopy, the testes is small, compact, regressed and the epididymis is coiled, but translucent, lacking sperm.

Adult male. Secondary sexual characters of tail fully developed; anterior margin of cloaca well clear of the posterior margin of carapace when extended; tail extends to cover 3.5–4.5 marginal scutes when folded around the upper thigh; penis usually extrudes when coaxed as above. Under laparoscopy, the testes are variable in condition depending upon the season, but the epididymides are distinct structures, coiled, opaque, white, containing abundant sperm throughout the year (except rarely: Kennett and Georges 1990).

The smallest mature male examined with laparoscope had a carapace length of 184.6 mm, and the largest immature male had a carapace length of 198.8 mm (midpoint 191.7 mm). This range corresponded closely with the range of sizes at which male attributes of the tail developed. The smallest adult male determined from external characteristics using the criteria above had a carapace length of 181.7 mm and the smallest juvenile male examined had a carapace length of 100.1 mm.

Turtles could be determined as female if they were larger in size than that at which males develop secondary sex characteristics; that is, with confidence when the anterior margin of the cloaca lies within the margin of the carapace at a carapace length greater than 135.9 mm. Immature females had small discrete ovaries with a distinct boundary, and numerous very small yellow ovarian follicles of uniform size and distribution within the stroma. The oviducts were a simple unconvoluted tube. Mature females, at the time we sampled, had enlarged developing follicles and sometimes other structures indicative of past breeding (corpora atresia, corpora albucantea); the ovary was an enlarged diffuse structure with no clear boundary. The oviducts were convoluted.

The smallest mature female examined with laparoscope had a carapace length of 249.1 mm, and the largest immature female had a carapace length of 285.1 mm. Females with carapace lengths in the range 249–285 mm were therefore taken to be mature. For practical purposes, a carapace length of 270 mm or greater can be used to assign mature female status to turtles where male secondary sexual characteristics are absent.

The Cooper Creek turtle shows pronounced sexual size dimorphism. Growth rates of males and females were similar for the first 15 years of life, but diverged thereafter with females growing to a much larger asymptotic size (398.7 ± 17.3 mm) than males (290.8 ± 7.8 mm). These asymptotes corresponded well with the median size of animals that showed no appreciable growth (females: 306.0 ± 2.5 (s.e.) mm; males: 245.6 ± 1.3 mm).

Using the sizes at sexual maturity and the age–size relationship established using the von Bertalanffy curves yielded estimates of ages at maturity for males at 12 years (11–13) and for females at 21 years (19–25).

Sex ratios

Raw adult sex ratios were biased in 10 of the 11 populations examined, with strong statistical significance in all 10 cases (Table 1). In all but one case (Springfield Waterhole), the bias was strongly in favour of males. Although exchange of individuals between waterholes within floodplain units is possible during periods of extensive flooding, there is no evidence in the data of differential assortment of the sexes across waterholes (Table 1). Part of the bias in sex ratio can be attributed to the differing ages of maturity of males and females – males mature younger than females – which leads to more male cohorts being included in the calculations of sex ratio than female cohorts (Gibbons 1990; Lovich and Gibbons 1990). We corrected for this effect by calculating the size of females at the age at which males mature, then calculating the sex ratio using females larger than that size (12 years or older), some of which would be immature, and mature males (12 years and older) only. The possibility that some males may not show the detectable beginnings of sexual dimorphism at the midpoint size of maturity (12 years), and so be counted as females, was considered negligible. The alternative of calculating the size of males at the age at which females mature, then calculating the sex ratio using males greater than that size (21 years old or older) and mature females (21 years or older) only, was considered unacceptable for several reasons. The age–size relationship is likely to become less accurate at greater sizes, leading to greater uncertainty in the cohorts included in the comparison. Also, many mature males, those with ages between 12 and 21 years, will be omitted from the analysis. The reduction in power would lead to ambiguity in the loss of significant sex ratio bias after correction.

The correction for differing ages at maturity brought the sex ratios of all populations closer to parity, as expected, and accounted for an overall 62% of the male surplus evident in the adult sex ratio. Even so, it was insufficient to explain the strong male bias (1.2–2.9) in five of the nine populations initially showing such bias (Table 1). Correction for differing ages at maturity exacerbated the female bias at Springfield Waterhole, with two females captured for every male ($n = 268$).

Discussion

Gibbons (1990), in a more comprehensive analysis than the one presented here, demonstrated considerable variation in sex ratio estimates across years and across locations for the slider turtle (*Trachemys scripta*). This species has temperature-dependent sex determination (TSD) and so it was difficult for Gibbons to disentangle the contribution to sex ratio variation caused by hatchling sex ratio bias from that caused by the range of other contributing factors he identified. He concluded that few species have been examined in sufficient detail to eliminate the many confounding factors, but an unaccounted-for component of the variation he observed may have resulted, not from these confounding factors, but from bias in the production of the sexes under TSD. *E. macquarii*, in contrast, has genotypic sex determination (GSD: Bull *et al.* 1985; Thompson 1988), as do all other chelid turtles examined (Georges 1988; Georges and McInnes 1998; Ezaz *et al.* 2006). We observed considerable and significant bias in adult sex ratio across most of the populations we sampled, and those that did not show statistically significant bias were those with low sampling intensity (admitting the possibly Type II error). Many of these biases were sustained when we corrected for differential ages of maturity for males and females. Significant bias in adult sex ratio of *Emydura* has been observed in several other studies (Table 2).

Possible sources of bias in observed captures in the absence of bias in the production of the sexes include (a) gear selectivity, where males and females have a different propensity to be caught when they encounter a trap; (b) differential encounter rates driven by differential home-range sizes, rates of movement within those home ranges, which will in turn influence the rate of encounter of traps within waterholes; (c) differential rates of dispersal across waterholes, which will interact with the trapping regime to produce bias; (d) differences in habitat preference, leading to differential propensity to be captured under a particular trapping regime; and (e) differential mortality of the sexes, arising through sex-specific differences in size and rate of passage through the most vulnerable size classes, and in behaviour, particularly nesting, but also in propensity to move through risk-prone habitat (Ream and Ream 1966; Palmisano *et al.* 1973; Gibbons 1990; Gibbs and Steen 2005).

Although Ream and Ream (1966) found that baited traps were biased in favour of males, we do not believe this to be the case for *Emydura*. Baited hoop traps did not yield biased sex ratios in an intensive study of *Emydura macquarii nigra* from Fraser Island (Table 2), nor did the sex ratio for individuals differ significantly from the sex ratio for captures, despite the turtles being captured, on average, 4.9 times each (Georges 1982). This suggests that the gear is not selective, and that males and females do not differ in their rate of encounter with traps. The male-biased sex ratios in our study are most likely to have arisen through higher mortality of

Table 2. Adult sex ratios reported for the *Emydura macquarii* complex across its range

None of the reported estimates has been corrected for differential age at maturity. The data are ordered from most female-biased to most male-biased

Location	Males	Females	M/F	χ^2	Significance	Reference
Fitzroy R. (impounded), Qld	514	791	0.6	58.4	<0.0001	Tucker 2000
Hunter R., NSW	77	136	0.6	15.8	<0.0005	Judge 2001
Murray R., SA	69	125	0.6	15.6	<0.0005	Thompson 1983
Ross R. (impounded), Qld	318	515	0.6	46.1	<0.0001	Trembath 2005
Burnett R. (impounded), Qld	631	759	0.8	11.6	<0.005	Tucker 2000
Kolan R., Qld	62	74	0.8	0.9	n.s.	Tucker 2000
Mary R. (impounded), Qld	93	120	0.8	3.2	n.s.	Tucker 2000
Ross R. (Stuart Creek), Qld	53	69	0.8	1.8	n.s.	Trembath 2005
Burnett R. (impounded), Qld	523	561	0.9	1.3	n.s.	Tucker 2000
Murray R., NSW	239	280	0.9	3.1	n.s.	Chessman 1978
Alligator Ck, Qld	119	115	1	0	n.s.	Trembath 2005
Fitzroy River, Qld	175	169	1	0.1	n.s.	Tucker 2000
Kolan R. (impounded), Qld	173	169	1	0	n.s.	Tucker 2000
Murray R., SA	94	91	1	0	n.s.	Judge 2001
Brisbane R., Qld	68	60	1.1	0.4	n.s.	Judge 2001
Burnett R., Qld	387	343	1.1	2.5	n.s.	Tucker 2000
Fraser Island, Qld	153	142	1.1	0.3	n.s.	Georges 1988
Macleay R., NSW	82	78	1.1	0.1	n.s.	Judge 2001
Mary R., Qld	97	81	1.2	1.3	n.s.	Tucker 2000
Burnett R., Qld	74	42	1.8	8.3		Georges 1988
Nepean R., NSW	134	62	2.2	25.7	<0.0001	Judge 2001

females by virtue of their nesting activity or because of differing dispersion of male and female turtles across waterholes comprising discrete floodplain units (Table 1). The strong and significant female bias in the Springfield Waterhole goes against the trend, and may have resulted from differential mortality among adults when the waterhole nearly dried in the 1980–83 drought. All other waterholes either persisted (e.g. Eulbertie Waterhole) or dried completely (e.g Tanbar Waterhole), killing all resident turtles. This proposition is supported by the observation that the sex ratio of the 102 animals to have been born since the drawdown (dramatic lowering of water level), and that have come into the size range at which correction for differential age at maturity can be made (12–22 years old), is not significantly biased (57 males to 45 females, $\chi^2 = 1.18$, d.f. = 1, $P > 0.05$).

TSD is thought to have serious demographic consequences in the face of climate change and habitat alteration, yet in long-lived species, such as turtles, the impact of such environmental change on adult populations may take many generations to manifest. Biased adult sex ratios may be our only early warning indicator of potential trouble ahead for many species as a consequence of regional changes in environmental temperatures. However, our study shows that even in the absence of temperature-dependent sex determination, sex ratio bias can occur in studies of freshwater turtles. As such, it reinforces the caveats placed on estimates of adult sex ratio in natural populations by Gibbons (1990). If we are to use estimates of sex ratio bias as an early warning of potential problems arising from climate change in species with TSD (Davenport 1989; Janzen 1994), or to predict responses of mothers engaging in facultative sex allocation (Olsson and Shine 2001; Robert and Thompson 2001), we need to attend first to issues of sampling design (individuals of both sexes must have equal exposure to the trapping regime across the entire population), gear selectivity compounded by differential encounter rates, differential mortality and differential ages at maturity. Some of these difficulties can be overcome by a focus on precision of estimates rather than accuracy in monitoring trends in sex ratio, as even strong systematic bias may not obscure a trend. Use of sex ratio data as an index to sex ratio (precise, but potentially inaccurate), rather than an estimate of sex ratio, assumes that any systematic bias is constant or that variation in the bias can be calculated and incorporated in the index. This can be achieved in part by standardisation of the gear and arrangement of the traps, but variation in differential mortality, dispersal and dispersion across multiple waterbodies, and inter-annual changes in rates of mortality will be more difficult to accommodate.

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