SKUTCH, A. F. 1961. Helpers among birds. Condor 63:198–226.

SKUTCH, A. F. 1984. Clutch size, nesting success, and predation on nests of neotropical birds. *In* P. A. Buckley et al. [eds.], Neotropical ornithology. Amer. Orn. Union (Orn. Monogr.) 36:575–595.

SKUTCH, A. F. 1986. Helpers at birds nests: a worldwide survey of cooperative breeding and related behavior. Univ. of Iowa Press, Iowa City, IA.

SKUTCH, A. F. 1989. Life of the Tanager. Cornell Univ. Press, New York.

SNOW, D. W., AND C. T. COLLINS. 1962. Social breeding behavior of the Mexican Tanager. Condor 64:161.

WILLIS, E. 1961. A study of nesting ant-tanagers in British Honduras. Condor 63:479–503.

WOOD, T. M., F. GALLO, AND P. K. DONAHUE. 1992. Observations at a Paradise Tanager nest. Wilson Bull. 104:360–362.

REPRODUCTIVE ANATOMY OF THE CHAFFINCH IN RELATION TO SPERM COMPETITION[1]

B. C. SHELDON[2] AND T. R. BIRKHEAD

*Department of Animal and Plant Sciences, The University of Sheffield,
P.O. Box 601, Sheffield S10 2UQ, U.K.*

Key words: Sperm competition; Fringilla coelebs; reproductive anatomy; sperm storage; testes.

Competition among male birds to fertilize the eggs of females has the potential to infuence many areas of avian biology (Birkhead and Møller 1992a). This is particularly true of reproductive anatomy and physiology which provides a link between behavior (such as copulations) and parentage. The study of male reproductive parameters, such as testis size, the number of sperm stored and ejaculate volume, has revealed numerous adaptations to sperm competition at the anatomical level (e.g., Møller 1988, Møller 1991, Birkhead et al. 1993). For example, relative testes mass is generally greater in species in which females engage in extra-pair copulations (Møller 1991).

One important factor that determines which male fertilizes eggs is the mechanism of sperm precedence (the way in which order of mating affects the chances of fertilization). All experimental studies to date have revealed that when copulations are separated by at least 4 hr the sperm of the last male to mate have precedence. For example, last male precedence averages 80% in the Zebra Finch *Taeniopygia guttata* (Birkhead et al. 1988) and between 77% and 93% in chickens *Gallus* (Warren and Gish 1943, Compton et al. 1978). The aim of this paper is to describe the reproductive anatomy of both male and female Chaffinches *Fringilla coelebs*, and to interpret features of their anatomy with reference to sperm competition and sperm precedence mechanisms.

METHODS

A single pair of Chaffinches was collected (under license) close to their nest in the early morning of 13 May 1992, on day +3 of the female's laying cycle (where day 0 is the day the first egg is laid). In addition, we dissected a freshly dead male (killed by a weasel *Mustela nivalis* in mid April), and a female (road kill in mid June). Methods for dissection and measurement of sperm storage tubules (SSTs) in females and testes and number of sperm in sperm stores of males followed Briskie (1993) and Briskie and Birkhead (1993). SSTs containing sperm were photographed under Normarski illumination using a Leica Laborlux microscope. Although the sample size is small, it is reasonable to draw general conclusions from such a sample as Briskie and Montgomerie (1992, 1993) found that variation between species accounted for most (60.1% or more) of the total variance in sperm length, SST length and SST number in a sample of 20 North American passerine species. Values are given as means (± 1 SD) unless otherwise stated.

RESULTS AND DISCUSSION

Male reproductive anatomy. Both males had enlarged testes and cloacal protuberances (CPs), indicating that they were reproductively active when collected (male 1: CP volume, following Briskie (1993), 308 mm^3; volume index following Birkhead et al. (1991), 20.3 mm^{3}g^{-1}; male 2: 322 mm^3 and 21.6 mm^{3}g^{-1} respectively). The right and left seminal glomera of male 1 weighed 0.0740 g and 0.0748 g respectively, a combined weight of 0.1488 g (0.73% of the male's body weight [20.25 g]) and contained an estimated total of 33.6 × 10^6 ($\pm 3.88 \times 10^6$ SE) sperm. The seminal glomera act as a store for matured sperm prior to ejaculation (Briskie 1993). The combined weight of the testes was 0.4779 g (right: 0.2333 g, 8.3 mm × 7.0

mm; left: 0.2446 g, 9.1 mm × 7.3 mm; 2.36% of body weight). The sperm examined were typical of passerine sperm, with 'corkscrew' heads (e.g., Quay 1985) and they measured 252.5 μm long (±10.5 μm, $n = 30$), with heads 15.2 μm long (±2.15 μm, $n = 30$).

The right and left seminal glomera of the second male weighed 0.0753 g and 0.0701 g respectively (combined weight 0.1454 g, or 0.76% of male body weight [19.0 g]), and were estimated to contain a total of 32.2 × 10^6 (±1.75 × 10^6 SE) sperm. The combined weight of the testes was 0.4070 g (right: 0.2014 g, 7.8 × 7.2 mm; left: 0.2056 g, 8.7 × 6.7 mm), 2.14% of the male's body weight. CP size was measured on four other male Chaffinches; two from males 35 and 50 days before egg-laying (volumes: 153 mm³ and 73 mm³) were much smaller than CPs from males closer to the laying dates of their females. The other two males were measured within a week of their females laying, and had CPs similar in size to those of the two dissected males. For the four males in reproductive condition the mean (SE) CP dimensions were: depth 8.08 (0.58); height 8.60 (1.32); width 8.18 (0.28), giving a mean volume of 446 mm³, or volume index of 28.39 mm³g⁻¹ (Birkhead et al. 1991).

In a comparative analysis, Møller (1991) demonstrated that birds that are subject to high levels of sperm competition, as determined by mating system, have larger testes than expected from their body weight. On the basis of Møller's (1991) regression of male body mass on testes size (log [testes mass] = −1.37 ± 0.67 log[body mass]), and given that the specific gravity of the testes in this study is less than that assumed by Møller, a 20 g bird is expected to have testes weighing 0.25 g; the mean testes mass (0.443 g) of the two males dissected is therefore 79% greater than expected. An impression of the relative size of this difference can be obtained by comparing the ratio between observed and expected testes mass in the Chaffinch (1.79) with those of two polyandrous species that are known to be subject to particularly intense sperm competition (Dunnock *Prunella modularis*: 2.13; Smith's Longspur *Calcarius pictus*: 2.98; Briskie 1993). Although male Chaffinches' testes are not as disproportionately large as these two polyandrous species, their relatively large size is an indication of the importance of sperm competition in this species.

Fewer data exist concerning the size of the seminal glomera in birds, or the number of sperm that males store within them. At 0.75% of male body weight the seminal glomera of these two male Chaffinches are intermediate in size between those of the two polyandrous species above (0.82% and 1.13% respectively) and a sample of three monogamous species in Briskie (1993) that had a mean seminal glomera size of 0.43% of male body mass (Yellow-headed Blackbird *Xanthocephalus xanthocephalus* 0.37%; Lapland Longspur *Calcarius lapponicus* 0.42%; American Tree Sparrow *Spizella arborea* 0.51%). The total number of sperm in the seminal glomera of the two male Chaffinches (mean 32.9 × 10^6 sperm) was considerably fewer than the number that a male Dunnock (1,060 × 10^6; Birkhead et al. 1991) or Smith's Longspurs (217 × 10^6; Briskie 1993) store, but considerably more than either Zebra Finches *Taeniopygia guttata* or Bengalese Finch-

es *Lonchura striata* (4.8 × 10^6 and 7.7 × 10^6 respectively; Birkhead et al. 1991). Males of these two species pairs (Smith's Longspur and Dunnock and Zebra and Bengalese Finches) probably lie near opposite ends of a continuum representing sperm competition intensity. The intermediate numbers of sperm in the seminal glomera of male Chaffinches fit in well with their position on this continuum as a monogamous species with a high level of sperm competition (Sheldon 1994), for which 17% of offspring are fathered through extrapair copulations (Sheldon and Burke 1994).

Female reproductive anatomy. The female collected during egg-laying had laid three eggs previously; there were two large, yolky follicles (diameters of 5.8 and 6.5 mm) in the ovary, indicating that there were at least two more eggs to be laid. However, this female would not have laid on the morning of capture as there was no shelled egg in the oviduct. SSTs were clearly visible in the primary mucosal folds under a low powered compound microscope. There were 11 primary mucosal folds, each of which contained an average of 68.6 SSTs (±4.18, $n = 5$), giving an estimated total of 755 SSTs. Under high power, many SSTs clearly contained sperm (e.g., Fig. 1 Top); of 93 SSTs examined, 86 (93%) contained a mean of 13.16 sperm (±15.01, range 1–100). As each SST contained an average of 11.43 sperm (including those with none), this female was estimated to be storing approximately 755 × 11.43 = 8,625 sperm. The SSTs were typical of passerines (pers. observ.), although they were relatively long and without branches. They averaged 508.5 μm in length (±177 μm, range 270–925, $n = 20$), diameter 76.8 μm (±15.3 μm, range 55–105, $n = 20$). The lumen of the tubules was clearly visible, and in many cases enlarged at the distal end; lumen width measured at the midpoint of the tubule was 9.6 μm (±3.2 μm, range 5–13.75, $n = 20$).

The distribution of the number of sperm per tubule was strongly negatively skewed. The observed distribution differed significantly from that expected if sperm distributed themselves randomly (calculated from a Poisson distribution; G-test, $G_{10} = 157.47$, $P < 0.0001$). Sperm were more aggregated than expected, since there were relatively more SSTs with fewer sperm and others with many more sperm than expected. This was not simply due to some SSTs being 'switched off' (and therefore not accessible to sperm), since when SSTs containing no sperm were excluded from the analysis the observed distribution was still significantly different from random ($G_{10} = 86.47$, $P < 0.0001$).

Birkhead et al. (1990) also reported that sperm were distributed non-randomly between SSTs in the Zebra Finch, and apparently clumped distribution of sperm within SSTs has also been shown to occur in the Dunnock (Birkhead et al. 1991) and the Japanese Quail *Coturnix japonica* (Birkhead and Møller 1992a). Since the 'clumping' is not due to some SSTs being inactive, it may be due to sperm travelling in discrete 'bundles' or due to some attraction between particular SSTs and sperm (Birkhead et al. 1990).

There was no evidence of the discrete stratification of sperm in the tubules as reported for some species (e.g., Briskie and Montogomerie 1993). Instead, sperm in SSTs containing a large number of sperm tended to occur in overlapping layers (Fig. 1 Top). In some cases
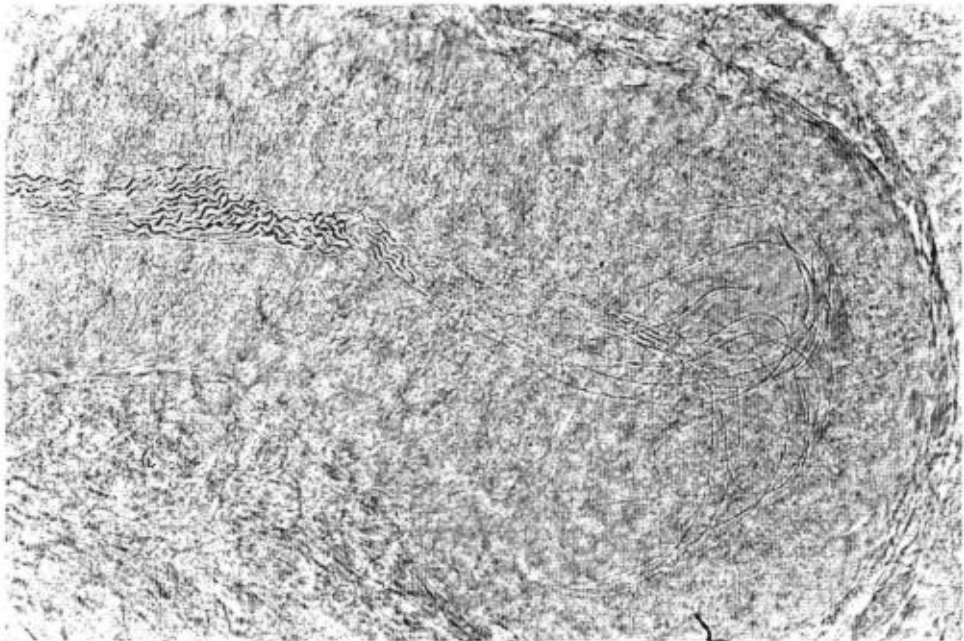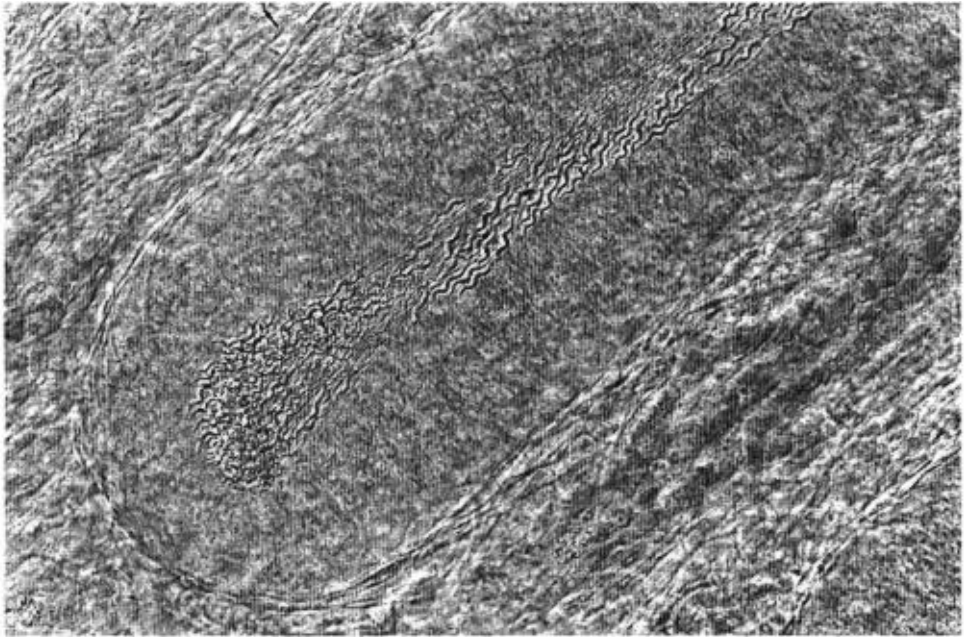
FIGURE 1. (Top) Sperm packed within a single sperm storage tubule. Note that they do not form discrete layers. (Bottom) Distal end of a sperm storage tubule, with turned sperm.

(approximately 10%) it appeared that sperm had turned in the enlarged distal end of the tubule, and were oriented with their heads facing towards the opening of the tubule (Fig. 1 Bottom); in these instances the heads of the 'turned' sperm had faced and sometimes overlapped the heads of other sperm oriented towards the distal end of the tubule (Fig. 1 Bottom).

The second female had an old, inactive, brood patch when examined, and on dissection the oviduct was much reduced compared to that of the first female. The follicles in the ovary were of almost uniform size (diameter approximately 1 mm) and, together with the late date (12 June), suggest that this female would not have renested that season. The brood patch was non-vascularized, and typical of a female with hatched young (pers. observ.). Although reduced in size, 16 primary mucosal folds were still visible. Examination under high power revealed the presence of SSTs although they were relatively indistinct. The mean number of SSTs present on five primary folds was 54.2 (± 8.13, range 49–70, $n = 5$), which was significantly fewer than for female 1 (Mann-Whitney U-test, $z = 2.034$, $P < 0.05$; treating folds as independent observations). SSTs were also shorter and clearly regressed compared to female 1 (mean length = 224.3 μm, $\pm$ 52.2, $n = 15$; $t_{33} = 5.85$, $P < 0.0001$; treating individual SSTs as independent observations). There were no sperm present in any of the SSTs ($n = 20$).

In contrast to males, functional explanations for the variation in female sperm storage anatomy, in terms of sperm competition, have proved elusive (Birkhead and Møller 1992a, 1992b; Briskie and Montgomerie 1993). Birkhead and Møller (1992b) found that female body mass accounted for a large proportion of the variance in SST number across species. On the basis of their relationship a 20 g bird is expected to have 1,058 SSTs (range 721–1,553), so the observed number of SSTs in female 1 (755) is within the predicted range, although close to the lower limit. In addition, Briskie and Montgomerie (1993) found an interspecific positive correlation between sperm length and SST length which they suggested may have evolved through competition between sperm for access to SSTs. The length of male Chaffinch sperm (252 μm) is close to that predicted on the basis of SST length from Briskie and Montgomerie (1993), although both sperm length and SST length are unusually large compared to other passerines for which this information is known. Only the Yellow Warbler *Dendroica petechia* and the Tree Swallow *Tachycineta bicolor* have longer sperm and SSTs respectively (Briskie and Montgomerie 1992, 1993). Birkhead and Møller (1992b) derived an equation that predicts the duration of sperm storage from the spread of laying and SST length; with spread of laying = 4.5 days, and SST length = 508.5 μm, the predicted sperm storage duration in the Chaffinch is 8.5 days. Since the first egg to be laid is fertilized early on day -1, sperm inseminated on day -9 could conceivably fertilize the first egg. This predicted figure accords well with the time at which males start mate guarding and the time at which females start soliciting for copulations (generally from day -8 onwards; Sheldon 1994).

All studies of sperm precedence in birds to date have indicated that last male sperm precedence (LMSP) oc-

curs when copulations are separated by more than 4 hours (Birkhead and Møller 1992a). The mechanism by which LMSP arises is unknown, but observations of sperm stratified into layers within female SSTs, with their heads oriented towards the distal end (e.g., Birkhead et al. 1990, Briskie and Montgomerie 1993), suggest that it might arise through a 'last in, first out' mechanism (Compton et al. 1978). In the present study the observations of sperm that had apparently turned within the SSTs of female 1 suggest that this mechanism may not operate in the Chaffinch, since sperm at the distal end of the tubule could perhaps gain access to the oviduct before sperm situated more proximally. As far as we can ascertain, these are the first observations of sperm apparently actively turning in any bird examined (although Mero and Ogasawara [1970] proposed that the enlarged distal lumen that they observed in preparations of chicken SSTs might allow sperm to turn in their ends).

The relatively large testes, seminal glomera and sperm stores of male Chaffinches suggest that they have been exposed to selection to produce large numbers of sperm at relatively frequent intervals. In addition, male Chaffinches have disproportionately large ejaculates for their body size (five times the volume of other small passerines: Thiede et al. 1981 in Møller 1988). It may therefore be possible to speculate about the sperm precedence mechanism in the Chaffinch. Observations of sperm apparently actively turning in the end of SSTs (Fig. 1 Bottom) suggest that last male sperm precedence is unlikely to occur in the Chaffinch by stratification (Compton et al. 1978). In addition, work on Zebra Finches (Birkhead et al. 1988), Mallard *Anas platyrhynchos* (Cheng et al. 1983) and chickens (Warren and Gish 1943) has shown that where copulations are separated by less than four hours, last male sperm precedence vanishes, and instead a 'fair raffle' (where chances of fertilization are proportional to the number of sperm inseminated) appears to operate. As Chaffinches copulate as frequently as four times per hour (Sheldon and Burke 1994), it may be that something more akin to a fair raffle may operate in this species (assuming that the "four hour rule" applies). The observations of turning sperm may be consistent with a raffle mechanism if sperm are continuously being cycled between the rest of the female reproductive tract and the sperm storage tubules; it is hard to see how such a mechanism could be consistent with last male precedence.

LITERATURE CITED

BIRKHEAD, T. R., J. V. BRISKIE, AND A. P. MØLLER. 1993. Male sperm reserves and copulation frequency in birds. Behav. Ecol. Sociobiol. 32:85–93.

BIRKHEAD, T. R., B. J. HATCHWELL, AND N. B. DAVIES. 1991. Sperm competition and the reproductive

organs of the male and female Dunnock. *Prunella modularis*. Ibis 133:306–311.

BIRKHEAD, T. R., AND A. P. MØLLER. 1992a. Sperm competition in birds: evolutionary causes and consequences. Academic Press, London.

BIRKHEAD, T. R., AND A. P. MØLLER. 1992b. Numbers and size of sperm storage tubules in birds: a comparative study. Biol. J. Linn. Soc. 45:363–372.

BIRKHEAD, T. R., J. E. PELLATT, AND F. M. HUNTER. 1988. Extra-pair copulation and sperm competition in the Zebra Finch. Nature 334:60–62.

BIRKHEAD, T. R., J. E. PELLATT, AND F. M. HUNTER. 1990. Number and distribution of sperm in the uterovaginal sperm storage tubules of the Zebra Finch. Condor 92:508–516.

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 T. R. BIRKHEAD. 1993. A review of the methods used to study the anatomy of avian sperm storage. Ornis Scand. 24:323–329.

BRISKIE, J. V., AND R. MONTGOMERIE. 1992. Sperm size and competition in birds. Proc. R. Soc. Lond. B 247:89–95.

BRISKIE, J. V., AND R. MONTGOMERIE. 1993. Patterns of sperm storage in relation to sperm competition in passerine birds. Condor 95:442–454.

CHENG, K. M., J. T. BURNS, AND F. MCKINNEY. 1983.

Forced copulation in captive mallards. III. Sperm competition. Auk 100:302–310.

COMPTON, M. M., H. P. VAN KREY, AND P. B. SIEGEL. 1978. The filling and emptying of the uterovaginal sperm-host glands in the domestic hen. Poultry Sci. 57:1696–1700.

MERO, K. N., AND F. X. OGASAWARA. 1970. Dimensions of uterovaginal sperm-storage tubules of the chicken and their possible significance in sperm release. Poultry Sci. 49:1304–1308.

MØLLER, A. P. 1988. Testes size, ejaculate quality and sperm competition in birds. Biol. J. Linn. Soc. 33:273–283.

MØLLER, A. P. 1991. Sperm competition, sperm depletion, paternal care and relative testis size in birds. Amer. Nat. 137:882–906.

QUAY, W. B. 1985. Cloacal sperm in spring migrants: occurrence and interpretation. Condor 87:273–280.

SHELDON, B. C. 1994. Sperm competition in the Chaffinch; the role of the female. Anim. Behav. 47:163–173.

SHELDON, B. C., AND T. BURKE. 1994. Copulation behavior and paternity in the Chaffinch. Behav. Ecol. Sociobiol. 34:149–156.

WARREN, D. C., AND C. L. GISH. 1943. Value of artificial insemination in poultry breeding work. Poultry Sci. 22:108–117.

CLIMBING ADAPTATIONS IN THE HINDLIMB MUSCULATURE OF THE WOODCREEPERS (DENDROCOLAPTINAE)[1]

ROBERT J. RAIKOW

Department of Biological Sciences, University of Pittsburgh, Pittsburgh, PA 15260, and Section of Birds, Carnegie Museum of Natural History, Pittsburgh, PA 15213

The woodcreepers (Furnariidae: Dendrocolaptinae) climb vertical tree trunks suspended by their forward toes and supported by their stiffened tails. They are one of several groups that independently evolved such scansorial behavior (Richardson 1942, Bock and Miller 1959, Storer 1971). This paper is part of a wider study of the woodcreepers (Raikow 1993, 1994; Raikow et al. 1993; Bledsoe et al. 1993) and its purpose is to consider whether the hindlimb muscles of the woodcreepers show structural adaptations for scansorial behavior.

Stolpe (1932) suggested that when birds assume perching or standing postures the center of gravity lies vertically above the hindlimbs, and gravity tends to flex the leg joints; this is counteracted by the postural activity of the extensor muscles of the legs. In a bird that is clinging vertically, however, the center of gravity is displaced horizontally relative to the substrate. The bird is anchored to the tree by flexion of the forward toes, whose claws penetrate the bark, and its tendency to fall extends the leg joints, and is resisted by the flexor muscles. Thus, in the evolution of scansorial behavior a functional reversal occurs as a major postural role is transferred from the extensor muscles to the flexors. Moreno (1991) analyzed climbing adaptations in treecreepers (*Certhia* spp.), and reiterated the idea, based on Stolpe (1932), Spring (1965), Winkler and Bock (1976), and Norberg (1986), that it is advantageous for a tail-braced bird to minimize the distance from its