

REPRODUCTIVE ANATOMY OF THE STRICTLY MONOGAMOUS CAPRICORN SILVEREYE *Zosterops lateralis chlorocephalus*

BRUCE C. ROBERTSON

Department of Zoology and Entomology, University of Queensland, Brisbane, Queensland, Australia 4072
Current address: School of Biological Sciences, University of Canterbury, PB 4800, Christchurch, New Zealand
e-mail: bruce.robertson@canterbury.ac.nz

Received: 16 October 2003

INTRODUCTION

The reproductive anatomy of birds, like many other facets of avian biology (Birkhead and Møller 1992), is under the influence of selection pressures associated with sperm competition (e.g. Møller 1991; Birkhead *et al.* 1993; Rising 1996; Briskie *et al.* 1997). Species subject to intense sperm competition possess reproductive structures that can produce and store large numbers of sperm (e.g. Briskie 1993; Mulder and Cockburn 1993; Castro *et al.* 1996). The reproductive anatomy of a bird, therefore, can be indicative of the intensity of sperm competition in that species.

The Capricorn Silvereye *Zosterops lateralis chlorocephalus* is a socially monogamous passerine of the islands of the southern Great Barrier Reef (Kikkawa 1997). Capricorn Silvereyes breed asynchronously at high density during a protracted breeding season (Kikkawa 1987), which suggests ample opportunity for sperm competition. However, extensive field observations (Kikkawa 1987; Robertson 1997) and a genetic parentage analysis (Robertson 1997; Robertson *et al.* 2001) have not found evidence for the presence of sperm competition. Here I examine the reproductive anatomy of the Capricorn Silvereye and compare the structures with those of other species with either high or low levels of sperm competition.

METHODS

The internal reproductive anatomy of a pair of Capricorn Silvereyes from the Heron Island population (see Kikkawa and Wilson 1983) was examined following the methods of Briskie (1993) and Briskie and Birkhead (1993). Given that most variation in sperm length, sperm storage tubule (SST) length and SST number is accounted for by between-species differences (e.g. Briskie and Montgomerie 1992, 1993), general conclusions can be reasonably drawn from a small sample (see Sheldon and Birkhead 1994). Furthermore, the well-established relationship between male sperm length and SST length (Briskie and Montgomerie 1992; Briskie *et al.* 1997) also provides us with a benchmark against which to assess the reliability of our measurements for the male and female Capricorn Silvereye.

The pair was determined by colour banding (Kikkawa 1997) and behavioural observations, and was collected by mist net on day +2 of the female's laying cycle (day 0 is the day the first egg is laid). Laying date was predicted from nest building and later confirmed by follicular development in the ovaries of the female. The birds were killed by cervical dislocation and dissected immediately.

Spermatozoa and SSTs were examined with a phase contrast microscope. In the male, spermatozoan size was measured from spermatozoa sampled from the seminal glomera. Total spermatozoon length, including both head and tail, was recorded for 20 haphazardly chosen spermatozoa (Briskie and Montgomerie 1993). Damaged spermatozoa (i.e. those with broken tails) were not measured. In the female, lengths and widths of SSTs were calculated for 20 clearly

visible SSTs sampled haphazardly under 400× magnification (Briskie and Montgomerie 1993) for each of the five mucosal folds. Only the lengths of relatively straight SSTs were measured. Lumen diameter was measured for ten of the 20 SSTs on each mucosal fold. All values are given as means \pm SE unless otherwise stated.

To investigate if the reproductive anatomy of the Capricorn Silvereye was consistent with either high or low levels of sperm competition, the values for the Capricorn Silvereye were compared with published values for similarly sized passerines (data in Briskie *et al.* 1997). These passerines were grouped by rate of extra-pair paternity (EPP) as having either high sperm competition (average EPP, $39.4 \pm 8.4\%$ and average mass, 12.6 ± 2.8 g): Reed Bunting *Emberiza schoeniclus*, Yellow Warbler *Dendroica petechia*, Red-faced Warbler *Cardellina rubrifrons*, or, low sperm competition (average EPP, $6.7 \pm 2.3\%$ and average mass, 12.2 ± 0.6 g): Blue Tit *Parus caeruleus*, Sedge Warbler *Acrocephalus schoenobaenus*, Zebra Finch *Taeniopygia guttata*.

RESULTS

The cloacal protuberance of male Capricorn Silvereyes was a predominantly unfeathered, barrel-shaped structure lacking any distinct features (cf. Birkhead *et al.* 1991; Mulder and Cockburn 1993), with the exception of a ring of feathers ranging in length from 6.0 to 8.0 mm, around the vent. A swelling, which contained the convoluted tubules of the seminal glomera, was located posteriorly on either side at the base of the protuberance. Tubules could not be seen through the skin in any male.

The testes of the sacrificed male weighed 0.2439 grams (right 0.1143 g, left 0.1296 g) or 1.74 per cent of the male's body weight (14 g). This was similar to the predicted value of 0.2499 grams for a passerine of this body mass (calculated following Møller 1991). Capricorn Silvereye spermatozoa were also similar in structure to other avian species (e.g. Quay 1985). When sperm length was compared to the high (255.8 ± 29.4 mm) and low (93.9 ± 12.4 mm) sperm competition groups, Capricorn Silvereye sperm (60.1 ± 0.7 μ m, $n = 20$) was consistent with low sperm competition.

The female's cloaca also was an unfeathered structure that showed some swelling, but no protuberance. SSTs were present on and between the mucosal folds (3 mm wide band) at the junction of the uterus and vagina. A mean of 81.8 ± 4.8 (range = 67–95) SSTs were counted in the lamina propria of five mucosal folds. As 14 mucosal folds were present in the utero-vaginal junction, it was estimated that this female had a total of 1 145 SSTs. SSTs of the Capricorn Silvereye were similar in structure to other bird species, except that no instances of branching were noted (Birkhead *et al.* 1991; Briskie and Montgomerie 1993). Some apparently empty SSTs were noted, but the

proportion of SSTs containing spermatozoa was not estimated. In all observed instances where spermatozoa were present in SSTs, they were stored in a single layer with the acrosomal regions forming a single clump facing the distal end of the tubule.

Capricorn Silvereye SSTs averaged 86.1 ± 18.3 micrometer ($n = 100$, range = 45.5–127.3) in length and 44.9 ± 7.5 micrometer ($n = 100$, range = 36.4–54.5) in width. The internal diameter of SSTs averaged 15.9 ± 2.9 micrometer ($n = 50$, range = 11.1–20.0). Both number and length of SSTs noted for the Capricorn Silvereye were consistent with a species showing low (no., 1270.7 ± 280.4 ; length, 211.9 ± 21.3 μm) rather than high (no., 542.3 ± 94.7 ; length, 535.2 ± 173.4 μm) sperm competition.

DISCUSSION

The anatomy of the male Capricorn Silvereye suggests that this species does not produce and store unusually large numbers of sperm. This is in contrast to other species that display frequent copulation, extra-pair copulation and intense sperm competition (Møller 1991; Briskie 1993). Capricorn Silvereye males display a cloacal protuberance for sperm storage (Robertson *et al.* 2001), however its size and the size of the testes are close to that expected for a passerine of this mass (Møller 1991; Briskie 1993). The cloacal protuberance of male Capricorn Silvereyes is probably more associated with sperm maturity (Wolfson 1954) than sperm competition (Birkhead *et al.* 1993).

The anatomy of the female Capricorn Silvereye was similar to that of other birds. The presence of SSTs in the junction of the uterus and vagina of the female suggests that Capricorn Silvereyes can store sperm between successive copulations. Field observations indicate that copulations in the Capricorn Silvereye are infrequent and limited to the time of ovulation, even between the members of a pair. Whilst sperm storage enhances the opportunity for sperm competition (Birkhead and Møller 1992), female Capricorn Silvereyes do not exploit this behavioural strategy (Robertson *et al.* 2001), hence it is possible that the SSTs found in females currently function in fertility insurance with the social mate rather than in sperm competition involving different males.

In passerines, sperm length depends on the morphology of the SSTs, which in turn, is influenced by sperm competition intensity (Briskie *et al.* 1997). Capricorn Silvereye sperm and SSTs are rather short in comparison to other passerines; both are characteristics of species with low intensity of sperm competition (Briskie and Montgomerie 1992; Briskie *et al.* 1997). It is also worth noting that the SSTs of the Capricorn Silvereye are barely longer than a single sperm, whereas most passerines possess SSTs that are two to three times the length of a single sperm (Briskie and Montgomerie 1992). A similar trend has been noted in the Least Flycatcher *Empidonax minimus* and the Red-eyed Vireo *Vireo olivaceus* (Briskie and Montgomerie 1992). Both species possess small testes (Briskie 1993) and, hence, potentially low intensities of sperm competition (Møller 1991; Briskie 1993).

In all comparisons with similarly sized passerines grouped as having either high or low sperm competition, the anatomy of the Capricorn Silvereye consistently placed the species into the group that displayed low rates of EPP. This finding is consistent with predictions based on the avian literature on sperm competition and the strictly monogamous mating system of the Capricorn Silvereye.

ACKNOWLEDGMENTS

I thank the staff of Heron Island Research Station for logistical support. Jiro Kikkawa, Anne Golidzen, Jim Briskie, Ed Minot, Bart Kempenars, Sandie Degnan and two anonymous reviewers made valuable comments on the manuscript. This study was conducted under permits from the Queensland Government and Australian Bird and Bat Banding Scheme, with ethical clearance from the University of Queensland and funding from the Australian Postgraduate Research Award Scheme (BCR) and an Australian Research Council large grant to Jiro Kikkawa.

REFERENCES

- Birkhead, T. R., Briskie, J. V. and Møller, A. P. (1993). Male sperm reserves and copulation frequency in birds. *Behav. Ecol. Sociobiol.* **32**: 85–93.
- Birkhead, T. R., Hatchwell, B. J. and Davies, N. B. (1991). Sperm competition and the reproductive organs of the male and female Dunnock *Prunella modularis*. *Ibis* **133**: 306–311.
- Birkhead, T. R. and Møller, A. P. (1992). 'Sperm competition in birds: Evolutionary causes and consequences'. (Academic Press: London.)
- Briskie, J. V. (1993). Anatomical adaptations to sperm competition in Smith's Longspurs and other polygynandrous passerines. *Auk* **110**: 875–888.
- Briskie, J. V. and Birkhead, T. R. (1993). A review of the methods used to study the anatomy of avian sperm storage. *Ornis Scand.* **24**: 323–329.
- Briskie, J. V. and Montgomerie, R. (1992). Sperm size and sperm competition in birds. *Proc. R. Soc. Lond. B. Biol. Sci.* **247**: 89–95.
- Briskie, J. V. and Montgomerie, R. (1993). Patterns of sperm storage in relation to sperm competition in passerine birds. *Condor* **95**: 442–454.
- Briskie, J. V., Montgomerie, R. and Birkhead, T. R. (1997). The evolution of sperm size in birds. *Evolution* **51**: 937–945.
- Castro, I., Minot, E., Fordham, R. and Birkhead, T. R. (1996). Polygynandry, face-to-face copulation and sperm competition in the Hihi, *Notiomystis cincta* (Aves: Meliphagidae). *Ibis* **139**: 765–771.
- Kikkawa, J. (1987). Social relations and fitness in Silvereyes. In 'Animal societies: theories and facts'. (Eds Y. Ito and J. Kikkawa). Pp. 253–266. (Japan Scientific Press: Tokyo.)
- Kikkawa, J. (1997). Individual colour banding for 8000 birds. *Corella* **21**: 26–31.
- Kikkawa, J. and Wilson, J. M. (1983). Breeding and dominance among the Heron Island Silvereyes *Zosterops lateralis chlorocephala*. *Emu* **83**: 181–198.
- Møller, A. P. (1991). Sperm competition, sperm depletion, paternal care, and relative testis size in birds. *Am. Nat.* **137**: 882–906.
- Mulder, R. A. and Cockburn, A. (1993). Sperm competition and the reproductive anatomy of male Superb Fairy-wrens. *Auk* **110**: 588–593.
- Quay, W. B. (1985). Cloacal sperm in spring migrants: occurrence and interpretation. *Condor* **87**: 273–280.
- Rising, J. D. (1996). Relationship between testes size and mating systems in American sparrows (Emberizinae). *Auk* **113**: 224–228.
- Robertson, B. C. (1997). The mating system of the Capricorn Silvereye, *Zosterops lateralis chlorocephala*: a genetic and behavioural assessment. PhD thesis, University of Queensland. (unpubl.)
- Robertson, B. C., Degnan, S. M., Kikkawa, J. and Moritz, C. C. (2001). Genetic monogamy in the absence of paternity guards: the Capricorn silvereye, *Zosterops lateralis chlorocephalus*. *Behav. Ecol.* **12**: 666–673.
- Sheldon, B. C. and Birkhead, T. R. (1994). Reproductive anatomy of the Chaffinch in relation to sperm competition. *Condor* **96**: 1099–1103.
- Wolfson, A. (1954). Sperm storage at lower-than-body temperature outside the body cavity in some passerines. *Science* **120**: 68–71.