Avian Testicular Structure, Function, and Regulation

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SUMMARY

In many birds, testes undergo dramatic annual changes in size and, as such, are among the most anatomically and physiologically plastic organs found in adult vertebrates. Adult testicular function is modulated by a myriad of external factors and orchestrated by numerous hormones that together enable birds to adapt to and breed in diverse habitats worldwide. These factors have generated a wide range of avian reproductive strategies, which has further shaped testicular structure and function. This chapter describes the mechanisms that control avian exocrine and endocrine testicular functions. It analyzes how these functions are regulated by ecological and behavioral factors and presents an overview of how environmental information is integrated and transduced into appropriate gonadal responses. It also discusses testicular dysfunction and the potential effects of anthropogenic disturbances on testis function. The chapter emphasizes areas where knowledge is lacking or incomplete, with the hope of fostering additional research on this exciting and fruitful area of avian biology.

1. CENTRAL MECHANISMS REGULATING TESTICULAR DEVELOPMENT

Current studies of the hormonal regulation of testicular function focus on elucidating neuroendocrine pathways that integrate environmental information and convey it to the testes to initiate or terminate reproduction. This research is spurred by the development of novel molecular techniques and the identification of new neuropeptides that together enable researchers to uncover a multitude of neural processes regulating avian male reproduction.

In vertebrates, the primary neural system responsible for regulating reproduction consists of hypothalamic neurons that secrete gonadotropin-releasing hormone (GnRH) into the median eminence. Of the three GnRH forms identified in birds thus far (King & Millar, 1982a; 1982b; Miyamoto et al., 1984; Berghman et al., 2000),

GnRH-I is considered the primary secretogogue of the gonadotropins (GTHs)—follicle-stimulating hormone (FSH) and luteinizing hormone (LH)—from the pituitary gland (Kuenzel, 2000). The production and secretion of these hormones is presumably regulated also by the inhibitary neuropeptide, gonadotropin-inhibiting hormone (GnIH) (Tsutsui et al., 2000). The mechanisms of action of GnIH are not fully elucidated, but mounting evidence suggests that this neuropeptide acts at multiple levels: hypothalamus, anterior pituitary gland, and potentially the gonads (Bentley, Tsutsui, & Wingfield, 2007; see also Chapter 1, this volume).

Several studies have also demonstrated an important role for thyroid hormones in regulating the seasonality of the male reproductive system (Dawson, Goldsmith, & Nicholls, 1984a, b; Goldsmith & Nicholls, 1984b; Lien & Siopes, 1991; Wilson & Reinert, 1993). Details of this regulatory action are not completely clear, but several lines of evidence support effects on GnRH production and secretion (Boulakoud & Goldsmith, 1991). Recent research has focused on how photic information is transduced into changes in GnRH cell function. One current model proposes that light-induced stimulation of neural thyrotropin (TSH) expression (Nakao et al., 2008) promotes the local conversion of thyroxine (T_4) to triiodothyronine (T_3) by the type 2 iodothyronine deiodinase (Dio2) (Yoshimura et al., 2003), which in turn stimulates GnRH release. The mechanism that controls this release is not fully understood and may involve a T_3-mediated reduction of the encasement by glial cells of nerve terminals located in the median eminence (Yamamura, Yasuo, Hirunagi, Ebihara, & Yoshimura, 2006).

The regulation of seasonal reproduction in birds may also involve a central role for brain-derived vasoactive intestinal peptide (VIP). Neurons producing VIP are thought to communicate directly with GnRH neurons and it has been proposed that they regulate the transduction of light signals to the reproductive system (Kiyoshi, Kondoh,

Hirunagi, & Korf, 1998; Teruyama & Beck, 2001). This mechanism remains poorly understood; some studies indicate an inverse relationship between VIP and GnRH expression (dark-eyed junco (*Junco hyemalis*) (Saldanha, Deviche, & Silver, 1994; Deviche, Saldanha, & Silver, 2000)) whereas other studies suggest that VIP stimulates the GnRH system (Li & Kuenzel, 2008).

2. ENDOCRINE INFLUENCE ON DEVELOPMENT OF THE AVIAN MALE PHENOTYPE

Sex determination has been studied in more detail in mammals than in birds. Birds differ from mammals in that avian females are heterozygotic (ZW genotype) and males are homozygotic (ZZ genotype) (Kirby & Froman, 2000). In mammals, the *sry* gene on the Y chromosome codes for the expression of genes related to the development of the male phenotype. The absence of an *sry* gene homolog in birds results in the default formation of the male reproductive tract (Kirby & Froman, 2000). A survey of steroidogenic genes in developing chickens (*Gallus gallus*) demonstrated that embryos are capable of androgen synthesis by day two of incubation, but around day five only females express the aromatase enzyme ($P450_{aro}$), which converts androgens to estrogens (Nomura, Nakabayashi, Nishimori, Yasue, & Mizuno, 1999). Sexual dimorphism in the expression of $P450_{aro}$ also has been observed in embryos of the Pekin duck (*Anas platyrhynchos*) (Koba et al., 2008b; 2008c), goose (*Anser anser*), and turkey (*Meleagris gallopavo*) (Koba et al., 2008b). A role for $P450_{aro}$ is further supported by studies utilizing $P450_{aro}$ inhibitors to convert genetic females to phenotypic males (Elbrecht & Smith, 1992) or individuals with mixed gender ovotestes (Koba et al., 2008a).

In male embryos, $P450_{aro}$ may be inhibited by anti-Müllerian hormone (AMH), named for its inhibitory effect on female Müllerian duct development. Expression of AMH mRNA is greater in male than female chickens (Nishikimi et al., 2000; Yamamoto, Tsukada, Saito, & Shimada, 2003) and Japanese quail (*Coturnix coturnix japonica*) embryos (Nakamura et al., 2008). As demonstrated by studies in the chicken, the molecular control of AMH transcription remains poorly understood (Oreal, Mazaud, Picard, Magre, & Carre-Eusebe, 2002). Current research on sex determination in birds focuses on the specific roles of several 'sex-determining' genes (e.g., *SF1*, *SOX9*, *DMRT1,* and *DAX1*) (Oreal et al., 2002; Sechman, 2005) and on whether sex is controlled by 'double dosing' with Z chromosome (two in males, one in females) or the presence of the W chromosome in females.

3. AVIAN TESTICULAR ANATOMY

Testes in birds are located deep in the abdominal cavity and are, therefore, visible only after removal of other organs, in particular the intestine. Testes are surrounded by a fibrous capsule that includes connective tissue and contractile fibers (Aire & Ozegbe, 2007). They contain interstitial tissue and seminiferous tubules, which are the site of spermatogenesis and, in developed testes, make up most of the testicular mass. Interstitial tissue includes Leydig or interstitial cells, the main source of testicular androgens (Dufty & Wingfield, 1986a; Galli, Irusta, & Wassermann, 1973; Halse, 1985; Madekurozwa, Chabvepi, Matema, & Teerds, 2002; Mauget, Jouventin, Lacroix, & Ishii, 1994; Nicholls & Graham, 1972; Rosenstrauch, Weil, Degen, & Friedlander, 1998; Woods & Domm, 1966) (see Section 3.1).

Testes in some species are of identical sizes (e.g., tree swallow (*Tachycineta bicolor*) (Kempenaers, Peer, Vermeirssen, & Robertson, 2002); chicken (Hocking, 1992)), but many species show testicular size asymmetry, with one testis normally being larger in adulthood than the other (Yu, 1998; Gunn, Champion, Casey, Teal, & Casey, 2008). As in other vertebrates, the direction of testis size asymmetry within a species is generally consistent (Yu, 1998; Merilä & Sheldon, 1999). An extreme case of avian testicular asymmetry is found in coucals (*Centropus* sp.), which develop a single testis (Rand, 1933; Chapin, 1939; Ligon, 1997). The potential significance of avian testicular asymmetry is discussed below (Section 7.3).

3.1. Leydig Cells

The ontogeny of Leydig cells has been described in the Japanese quail (Ottinger & Bakst, 1981). In this species, Leydig cells before and during hatching have a fibroblast-like appearance and are characterized by a smooth endoplasmic reticulum and lipid droplets, appearing two to three weeks posthatching, when plasma testosterone (T) increases. Consistent with this observation, steroidogenic activity of quail Leydig cells, as measured by 3β-hydroxysteroid dehydrogenase (3β-HSD), an enzyme that plays a key role in the conversion of cholesterol to androgens (Madekurozwa et al., 2002), is low during the first three weeks posthatching and then rapidly increases (Scheib, 1973).

The ultrastructure of adult Leydig cells has been characterized in several species including the Mallard duck (*A. platyrhynchos*), chicken, budgerigar (*Melopsittacus undulatus*), white-crowned sparrow (*Zonotrichia leucophrys*), and Japanese quail (Connell, 1972; Humphreys, 1975; Lam & Farner, 1976; Aire, 1997; Rosenstrauch et al., 1998). Cells in these species show morphological changes that generally parallel their androgen secretion. For example, highly fertile, young adult chickens have

numerous tightly packed and functionally active Leydig cells and elevated plasma T. By contrast, older and less fertile chickens with low plasma T have fewer Leydig cells that show morphological signs of decreased androgen secretion (Rosenstrauch et al., 1998). Similar changes are observed when comparing Leydig cells during and outside the reproductive season in seasonal breeders (Humphreys, 1975; Lam & Farner, 1976; Rohss & Silverin, 1983; Tae et al., 2005). Photomanipulations of captive birds also support this conclusion. For example, in white-crowned sparrows, photostimulation increases plasma T and Leydig cell numbers (Lam & Farner, 1976). The morphology of these cells in photostimulated birds—numerous large mitochondria containing tubular cristae, a round nucleus, and a well-developed smooth endoplasmic reticulum—indicates elevated secretory activity. As sparrows become photorefractory, these effects are reversed. Similarly, gonadally quiescent budgerigars (Humphreys, 1975) and chickens (Aire, 1997) differ from reproductively active birds in having fewer Leydig cells, many showing signs of degeneration. The time course of differentiation and ultrastructural changes of Leydig cells during photo-stimulation have been described in detail in the Japanese quail (Nicholls & Graham, 1972).

3.2. Seminiferous Tubules

Seminiferous tubules in birds are anastomosed and sur-rounded by a basal lamina consisting of fibroblasts, myoepithelial cells, and connective tissue. They contain Sertoli cells and the seminiferous epithelium, where germ cells divide and then differentiate while migrating from the basal lamina to the tubule lumen.

Sertoli cells are elongated cells that extend from the basal lamina of seminiferous tubules to the lumen. Adjacent Sertoli cells are joined by tight junctions, thereby dividing the seminiferous epithelium into basal and distal (adlumi-nal) regions, which form an effective blood−testis barrier (Osman, Ekwall, & Ploen, 1980; Bergmann & Schindel-meiser, 1987). Sertoli cells play an essential role in the development and maturation of gametes and also serve an endocrine function, as they produce inhibin (Sedqyar et al., 2008). Some studies indicate that Sertoli cells multiply during a limited posthatching period and therefore do not proliferate in adulthood (De Reviers et al., 1980; Bozkurt, Aktas, Ulkay, & Firat, 2007). Other studies, however, describe extensive apoptosis of Sertoli cells at the end of the reproductive period in seasonally breeding birds (Section 4.4), suggesting the potential for these cells to regenerate in adulthood in preparation for the following breeding season. Sertoli cells express androgen receptors (Dornas, Oliveira, Dias, Mahecha, & Oliveira, 2008) and their adult size and function are hormonally regulated (Brown, Bayle, Scanes, & Follett, 1975; Ishii & Yamamoto, 1976). As demonstrated

in Japanese quail, FSH and T act synergistically to increase testicular weight by inducing Sertoli cell hypertrophy (Tsutsui & Ishii, 1978) (Section 5.2).

4. ENDOCRINE AND EXOCRINE FUNCTIONS OF AVIAN TESTES

4.1. Testicular Androgen Hormone Synthesis and Secretion

Following Fevold and Eik-Nes' (1962) initial work on house sparrows (*Passer domesticus)*, several studies used *in-vitro* incubation of gonadal tissue in the presence of radioactive precursors to identify the biosynthetic pathways involved in T synthesis (chicken (Delrio, Lupo, & Chieffi, 1967; Nakamura & Tanabe, 1972b; Galli et al., 1973); Japanese quail (Nakamura & Tanabe, 1972b); Wilson's phalarope (*Phalaropus tricolor*) (Fevold & Pfeiffer, 1968); red-winged blackbird (*Agelaius phoeniceus*) (Kerlan, Jaffe, & Payne, 1974)). Depending on the presence of cofactors (nicotinamide adenine dinucleotide (NAD^+) or its reduced form (NADH)), testicular tissue of the chicken converts pregnenolone to T following the Δ^4 or Δ^5 pathway (Nakamura & Tanabe, 1972a). Even though the conversion of androstenedione (AND) to T by 17β-hydroxysteroid dehydrogenase (17β-HSD) is reversible, T is usually the quantitatively main end product in adults (Fevold & Pfeiffer, 1968; Nakamura & Tanabe, 1972a). The testes of immature birds, however, can produce more AND than T, presumably as a result of lower 17β-HSD activity than in adults (Fevold & Pfeiffer, 1968; Galli et al., 1973).

4.2. Spermatogenesis

As in mammals, spermatogenesis in birds is defined as the formation of mature spermatozoa from spermatogonia and it includes three sequential steps: spermatocytogenesis, spermatidogenesis, and spermiogenesis. The anatomical characteristics and physiological control of avian sper-matogenesis have been the object of extensive studies (Thurston & Korn, 2000; Aire, 2007; Jamieson, 2007). Early work identified one or two types of spermatogonia (e.g., Zlotnik, 1947; Kumaran & Turner, 1949; Lake, 1956), but subsequent work on Japanese quail found seminiferous tubules to contain four types of spermatogonia (Ad, Ap1, Ap2, and B) that differ with respect to their staining intensity and ultrastructural characteristics (Lin & Jones, 1992). More recently, Bakst, Akuffo, Trefil, and Brillard (2007) described three types of spermatogonia in the turkey. During spermatocytogenesis, a spermatogonium (Ad germ cell) undergoes mitosis to generate a new Ad cell and an Ap1 cell, which further divides into two daughter Ap2 cells. Each Ap2 cell divides into two B spermatogonia, which themselves each divide into two primary

spermatocytes. Primary spermatocytes undergo two meiotic divisions, thus giving birth to secondary spermatocytes, which each divide into spermatids (spermatidogenesis) (Aire, 2007). As a result of these cell divisions, each Ad spermatogonium can generate 32 spermatids. (To contrast this process in birds with that in mammals, see Volume 5, Chapter 5.)

Spermatids transform into sperm cells during spermiogenesis, which has been best studied in Japanese quail (Lin & Jones, 1993) and chickens (Sprando & Russell, 1988). Spermiogenesis is characterized by a dramatic reduction of the amount of cytoplasm and a profound morphological transformation that results in mature sperm cells consisting of a head (acrosome, cylindrical nucleus, and mitochondria) and tail (flagellum), and spermiation is the release of sperm from Sertoli cells into the seminiferous tubule lumen. The structure of mature sperm in passerines is relatively conserved, but differs in several respects from that in nonpasserines (for details see Jamieson, 2007).

The duration of spermatogenesis in mammals varies considerably from one species to another (e.g., prairie vole (*Microtus ochrogaster*): 29 days (Schuler & Gier, 1976); dog (*Canis lupus familiaris*): 42 days (Ghosal et al., 1983); chimpanzee (*Pan troglodytes*): 63 days (Smithwick, Young, & Gould, 1996)). Limited information in birds suggests a shorter and perhaps more consistent duration of spermatogenesis than in mammals (chicken: 12−13 days (De Reviers, 1975); Japanese quail: 13 days (Lin & Jones, 1992)).

4.3. Sperm Maturation, Transport, and Storage

Sperm released into the seminiferous tubules are suspended in seminiferous fluid and carried to the cloaca through excurrent ducts consisting of the rete testis, which comprises an intra- and an extratesticular region; the efferent duct; the connecting duct; the epididymis; and the deferent duct (Kirby & Froman, 2000). The ontogeny and adult cytological characteristics of excurrent ducts have been described in detail (Tingari, 1971; 1972; Aire, 1979; Aire, Ayeni, & Olowo-okorun, 1979; Aire, 1982). Sperm in birds are transported rapidly along the reproductive tract (Clulow & Jones, 1982; 1988). In Japanese quail, this transport requires approximately 24 hours (Clulow & Jones, 1988). During this time, sperm undergo final maturation (Esponda, 1991), most of the seminiferous fluid is reabsorbed by pinocytosis (Tingari & Lake, 1972; Nakai, Hashimoto, Kitagawa, Kon, & Kudo, 1989), and the composition of the fluid is altered to produce seminal plasma (Lake & Hatton, 1968; Stratil, 1970). Sperm in the seminiferous tubules, epididymis, and deferent duct in chickens lack motility (Ashizawa & Sano,

1990), but, as they are transported along the excurrent ducts, chicken and quail sperm acquire the potential for motility due to the influence of factors, including presumably Ca^{2+} and glutamate, that are secreted into the accessory gland reproductive fluids (Ashizawa & Sano, 1990; Ashizawa, Wishart, Ranasinghe, Katayama, & Tsuzuki, 2004; Clulow & Jones, 1982; Froman & Feltmann, 2005). In the chicken, flagellar movement is temperature-dependent and actual sperm motility is thought to be acquired by a temperature decrease at the time of ejaculation and ejaculate transfer into the female cloaca (Ashizawa & Sano, 1990; Ashizawa et al., 2004). Sperm motility in the rock pigeon (*Columba livia*) is highest between 18 and 24°C and declines at 28°C (Cheng et al., 2002). Sperm motility in the chicken also depends on genetic factors that influence mitochondrial morphology and function (Froman & Kirby, 2005).

In passerines, the distal end of the vas deferens forms the seminal glomus, a specialized sperm storage accessory structure (Gupta, Bhat, & Maiti, 1984; Samour, Spratt, Holt, & Smith, 1988). The glomus in passerines may have evolved as a result of these birds' aerial lifestyle, which is incompatible with very large testes (Aire, 2007). The number of sperm in the seminal glomus of the house sparrow declines during the course of the day (Birkhead, Veiga, & Moller, 1994). Thus, the glomus may accumulate sperm during the night for use during the day in the course of multiple copulations. Nonpasserines have a limited capacity for extragonadal sperm storage (Clulow & Jones, 1982; Cecil, Bakst, & Monsi, 1988; Jones, 1999).

4.4. Seasonal Testicular Regression and Programmed Cell Death

The testicular involution that takes place at the end of the reproductive season in seasonal breeders was originally attributed to tissue necrosis brought about by the failure of androgens to maintain the integrity of the seminiferous tubules (Thurston & Korn, 2000). Since then we have learned that seasonal testicular regression results from a precisely controlled process of programmed cell death (apoptosis) that is regulated by complex signaling mechanisms. Despite the large seasonal variation in testis size observed in many bird species, few studies have examined apoptosis in the avian testes. At the end of the breeding season, the American crow (*Corvus brachyrhynchos*) shows a 19-fold and 9-fold decrease in testis size and spermatogenetic activity, respectively (Jenkins, Ross, & Young, 2007). The decrease in size likely results primarily from Sertoli cell apoptosis (Rodriguez, Ody, Araki, Garcia, & Vassalli, 1997). In the European starling (*Sturnus vulgaris*), apoptosis associated with seasonal testicular regression was similarly limited to Sertoli and germ cells (Young, Ball, & Nelson, 2001).

5. ENDOCRINE AND PARACRINE CONTROL OF AVIAN TESTICULAR FUNCTION

Two anterior pituitary hormones, LH and FSH, play a primary role in the control of testicular endocrine and exocrine functions. The importance of these hormones is underlined by the results of studies involving hypophysectomy. This surgery causes testicular involution in the chicken (Brown et al., 1975; Tanaka & Fujioka, 1981) and Japanese quail (Bayle, Kraus, & Van Tienhoven, 1970; Brown & Follett, 1977), whereas administration of chicken purified LH but especially chicken purified FSH to hypophysectomized Japanese quail stimulates testicular development and growth (Brown et al., 1975). Testes in T-treated hypophysectomized immature quail remain undeveloped, but increase in size when birds also receive LH and especially FSH (Brown & Follett, 1977). This observation provides no evidence for a role for T in regulating testicular development. However, a role for T in adult testicular function is suggested by the finding in mature hypophysectomized quail that administration of large doses of T, while insufficient to maintain spermatogenesis, retards testicular regression resulting from the surgery (Brown & Follett, 1977).

Avian testes synthesize various chemical mediators (Table 2.1) and their receptors (Table 2.2), suggesting direct, but as yet poorly understood, physiological regulation of testicular function by factors other than LH, FSH, and androgens. Receptors for these mediators in Sertoli cells and seminiferous tubules presumably influence aspects of spermatogenesis; those in Leydig cells may control steroid production and those in epididymal tissue may regulate sperm maturation and seminal fluid composition.

The expression of various chemical messengers and their receptors by testes is not entirely surprising as testes are sites of extensive cell proliferation, differentiation, steroid synthesis, and apoptosis. These complex processes presumably require the participation of numerous regulatory hormones and growth factors, particularly as birds often exhibit large seasonal variation in testis size. The following sections summarize avian research on the direct regulation of steroidogenesis and spermatogenesis by LH, FSH, and some other mediators, and they outline potentially promising future avenues for research on this topic.

5.1. Luteinizing Hormone (LH)

The primary action of LH on testes is to increase the secretion of androgens by Leydig cells (Kirby & Froman, 2000). The presence of 3β-HSD in Leydig cells and the generally hydrophobic nature of steroids suggest that LH stimulates androgen production and not just release.

Supporting this role, plasma LH, in response to photo-stimulation and ensuing photorefractoriness in captive white-crowned sparrows, changes in parallel with Leydig cell number and ultrastructure (Lam & Farner, 1976). In domestic ducks, plasma LH and T follow the same general time course of changes during constant light exposure starting at 60 days of age and lasting until puberty (160 days of age) (Yang, Medan, Watanabe, & Taya, 2005). In several species, seasonal changes in plasma LH parallel changes in plasma T (Magellanic penguin (*Spheniscus magellanicus*) (Fowler, Wingfield, Boersma, & Sosa, 1994); rufous-winged sparrow (*Aimophila carpalis*) (Deviche, Small, Sharp, & Tsutsui, 2006); emperor (*Aptenodytes forsteri*) and Adelie (*Pygoscelis adeliae*) penguins (Groscolas, Jallageas, Goldsmith, & Assenmacher, 1986); king penguin (*Aptenodytes patagonicus*) (Mauget et al., 1994)), although in other species seasonally maximal plasma LH precedes peak plasma T (great tit (*Parus major*) (Rohss & Silverin, 1983); ostrich (*Struthio camelus*) (Degen, Weil, Rosenstrauch, Kam, & Dawson, 1994); white-winged crossbill (*Loxia leucoptera*) (Deviche & Sharp, 2001)).

A direct action of LH on Leydig cells is supported by the presence of putative LH receptors on these cells (ostrich (Madekurozwa et al., 2002); embryonic chicken (Akazome, Abe, & Mori, 2002)) and with the observation that LH rapidly increases the *in-vitro* testicular secretion of T (garden warbler (*Sylvia borin*) (Bluhm et al., 1991); ring-necked pheasant (*Phasianus colchicus karpowi*) (Tae et al., 2005)). The effects of *in-vivo* GTH treatment on testicular function were studied by Brown et al. (1975) in Japanese quail. Repeated injections of purified chicken LH to young males of this species induce differentiation of the interstitium and Leydig cell maturation. These injections also stimulate spermatogonial division and differentiation of Sertoli cells, but whether these effects are direct or result from increased androgen secretion has not been determined. The testicular effects of LH in Japanese quail are specific as they are not replicated by treatment with purified chicken FSH fractions. The specificity of LH action on androgen production *in vivo* and *in vitro* was confirmed by measuring the effects of purified chicken, turkey, and ostrich LH in several avian species (chicken, Japanese quail, mallard duck, and turkey (Chase, 1982)). In these species, LH generally induces a dose-related increase in androgen production, but FSH is inactive when given alone and does not alter the response to LH when both are administered together.

5.2. Follicle-stimulating Hormone (FSH)

The production and maturation of sperm in mammals primarily depends on FSH acting on Sertoli cell receptors through cyclic adenosine 3',5'-monophosphate (cAMP)

TABLE 2.1 Hormones reported within the testes of birds

Hormone	Species	Stage	Whole testes	Leydig cells	Sertoli cells	Seminiferous tubules	Spermatogonia or spermatocytes	Epididymis or vas deferens	References
Growth hormone	Chicken	E, A		+	−	+	+	+	Luna et al. (2004)
		A	+			+	+	+	Harvey et al. (2004)
Insulin-like growth factor-1	Chicken	A	+						Harvey et al. (2004); Tanaka et al. (1996)
Prepro-orexin	Chicken	A	+						Ohkubo et al. (2003)
Adiponectin	Chicken	A		+	−	−	−		Ocon-Grove et al. (2008)
Gonadotropin-releasing hormone-I	Chicken	A	+						Sun et al. (2001)
D-aspartate	Mallard	A		+	+	+			Di Fiore et al. (2008)
Nitric oxide	Mallard	A		+	+	+			Di Fiore et al. (2008)
Inhibin	Chicken	A	+						Lovell et al. (2000); Bandivdekar et al. (1982)
		J, A	+						Davis and Johnson (1998)
		J	+						Onagbesan et al. (2004)
	Quail	E, J, A		+	+				Sedqyar et al. (2008)
	Duck	E, J		+	+	+			Yang et al. (2005)
Activin	Chicken	A	+						Lovell et al. (2000)
		J, A	+						Davis and Johnson (1998)
		J	+						Onagbesan et al. (2004)
	Quail	E, J, A		+	+				Sedqyar et al. (2008)
	Duck			+	+				Yang et al. (2005)

Follistatin	Chicken	J, A	+					Davis and Johnson (1998)
Myostatin	Chicken	E	+					Kubota et al. (2007)
Agouti-related protein	Chicken	A	+					Takeuchi et al. (2000)
Anti-Müllerian hormone	Chicken	E	+	−	+	−	−	Eusebe et al. (1996)
		E	+					Oreal et al. (2002)
	Quail	E	+					Koba et al. (2008a)
	Quail	J	+					Koba et al. (2008a); Nakamura et al. (2008)
	Duck	E	+					Koba et al. (2008c)
	Turkey; goose	J	+					Koba et al. (2008b)
Gonadotropin-inhibiting hormone	Starling	A	+					Bentley et al. (2008)
	Quail	A	+	+		+	+	+	Bentley et al. (2008)
	House sparrow	A	+	+		+		McGuire and Bentley (2010)

+ indicates the presence of hormone as determined by methods including radioligand binding assays, immunocytochemistry, and *in-situ* hybridization; − indicates hormone presence was tested for but found absent. Abbreviations for life stages are as follows: E, embryo; J, juvenile; A, adult.

TABLE 2.2 Hormone receptors reported within the testes of birds

Ligand	Species	Stage	Whole testes	Leydig cells	Sertoli cells	Seminiferous tubules	Spermatogonia or spermatocytes	Epididymis or vas deferens	References
Prolactin	Turkey	A, E	+						Mao et al. (1999); Pitts et al. (2000)
	Chicken	E	+						Pitts et al. (2000)
		A	+						Mao et al. (1999); Tanaka et al. (2000)
	Pigeon	A	+						Mao et al. (1999)
	Quail	A	+						Mao et al. (1999)
Orexin	Chicken	A	+						Ohkubo et al. (2003)
Progesterone	Chicken	J, A	+						González-Morán et al. (2008)
Androgen	Chicken	A		+	−				Shanbhag and Sharp (1996)
		A		+	+			+	Dornas et al. (2008)
		J, A	+						González-Morán et al. (2008)
	Canary	A		−	+				Nastiuk and Clayton (1994)
	Duck	A		+	+			+	Dornas et al. (2008)
		E	+						Koba et al. (2008b)
	Quail	J	+						Nakamura et al. (2008)
Estrogen	Chicken	A						+	Kwon et al. (1997)
		J, A	+						González-Morán et al. (2008)
	Turkey	E	+						Koba et al. (2008a)
	Duck	E	+						Koba et al. (2008a; 2008b)
	Goose	E	+						Koba et al. (2008a)
	Quail	J	+						Koba et al. (2008c); Nakamura et al. (2008)
Adiponectin	Chicken			+	+	+	+		Ocon-Grove et al. (2008)
Gonadotropin-releasing hormone	Chicken		+						Sun et al. (2001)
Growth hormone	Chicken		+					+	Harvey et al. (2004)

Hormone	Species	Stage					Reference
Glucocorticoid	Chicken	A	+				Kwok et al. (2007)
Corticotropin-releasing hormone	Chicken	J	+				De Groef et al. (2004)
Melatonin	Chicken	A	+				Ayre et al. (1992)
	Duck	A	+				Ayre et al. (1994)
	Quail	A	+				Wang et al. (1992)
Retinoic acid	Quail	J, A	+				Fu et al. (2001)
Gonadotropin-inhibiting hormone	Starling	A		+	+		Bentley et al. (2008)
	Sparrow	A		+	+		Bentley et al. (2008)
	House sparrow	A	+	+		+	McGuire and Bentley (2010)
Prostaglandin	Chicken	A	+				Kwok et al. (2008)
Aryl hydrocarbon	Cormorant	A	+				Lee et al. (2007)
Motilin	Chicken	J	+				Yamamoto et al. (2008)

+ indicates the presence of hormone receptor as determined by a variety of methods including radioligand binding assays of whole testes, immunocytochemistry, and *in-situ* hybridization. − indicates receptor presence was tested for but found absent. Abbreviations for life stages are as follows: E, embryo; J, juvenile; A, adult.

activation of protein kinases (see Hadley, 2000). Several studies demonstrate that FSH likewise plays a major role in the control of avian Sertoli cell function and spermatogenesis.

In captive mallard ducks exposed to natural photoperiod, plasma FSH is elevated during the vernal period of testicular growth, reaches a maximum when testes are fully developed during the breeding season, and then rapidly declines when birds become photorefractory and begin to molt (Haase, 1983; Haase, Sharp, & Paulke, 1985). Plasma FSH and testicular size undergo parallel changes during the annual cycle also in other species (great tit (Silverin, Kikuchi, & Ishii, 1997); European starling (Dawson & Goldsmith, 1983)). Photomanipulation experiments likewise show a correlation between plasma FSH and testicular development. Plasma FSH is low in white-crowned sparrows held on short days and with undeveloped testes (Wingfield, Follett, Matt, & Farner, 1980). Following photostimulation, plasma FSH increases gradually for approximately four weeks, concurrently with testicular development and the initiation of spermatogenesis. It should be noted that in these sparrows, as in the Japanese quail (Follett, 1976), photoinduced plasma FSH decreases despite testes remaining fully developed for several weeks, suggesting that early but not late stages of spermatogenesis require elevated plasma FSH. Further, plasma FSH is often higher than baseline in birds with regressed testes. For example, great tits in the fall, when these birds regain photosensitivity, show a small peak in plasma FSH (Silverin et al., 1997). Further research is needed to fully understand the significance of this observation.

The most detailed work on the time course of photoinduced changes in plasma FSH and testicular development has been performed in Japanese quail (Follett & Maung, 1978). In this species, plasma FSH increases in parallel with testis development following photostimulation with photoperiods of various durations. For example, males exposed to 14 or more hours of light daily develop their testes fully and achieve peak plasma FSH after 10 long days. By contrast, quail exposed to 12 hours of light daily show reduced testicular development and lower plasma FSH than birds exposed to longer photoperiods.

The role of FSH also has been studied through hormone-administration experiments (e.g., Purcell & Wilson, 1975; Balthazart, Massa, & Negri-Cesi, 1979). Administration of chicken purified FSH to hypophysectomized Japanese quail stimulates Sertoli cells and germ cell differentiation, resulting in enlarged seminiferous tubules and increased testicular weight, but the treatment does not lead to differentiation of Leydig cells (Brown et al., 1975). The hormonal specificity of these effects of exogenous FSH is revealed by the fact that they are not observed following treatment with chicken purified LH rather than FSH. Similarly, treatment of neonatal chickens with ovine FSH, but not LH, dose-dependently increases their seminiferous tubule diameter (Ishii & Yamamoto, 1976).

The effects of GTHs on testes depend on circulating concentrations of these hormones but also on their receptors. Beginning with Ishii and Yamamoto's (1976) study of white-crowned sparrows, a number of studies used radioligand binding of mammalian FSH to avian testicular tissue preparations to characterize FSH receptors (Japanese quail (Ishii & Adachi, 1977); chicken (Tsutsui & Ishii, 1978); mallard duck (Bortolussi, Deviche, Colombo, & Marini, 1979); Indian weaver bird (*Ploceus philippinus*) (Tsutsui, Kawashima, Saxena, & Ishii, 1992; Tsutsui, Kawashima, V. Saxena, & A. Saxena, 1992; Kawashima, Tsutsui, Saxena, & Ishii, 1993)). It was found that testes contain specific, high affinity (nanomolar range) binding sites for FSH and these sites have a reduced binding affinity for LH (Ishii & Yamamoto, 1976; Ishii & Adachi, 1977; Tsutsui & Ishii, 1978; Kawashima et al., 1993). In white-crowned sparrows that are transferred from short to long days to stimulate gonadal development, FSH binding capacity (number of binding sites per testis) and plasma FSH increase (Ishii & Yamamoto, 1976). Similar observations have been made in Indian weaver birds (Tsutsui et al., 1992a; 1992b; Kawashima et al., 1993). Research on Japanese quail suggests that photoinduced increases in gonadal FSH binding capacity result from upregulation of binding sites by the hormone itself (self-potentiation), in addition to synergistic actions with T (Tsutsui & Ishii, 1978; but see Ottinger, Kubakawa, Kikuchi, Thompson, & Ishii, 2002). The mechanism mediating this putative synergism is unknown and its physiological importance remains in question, especially in view of the fact that T administration, alone or with FSH treatment, decreases the incorporation of ^{32}P into testes of the chicken (Breneman & Zeller, 1982). The gene coding for avian testicular FSH receptors has been sequenced and cloned, and the putative amino-acid sequence of the receptor has been identified (chicken ovarian follicle (Wakabayashi, Suzuki, Hoshino, Nishimori, & Mizuno, 1997)), offering new opportunities to study the regulation of these receptors.

5.3. Gonadotropin-inhibiting Hormone (GnIH)

The discovery of the hypothalamic inhibitory neuropeptide GnIH (Tsutsui et al., 2000) has stimulated considerable research into the physiological roles and mechanisms by which this neurohormone influences the hypothalamo—pituitary gland axis (Bentley et al, 2009; Tsutsui et al., 2010). As shown recently, avian testes also contain GnIH and its receptors (Bentley et al., 2008; McGuire & Bentley, 2010). Receptors are located in interstitial and germ cells, suggesting that GnIH controls testicular steroid production

and germ cell function through autocrine and/or paracrine actions. Supporting this proposition, GnIH decreases the gonadotropin-induced *in-vitro* stimulation of testosterone secretion by house sparrow testes (McGuire & Bentley, 2010). Stress in rodents (Kirby, Geraghty, Ubuka, Bentley, & Kaufer, 2009) and probably birds (Calisi, Rizzo, & Bentley, 2008) increases the brain expression of GnIH. A similar increase, if taking place in testes, may contribute to mediating the rapid *in-vivo* inhibition of T secretion that is observed in response to acute stress in the white-crowned (Wingfield, Smith & Farner, 1982) and rufous-winged (Deviche et al., 2010) (Section 5.7) sparrow.

5.4. Inhibin and Activin

Gonadotropin-releasing hormone stimulates LH and FSH, but the secretion of the two GTHs is thought to be differentially regulated due to the negative feedback effects of inhibin on FSH secretion and to a lesser degree the stimulatory action of activin on FSH secretion (Davis & Johnson, 1998). Inhibin and activin are dimeric glycoproteins that share a common α subunit but differ with respect to their β subunit; inhibin has either a single β_A or β_B subunit, whereas activin has a homodimeric β subunit (Davis & Johnson, 1998). These structural similarities have made separating the biological effects and responses of the two hormones to FSH at the testis level challenging. Studies involving immunization against the inhibin α subunit have found immunized birds to have elevated testicular weights compared to control birds (chicken (Lovell, Knight, Groome, & Gladwell, 2000); Japanese quail (Satterlee, Castille, & Fioretti, 2006)). In the latter species, immunization also advances puberty and delays age-associated testicular involution. The mechanism that mediates inhibitory effects of inhibin on the reproductive system is unclear because, in the chicken, the increase in testicular weight resulting from immunization against inhibin α subunit is associated with decreased plasma LH but no change in plasma FSH or testicular morphology (Lovell et al., 2000). As these authors suggest, inhibin may act on testes to reduce their sensitivity to FSH, but this hypothesis warrants further research. A paracrine role of inhibin and activin on testes is indicated by studies suggesting that these hormones influence gamete growth and differentiation (Onagbesan, Safi, Decuypere, & Bruggeman, 2004; Sedqyar et al., 2008) and fetal steroidogenesis (Rombauts, Vanmontfort, Decuypere, & Verhoeven, 1996).

5.5. Melatonin (MEL)

Melatonin (MEL) in birds is produced primarily by the pineal gland and the retina (Underwood, Binkley, Siopes, & Mosher, 1984) and exerts complex effects on the male reproductive system (Gupta, Haldar-Misra, Ghosh, & Thapliyal, 1987; Ohta, Kadota, & Konishi, 1989; Sackman, 1977; Singh & Haldar, 2007). Studies have revealed an important modulatory role for MEL in the regulation of seasonal reproductive cycles, but much remains to be learned about the mechanisms involved (see also Chapter 8, this volume).

Melatonin stimulates the reproductive axis under some conditions. For example, MEL pretreatment to red-headed buntings (*Emberiza bruniceps*) blocks the suppressive effect of prolactin (PRL) on testis growth (Trivedi, Rani, & Kumar, 2004). By contrast, other investigations found no evidence for an obligatory role of the pineal gland or its secretions in the regulation of seasonal reproduction (Wilson, 1991; Pant & Chandola-Saklani, 1992). In yet other studies, seasonal changes in pineal gland activity as measured cytologically (Indian weaver bird (Chakraborty, 1993)), enzymatically (house sparrow (Barfuss & Ellis, 1971)), or through plasma MEL (jungle bush-quail (*Perdicula asiatica*) (Singh & Haldar, 2007)) was inversely related to the activity of the reproductive system, suggesting inhibitory effects of pineal gland secretions on this activity. In the adult male Japanese quail, blinding results in elevated plasma LH (Konishi, Iida, Ohta, & Takahashi, 1988). This observation is consistent with an inhibitory effect of MEL on the reproductive system but does not rule out alternate mechanisms. More direct evidence for an inhibitory role for MEL comes from the demonstration that administration of this hormone inhibits testicular recrudescence in the rose-ringed parakeet (*Psittacula krameri*) (Sengupta & Kumar, 2006) and can delay reproductive maturation in the cockerel (Balemans, Van de Veerdonk, & Van de Kamer, 1977; Lewis, Middleton, & Gous, 2006; but see John, George, & Etches, 1986). Inhibitory effects of MEL may involve direct actions on the hypothalamus and/or pituitary gland (Gupta et al., 1987). Supporting this hypothesis, GnIH neurons express MEL receptors and MEL mediates the increase in GnIH expression seen in Japanese quail in response to short days (Ubuka, Bentley, Ukena, Wingfield, & Tsutsui, 2005). Melatonin may also affect gonadal tissue directly. Indeed, MEL decreases the *in-vitro* production of steroids from labeled precursors by testis homogenates (Mallard duck (Cardinali & Rosner, 1971)), and the testes of several avian species contain specific, high affinity binding sites for ^{125}I-labeled MEL (Ayre, Yuan, & Pang, 1992; Wang, Cheng, Brown, Pang, & Pang, 1992; Ayre & Pang, 1994; Ayre, Wang, Brown, & Pang, 1994; Cheng et al., 1994). In the Japanese quail, the number of testicular MEL binding sites is photoperiodically regulated; birds have fewer such sites when exposed to short rather than long days (Pang et al., 1993). This difference may result from down- (short days) or up- (long days) regulation of MEL receptors.

5.6. Prolactin (PRL)

Prolactin in birds often exerts an antigonadal influence (e.g., Bates et al., 1935; Nalbandov, 1945; Bailey, 1950; Bar, 2006) that is thought to play an important role in the control of seasonality (Dawson, King, Bentley, & Ball, 2001; Sharp & Blache, 2003). This influence presumably results in part from central effects of PRL. Indeed, in the ring dove (*Streptopelia risoria*), an intracerebroventricular PRL injection dose-dependently decreases plasma LH and induces testicular regression (Buntin, Lea, & Figge, 1988). Further, the preoptic region of the brain in this species (Fechner & Buntin, 1989; Buntin, Ruzycki, & Witebsky, 1993) and in Wilson's phalarope (Buntin, El Halawani, Ottinger, Fan, & Fivizzani, 1998) contains specific, high-affinity PRL binding sites. It remains to be determined whether PRL reaches these sites after secretion from the pituitary gland into the blood or is produced within the brain itself (Buntin, Hnasko, & Zuzick, 1999; Ramesh, Kuenzel, Buntin, & Proudman, 2000).

In most species examined, PRL secretion is photoinduced (Goldsmith & Nicholls, 1984a; Sharp, Klandorf, & McNeilly, 1986; Silverin & Goldsmith, 1997; Sharp, Dawson, & Lea, 1998; Sreekumar & Sharp, 1998). Maximal circulating PRL concentrations are reached toward the end of the reproductive season, coinciding with the onset of photorefractoriness, suggesting that PRL contributes to the gonadal regression taking place at this time (Dawson & Goldsmith, 1983; 1984; Haase et al., 1985; Stokkan, Sharp, Dunn, & Lea, 1988; Bluhm, Phillips, & Burke, 1989; Sharp et al., 1998). Experimental evidence, however, shows that PRL facilitates seasonal testicular involution but does not cause photorefractoriness. This evidence comes, in particular, from studies on the European starling, a species that responds to chronically long days by completely losing sensitivity to this stimulus (absolute photorefractoriness). Active immunization of starlings against VIP (see Section 1), the main PRL secretagogue in birds, slowed but did not prevent testicular regression associated with photorefractoriness (Dawson & Sharp, 1998). Further, plasma PRL in chronically refractory mallards increases but then returns to baseline values, indicating that it is not required for long-term maintenance of photorefractoriness (Sharp et al., 1986). Other species, including the Japanese quail (Robinson & Follett, 1982; Follett & Pearce-Kelly, 1990) and *Aimophila* sparrows (Deviche, Sabo, & Sharp, 2008; Small, Sharp, Bentley, & Deviche, 2008a; 2008b), respond to prolonged exposure to long days by losing sensitivity to these long days gradually, but incompletely (relative photorefractoriness). As in other species, PRL in the Japanese quail increases during photostimulation (Goldsmith & Hall, 1980). Contrary to the situation in the European starling, however, PRL may play a critical role in the induction of photorefractoriness in relatively photorefractory species (Dawson et al., 2001).

Mammalian testes contain GTH-dependent PRL receptors (Fishback, Arimura, & Turkelson, 1982) and, in humans, PRL is thought to decrease T secretion through an LH-independent mechanism, suggesting direct testicular effects in this species (Suescun et al., 1985). Prolactin receptors (PRL-Rs) are expressed in avian testes as well (Zhou, Zadworny, Guemene, & Kuhnlein, 1996; Leclerc, Zadworny, Bedecarrats, & Kuhnlein, 2007; see Table 2.2). Research in chickens has identified testis-specific PRL-R truncated transcripts that are expressed in an age-related fashion (Mao et al., 1999). These data suggest direct actions of PRL on avian testicular tissue. In one of the few studies on this subject, Stetson and Erickson (1970) found in cockerels that treatment with large doses of mammalian PRL alone has no effect on testicular incorporation of ^{32}P, but acts synergistically with exogenous LH to increase this incorporation. Additional research is necessary to clarify whether PRL exerts a direct physiological influence on avian testicular function and to elucidate potential interactions between this hormone and LH at the testicular level.

5.7. Glucocorticoids and Metabolic Hormones

Research on the effects of stress on the male reproductive system has demonstrated a generally negative relation between plasma corticosterone (CORT), the primary avian glucocorticoid, and T (reviewed by Wingfield & Sapolsky, 2003). During a prolonged stressful situation, plasma T and LH levels are thought to decline as a result of elevated plasma CORT. Supporting this hypothesis, CORT administration blocks photoperiod-induced testicular development in the male Japanese quail (Deviche, Massa, Bottoni, & Hendrick, 1982), and, in the red-headed bunting, pharmacological blockade of CORT secretion delays seasonal testicular regression (Bhatt, Patel, & Chaturvedi, 2001). The mechanism that mediates these effects remains speculative. Testes express glucocorticoid receptors (Table 2.2) and CORT may, therefore, act directly on testes to inhibit their function, but the decline in plasma LH that follows CORT treatment (Deviche et al., 1982) suggests actions also on the hypothalamus and/or pituitary gland. Inhibitory effects of stress may also involve GnIH because stress can in some circumstances increase the number of hypothalamic GnIH-expressing neurons (house sparrow (Calisi et al., 2008) (Section 5.3)).

Acute stress can also have inhibitory effects on reproductive hormones. In the white-crowned (Wingfield et al., 1982) and rufous-winged (Deviche et al., 2010) sparrows, plasma T decreases within one hour and fifteen minutes, respectively, of capture and handling. In neither study was

this decrease associated with a decrease in plasma LH, suggesting a stress-mediated inhibition of testicular endocrine function. In contrast to these studies, other research has found a positive relation between plasma T and short-term stress. This increase in roosters is not seen in castrated birds, indicating that T is presumably secreted by testes and not adrenal glands (Heiblum, Arnon, Gvaryahu, Robinzon, & Snapir, 2000). Several hypotheses have been proposed to explain the stimulatory effects of stress on plasma T: changes in adrenal androgen biosynthesis (Robinzon & Cutolo, 1999), natural temporal variation of T resulting from GnRH pulsatility (Wilson, Rogler, & Erb, 1979), and a direct stimulation of Leydig cells by catecholamines (Landsberg & Young, 1992). More research is warranted to clarify the effects of stress on the hypothalamo–pituitary–testicular axis and in particular the specific role in this respect of glucocorticoids, the reasons for stress having either stimulatory or inhibitory actions on reproductive hormones, and the peripheral and central sites involved.

Interesting opportunities to investigate relations between stress and reproduction come from genetic lines selected for divergence in adrenocortical activity. Selection of Japanese quail for reduced adrenocortical response to restraint stress (Satterlee, Truax, Jacobsperry, & Johnson, 1982; Satterlee, Johnson, & Jacobsperry, 1983; Satterlee & Johnson, 1988; Satterlee & Jones, 1997) has resulted in individuals that show accelerated development of the cloacal gland (Marin & Satterlee, 2004; Satterlee & Marin, 2004; Satterlee, Cole, & Castille, 2006; Satterlee, Tong, Castille, & Marin, 2007), larger testis weight relative to body mass (Marin & Satterlee, 2004; Satterlee & Marin, 2004; Satterlee et al., 2006b), and increased frequencies of male androgen-dependent sexual behaviors (Marin & Satterlee, 2003).

An important consideration is that stress effects on testicular function may be difficult to identify when stress results from metabolic challenges (Wingfield & Sapolsky, 2003). Studies in laboratory rodents found that anabolic hormones (growth hormone (GH) and insulin-like growth factor (IGF)) associated with energy balance and growth exert local effects on testicular steroidogenesis. In mammals, GH is thought to influence gametogenesis through IGF-1 and stimulates T synthesis by inducing the production of steroidogenic enzymes such as 3β-HSD (reviewed in Hull & Harvey, 2000a; 2000b; Chandrashekar, Zaczek, & Bartke, 2004). Indeed, evidence from mammals supports the hypothesis that both GH and IGF-1 are synthesized *de novo* in testes and act independently or in concert via receptors on both Sertoli and Leydig cells (Hull & Harvey, 2000b). Avian testes contain immunoreactive GH and IGF-1, and receptors for these peptides (Harvey et al., 2004). Similar mechanisms as in mammals may, therefore, operate in birds. The recent characterization of the GH gene sequence in the chicken (Kansaku, Hiyama, Sasanami, &

Zadworny, 2008) and pied flycatcher (*Ficedula hypoleuca*) (Buggiotti, Hellstrom, & Primmer, 2006) will hopefully lead to the development of probes that can be used to address the specific role of GH on avian testicular function.

5.8. Nitric Oxide (NO) and D-aspartate (D-Asp)

It has been proposed in mammals that nitric oxide (NO) serves as a paracrine inhibitor of Leydig cell T synthesis (Adams, Nock, Truong, & Cicero, 1992; Lamanna, Assisi, Vittoria, Botte, & Di Fiore, 2007). This inhibition is opposed by the amino acid D-aspartate (D-Asp), which in mammals stimulates steroidogenesis (D'Aniello et al., 1998; Lamanna, Assisi, Botte, & Di Fiore, 2006; 2007a; Lamanna et al., 2007b). A potential role for NO in avian reproduction has been investigated in two species, the Japanese quail (regulation of GTH release (Chaturvedi & Kumar, 2007; Kumar & Chaturvedi, 2008)) and the mallard duck (regulation of T production by NO and D-Asp (Di Fiore, Lamanna, Assisi, & Botte, 2008)). In the latter study, D-Asp and NO were localized in Leydig cells, with D-Asp more prevalent during the reproductive period and NO more prevalent outside this period. This observation supports a stimulatory and inhibitory role, respectively, of these chemical mediators in testicular function (Di Fiore et al., 2008).

5.9. An Avian Androgen-binding Protein?

Testosterone in vertebrates is thought to regulate spermatogenesis by binding to a testicular androgen-binding glycoprotein (ABP) that concentrates T within the seminiferous tubules, resulting in the elevated luminal T levels necessary to promote sperm maturation in the epididymis (Norris, 2007). Although evidence supports an important role for T in sperm maturation in birds, it is unknown whether avian seminiferous tubules contain ABP. Human ABP and sex hormone-binding globulin (SHBG) (Gershagen, Lundwall, & Fernlund, 1989) are products of the same gene, have identical amino-acid sequences, and differ only with respect to the oligosaccharides attached to them (Hammond & Bocchinfuso, 1996). Early studies concluded that SHBG is absent in birds (Murphy, 1968; Corvol & Bardin, 1973) but more recent work suggests that 90–95% of plasma androgens circulate bound to a CORT-binding globulin (CBG), raising the possibility that avian CBG acts as the primary SHBG in circulation (Deviche, Breuner, & Orchinik, 2001; Breuner & Orchinik, 2002). The amino-acid sequence of avian CBG has not been identified (but see Noel, Ramsey, Crews, & Breuner, 2004) and whether testes produce this protein is unknown. Corticosterone-binding globulin is, however, the most likely candidate for an ABP in the avian male reproductive system.

6. EXOGENOUS REGULATION OF TESTICULAR FUNCTION

In many avian species, testes are maximally developed during the breeding season, which is preceded and followed by a period of reproductive quiescence during which testes are regressed and do not produce gametes (Figure 2.1) (Dawson et al., 2001; Meddle, Wingfield, Millar, & Deviche, 2006; Dawson & Sharp, 2007; Leska & Dusza, 2007). As a result, testicular size can change several-hundred-fold during the year (Table 2.3) as compared to the less-than-five-fold change often seen in seasonally breeding mammals (e.g., Lincoln & Short, 1980; Nicholls, Goldsmith, & Dawson, 1988; Urbanski, Fahy, & Collins, 1993; Dawson, 2002). The dramatic morphological and physiological changes associated with seasonal (in-)activation of the avian reproductive system require time. Males must, therefore, be able to anticipate the start and end of the optimal time for breeding to maximize their chances of successful reproduction. The specific cues used to predict seasonal environmental changes vary among species. This section discusses abiotic cues used to determine the annual cycle of testicular development, with particular emphasis on birds exhibiting different breeding schedules and life histories.

6.1. Abiotic Factors

6.1.1. Photophase

The annual change in daylength (photophase) is the primary initial predictive cue that many birds use to time reproduction. Changes in testicular size/weight stimulated by a change in photoperiod are species-specific and often associated with differences in breeding phenology and mating system (Section 6.2) (Garamszegi, Eens, Hurtrez-Bousses, & Moller, 2005; Pitcher, Dunn, & Whittingham, 2005). To our knowledge, no avian species has been identified that relies exclusively on nonphotic cues to time

reproduction. Thus, photoperiod exerts at least a permissive effect on the reproductive system (see Section 6.1.4 for discussion of reduced reliance on photic cues). In many species, increasing photoperiod from short winter days stimulates testicular recrudescence (Hamner, 1968; Dawson et al., 2001; Sharp, 2005; Dawson & Sharp, 2007). However, the short-day-breeding emu (*Dromaius novaehollandiae*) shows a similar increase in testicular development, but in response to decreasing photoperiod (Malecki et al., 1998). Little work has been done on the effect of photoperiod on the reproductive system of nocturnal species (Guchhait & Haldar, 1999) and the mechanisms that regulate seasonal gonadal cycles in these species are largely unknown.

Birds can respond to even small photoperiodic changes around the critical day length, defined as the shortest photoperiod that stimulates testicular development. The duration of the critical day length varies intra- and interspecifically. For example, the critical day length in starlings is 12 hours light (L) and birds kept under a 12L : 12 dark (D) light schedule show normal testicular cycling (Dawson, 2006). However, a 30-minute shift in photoperiod (increasing to 12.5L and then decreasing to 11.5L) results in a permanently photorefractory or photosensitive state, respectively. Thus, the directionality, rather than only the magnitude of a change in photoperiod, is important for photoperiodic regulation of testicular development (Dawson, 2006). The same applies to equatorial species, in which small changes in both photoperiod (i.e., 17 minutes) and light intensity can suffice to induce testicular development (spotted antbird (*Hylophylax naevioides*) (Hau, Wikelski, & Wingfield, 1998; Wikelski, Hau, & Wingfield, 2000)).

6.1.2. Precipitation

The average amount of precipitation in most temperate regions varies seasonally. In these regions, a seasonal increase in photophase, and rising temperatures, are often
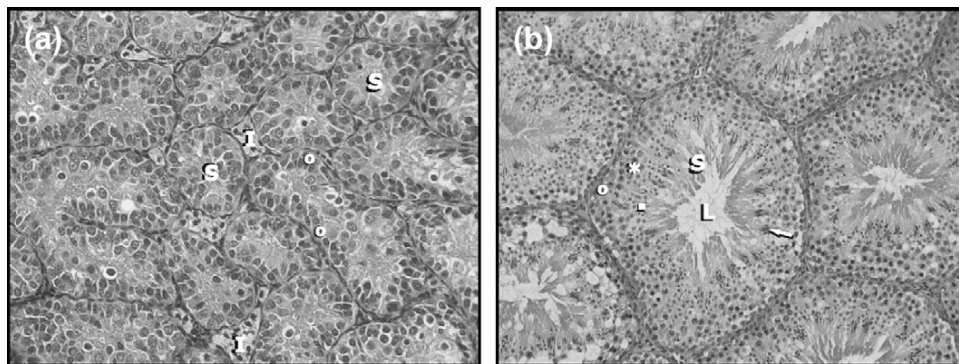

FIGURE 2.1   Photomicrographs of (a) nonbreeding and (b) breeding variegated fairy-wren (*Malurus lamberti assimilis*) testis sections. I, interstitium; L, lumen; S, seminiferous tubule; o, spermatogonium; *, secondary spermatocytes; ■, spermatids; →, elongating spermatids. Pictures taken at 20× magnification. *From M. Rowe, unpublished data.*

TABLE 2.3 Breeding to non-breeding testis mass and volume ratios in birds and mammals as reported in or estimated from cited publications

Common name	Scientific name	Mass ratio	Volume ratio	Citation
Emu	*Dromaius novaehollandiae*	1.9		Malecki et al. (1998)
Korean ring-necked pheasant	*Phasianus colchicus karpowi*	15.8		Kim and Yang (2001)
Chicken	*Gallus gallus domesticus*	40		González-Morán et al. (2008)
Japanese quail	*Coturnix coturnix japonica*	5—11		Artoni et al. (1999); Sudhakumari et al. (2001)
Turkey	*Meleagris gallopavo*	22.2		Noirault et al. (2006)
Mallard duck	*Anas Platyrhynchos*	100.4		Johnson (1961)
Indian rose-ringed parakeet	*Psittacula krameri*	50		Krishnaprasadan et al. (1988)
Spotted antbird	*Hylophylax n. naevioides*		11	Hau (2001)
American crow	*Corvus brachyrhynchos*	19		Jenkins et al. (2007)
Brahminy myna	*Sturnus pagodarum*		60—90	Kumar and Kumar (1993)
Starling	*Sturnus vulgaris*	160	190.5—250	Dawson et al. (2002); Dawson (2003; 2005)
Canary	*Serinus canaria*		50	Bentley et al. (2003); Hurley et al. (2008)
House sparrow	*Passer domesticus*	166.7	46.4	Hegner and Wingfield (1986); Trivedi et al. (2006)
Redheaded bunting	*Emberiza bruniceps*		45	Kumar et al. (2002); Rani et al. (2005)
Song sparrow	*Melospiza melodia*	12.5	50—125	Wingfield (1984); Perfito et al. (2004)
White-crowned sparrow	*Zonotrichia leucophrys pugetensis*		38—80	Wingfield et al. (1997)
Rufous-collared sparrow	*Zonotrichia capensis*		11.9	Moore et al. (2004; 2005)
Syrian/golden hamster	*Mesocricetus auratus*	5	3.0—5.0	Donham et al. (1996); Kawazu et al. (2003)
Siberian hamster	*Phodopus sungorus*		5.3—5.8	Gorman and Zucker (1995); Prendergast et al. (2000)
Vole	*Microtus agrestis*	1.9		Król et al. (2005)
Ram	*Ovis musimon*		1.4	Lincoln (1998)
Deer	*Axis axis*	1.6		Willard and Randel (2002)
	Cervus elaphus		1.8	Suttie et al. (1992)

associated with increased rainfall, and these factors combine to increase plant and insect food resources. Increased food availability in turn provides energetic resources that birds can use to develop testes and for other aspects of reproduction. Indeed, unusually heavy winter rains that cause early greening of vegetation can advance the timing of breeding even in strictly seasonal breeders (canary (*Serinus canaria*) (Leitner, Van't Hof, & Gahr, 2003; Voigt, Goymann, & Leitner, 2007); zebra finch (*Taeniopygia guttata*) (Perfito, Zann, Bentley, & Hau, 2007)). By contrast, in regions such as the Sonoran Desert, the vernal increase in photophase and temperature is not typically associated with increased precipitation (Small, Sharp, & Deviche, 2007) and, in other areas (e.g., central Australia), rains are unpredictable and do not follow a consistent seasonal pattern (Immelmann, 1963; Zann, Morton, Jones, & Burley, 1995). In such situations, male birds are often flexible breeders and their reproductive physiology can rapidly respond to stimuli associated with irregular rainfall.

For example, zebra finches breed seasonally along the southeast Australian coast, where rains are relatively predictable. Birds in this region have moderately developed testes in preparation for the breeding season and regressed testes outside this season (Perfito et al., 2007). By contrast, in the arid center of the continent, where rains are unpredictable, zebra finches breed opportunistically, maintaining semideveloped, yet functional, testes year-round, even when their body condition deteriorates as a result of poor environmental conditions (Perfito et al., 2007). In drought-simulated captive conditions, zebra finches reduce their testis size but testes retain the capacity to produce sperm (Vleck & Priedkalns, 1985; Perfito, Bentley, & Hau, 2006). More predictably, in the Sonoran Desert, male rufous-winged sparrows start developing their testes in the spring in response to increasing photoperiod, but do not normally breed until the onset of the summer monsoon (Deviche & Small, 2006; Deviche et al., 2006; Small et al., 2007).

In both zebra finches and *Aimophila* sparrows, it remains unclear whether reproductive responses to precipitation are mediated directly by rainfall (e.g., increased humidity, sound of rain, physical contact with water) or indirectly and through an increase in food resources. Suggesting direct effects, testicular regression in captive rufous-winged sparrows is delayed in birds that receive food and water *ad libitum* and are exposed to artificial rain under fall-like photoperiod, compared to control sparrows that are not exposed to artificial rain (Deviche, unpublished observation). By contrast, other research suggests that rain influences testicular function indirectly, by acting as a predictive cue for future increase in biomass availability (Zann et al., 1995). These authors found a lag (four months showing the most profound effect) between when the first rains fell and breeding, suggesting that birds use rain to time reproduction so that young hatch when grass seeds are first ripening (Zann et al., 1995). Research on the zebra finch also shows that increased humidity and water availability lead to an increase in testicular size (Priedkalns, Oksche, Vleck, & Bennett, 1984; Vleck & Priedkalns, 1985).

6.1.3. Temperature

In seasonal environments, changes in ambient temperature provide a secondary cue that birds can use to predict future breeding conditions. We have little information on whether temperature influences testicular development directly or indirectly. Further, as average temperature in many regions changes seasonally in parallel with the photophase (e.g., Deviche & Sharp, 2001), separating the influence of these two factors on reproductive functions in natural conditions can be difficult.

Temperature exerts complex effects on testicular function and development. For example, in chickens, high ambient temperatures impair testicular function and decrease semen output (Wilson, Siopes, & Itho, 1972), and cold temperatures suppress testicular growth and fertility (Huston, 1975). By contrast, comparative studies using several subspecies of white-crowned sparrows that breed at different latitudes found that temperature does not influence testicular development in high-latitude breeders with short, predictable breeding seasons. However, lower-latitude breeders with more flexible breeding seasons than arctic breeders show a positive association between temperature and testicular development (Wingfield, Hahn, Wada, Astheimer, & Schoech, 1996; Wingfield et al., 2003). Captive studies examining the effects of temperature on testicular development found that cold temperatures can delay reproductive readiness and the onset of photorefractoriness in male black-billed magpies (*Pica pica*) (Jones, 1986), song sparrows (*Melospiza melodia morphna*) (Perfito et al., 2004), and tits (*Parus* spp.) (Silverin & Viebke, 1994; Silverin et al., 2008). Conversely, warmer temperatures can advance testicular development in southern-breeding great tits (Silverin et al., 2008) and seasonal testicular regression in European starlings (Dawson, 2005).

Research comparing species inhabiting environments differing in seasonal temperature patterns, combined with captive studies manipulating ambient temperatures and photoperiod, should help untangle the role and mechanism of action of temperature on testicular function.

6.1.4. Food

The type, amount, quality, and predictability of food resources can exert complex effects on the reproductive system (Hahn, Pereyra, Katti, & Ward, 2005). In environments where food availability is relatively predictable and breeding flexible, food supplementation can advance or enhance testicular development (Newton, 1998; Hau, Wikelski, & Wingfield, 2000; Hahn et al., 2005). For example, in free-ranging song sparrows inhabiting coastal and mountain habitats that differ with respect to seasonal food availability, testicular growth rates and maximal testicular size differ between years and as a function of altitude and presumably food availability (Perfito et al., 2004). Similarly, food restriction at the onset of the breeding season can delay seasonal testicular regression (Dawson, 1986), and restriction during reproduction can cause a decrease in testicular weight (Kobayashi & Ishii, 2002; Kobayashi, Cockrem, & Ishii, 2002). These observations indicate that food availability may serve as a secondary cue for reproduction.

For most of the year, crossbills (*Loxia* spp.) consume primarily conifer seeds, the availability of which often varies unpredictably in time and space. As a result, reproduction in these birds is not thought to be tightly regulated by photoperiod (Hahn, 1995). Instead, access to sufficient

food resources can lead to testicular development even when birds are exposed to short winter days (Hahn, 1995; Hahn, Wingfield, Mullen, & Deviche, 1995; Hahn, 1998; Deviche & Sharp, 2001). Despite this, food alone does not act as the primary cue (Hahn et al., 2005) because testicular development occurs only in the presence of a mate (Hahn et al., 1995). The only time of year that crossbills have small testes and appear limited in their ability to breed, even if food is available, is during autumnal molt. This limitation may be photoperiod-mediated (Deviche & Sharp, 2001; MacDougall-Shackleton, Deviche, Crain, Ball, & Hahn, 2001).

Uniquely, zebra finches may use food as a primary cue, as males exposed to short or long days do not develop their testes when food-restricted (Perfito, Kwong, Bentley, & Hau, 2008). However, exposure to long photoperiod and *ad-libitum* food availability induce maximal testicular development (Perfito et al., 2008). More research is needed in order to understand the importance of food and interactions between food availability and photoperiod in this species.

6.2. Life History

6.2.1. Breeding strategy

Seasonal breeders are often categorized based on the development of a refractory state at the end of their breeding period rather than by the cues used to stimulate reproductive development. These categories, although often presented as discrete units, exist on a continuum that sometimes makes it difficult to clearly categorize a species' breeding strategy. A combination of studies on free-ranging (e.g., Silverin, Massa, & Stokkan, 1993; Deviche & Sharp, 2001; Leitner et al., 2003; Silverin et al., 2008) and captive birds (e.g., Macdougall-Schackleton et al., 2001; Bentley, Audage, Hanspal, Ball, & Hahn, 2003; Hahn, Pereyra, Sharbaugh, & Bentley, 2004; Voigt et al., 2007; Hurley, Wallace, Sartor, & Ball, 2008) is often required to do so.

The seasonal breeders that are most easily defined are the absolutely photorefractory species. In these species, transfer from short to long (i.e., longer than the critical day length) photoperiod induces testicular growth, but testes then spontaneously regress even during exposure to increasing or previously stimulatory day lengths (Hamner, 1968; Nicholls et al., 1988). Termination of absolute photorefractoriness requires exposure to short days and coincides with an increase in hypothalamic GnRH-I expression, but not testicular size (Dawson & Goldsmith, 1997).

Less clearly categorized are species the testicular cycle of which does not obligatorily include spontaneous regression in response to prolonged exposure to long days. These species, such as the Japanese quail (Robinson & Follett, 1982) and sparrows of the genus *Aimophila* (Deviche et al., 2008; Small et al., 2008a), are said to be relatively photorefractory. Their testicular growth is stimulated by long days, but testicular regression does not begin until day length decreases. In these species, exposure to artificial long days can increase testicular size even during natural testicular involution (rufous-winged sparrow (Small et al., 2008c)). Testicular regression in the Japanese quail is not associated with decreased hypothalamic GnRH-I (Foster, Plowman, Goldsmith, & Follett, 1987).

A third category consists of species that exhibit considerable reproductive flexibility or breed opportunistically, some of which may be relatively photorefractory. *Flexible* breeders tend to breed seasonally and use day length to time gonadal functioning, but the exact timing of reproduction is largely dependent on nonphotic secondary cues such as rainfall or temperature (Leitner et al., 2003; Wingfield et al., 2003). *Opportunistic* breeders breed less seasonally, respond minimally to day length, and primarily rely on nonphotic cues, such as food or mates, as signals to stimulate testicular function (Deviche & Sharp, 2001; Perfito et al., 2008). These birds typically inhabit environments where the cues used to time reproduction are largely unpredictable. They must be capable of rapidly developing their gonads when conditions become favorable (Perfito et al., 2007; Hahn et al., 2008).

The degree to which a given species exhibits absolute or relative photorefractoriness varies within and between species. For example, within cardueline finches, common redpolls (*Carduelis flammea*) breed seasonally, pine siskins (*Carduelis pinus*) breed flexibly but show spontaneous testicular regression, and white-winged crossbills breed almost opportunistically (Hahn et al., 2004) (see Section 6.1.4). Another study on cardueline finches found that red crossbills (*Loxia curvirostra*), pine siskins, and gray-crowned rosy-finches (*Leucosticte tephrocotis*), but not Cassin's finches (*Carpodacus cassinii*), develop testes and have elevated plasma LH when exposed to constant light in autumn (MacDougall-Shackleton, Katti, & Hahn, 2006). The closely related canary (*Serinus canaria*), breeds flexibly in the wild (Leitner et al., 2003), but artificial selection has generated genetic lines with characteristics of absolute photorefractoriness (Hurley et al., 2008) and breeders with a variable photorefractory response (Bentley, Wingfield, Morton, & Ball, 2000; Bentley et al., 2003). Studies on cardueline finches illustrate the diversity and complexity that need to be considered in order to understand mechanisms that regulate avian reproductive cycles.

6.2.2. Migratory vs. sedentary species

Many species migrate before and after their breeding season. Preparation for migration limits the duration of the reproductive period (Lofts & Murton, 1973). Other birds do not migrate, which may extend their breeding season and allow maintenance of territories year-round (Silverin et al.,

1993; Hau et al., 2000; Hau, 2001). Still other species exhibit nomadic behavior with large home ranges and unpredictable annual movements (Hahn 1995; Hahn et al., 1995; Hahn, 1998; Perfito et al., 2007).

Migration is energetically demanding and thus may constrain the energy available for testicular growth (Drent, Both, Green, Madsen, & Piersma, 2003; Battley & Piersma, 2005). Therefore, migrants must balance the energetic constraints associated with migration with the need to develop their reproductive system so as to minimize the impact on reproductive success and body condition (Bauchinger, Van't Hof, & Biebach, 2007; 2008). Testicular development in migratory species appears closely tied to changes in photoperiod, particularly on wintering grounds (e.g., Gwinner, 1987; 1989; Silverin, 1995; Rödl, Goymann, Schwabl, & Gwinner, 2004), and short- and long-distance migrants may differ with respect to their responsiveness to small changes in day length. This difference may in turn enable long-distance migrants to initiate migration earlier than short-distance migrants (e.g., stonechats (*Saxicola torquata*) (Helm & Gwinner, 2005; Raess & Gwinner, 2005)).

In many migratory species, males reach breeding grounds before females, which provides time to complete testicular recrudescence and establish territories before females arrive (Kokko, Gunnarsson, Morrell, & Gill, 2006). In these species, particularly long-distance migrants with brief breeding seasons, testicular growth often begins during migration and, as a result, testes can become fully developed shortly after arrival on breeding grounds (Bauchinger et al., 2007). Some species even produce sperm and mate during migration, but it is unclear whether sperm produced at this time are viable enough to ensure fertilization (Quay, 1985; 1989). Ample food supplies at 'stopover' sites may contribute to partial or advanced testicular development (Bauchinger et al., 2008).

Sedentary species show a diversity of testicular cycles and greater variation than migratory species in their onset of reproduction, depending on whether they are paired and maintain year-round territories or defend territories only during the breeding period (Small et al., 2007; Hahn et al., 2008; Jawor & MacDougall-Shackleton, 2008; Wingfield, 2008). The latter species in temperate regions typically exhibit an annual testicular cycle that parallels changes in day length, but with greater flexibility than seen in migratory species (Phillmore, Hoshooley, Sherry, & MacDougall-Shackleton, 2006; Jawor & MacDougall-Shackleton, 2008; Wingfield, 2008). In species such as the rufous-winged sparrow that maintain pair bonds and territories year-round (Ohmart, 1969; Lowther, Groschupf, & Russell, 1999), males develop testes in spring but generally do not breed until the summer monsoon, when day length is decreasing (Small et al., 2007). The timing of final testicular maturation is flexible, which is advantageous as the

onset and intensity of the monsoon varies considerably from one year to another. Similarly to the rufous-winged sparrow, in sedentary tropical species, factors such as spatial and temporal shifts in food availability play important roles in the control of testicular cycles (Kumar, Singh, Misra, Malik, & Rani, 2002; Wikelski, Hau, Robinson, & Wingfield, 2003; Rödl et al., 2004; O'Brien & Hau, 2005; Hahn et al., 2008). However, in these species there appears to be an annual cycle of testicular recrudescence and involution that is minimally influenced by photoperiod (Hau et al., 1998; Wikelski et al., 2000). Nomadic species such as crossbills and zebra finches, which travel widely in search of food resources, rely heavily on nonphotic factors to time reproductive development (Hahn, 1995; Hahn et al., 1995; Zann et al., 1995; Hahn, 1998; Perfito et al., 2007). Species exhibiting this breeding strategy constitute particularly interesting models to investigate the role of secondary cues in the timing of reproduction.

Our understanding of the role of life strategies in testicular cycles is constrained by the paucity of data on this subject for free-ranging birds. Replicating the energetic demands of migration in captive birds is difficult and limits our ability to study how migration impacts testicular functions. More studies are needed that sample birds prior to migration, during stopovers, and shortly after arrival on breeding grounds (Bauchinger et al., 2007; 2008). Identifying factors that influence the flexibility of the annual testicular cycle should enable us to better predict how environmental perturbations such as global climate change (Section 9.2) may impact avian reproduction.

6.2.3. Brood parasitism

Brood parasites lay their eggs in the nests of other birds and rarely build nests or rear their own young. In the few studies on this subject, testicular development in brood parasites apparently matched that of their primary host species, suggesting control by similar factors (Payne, 1967; Scott & Middleton, 1968; Payne, 1973a; 1973b; 1977). In the brown-headed cowbird (*Molothrus ater*), an increase in photophase stimulates testicular development (Dufty & Wingfield, 1986a). In this study, captive and free-ranging males developed larger testes when mated than when unpaired, demonstrating a role for social cues in testicular development (Dufty & Wingfield, 1986b).

6.2.4. Social cues

Numerous studies have investigated the role of social factors in avian reproduction. Many investigations on this topic have emphasized effects of auditory and pairing cues (reviewed in Helm, Piersma, & Van der Jeugd, 2006). Studies on the role of auditory cues have primarily focused

on how male song production in passerines enhances the reproductive system development of conspecific females (Kroodsma, 1976; Leboucher, Depraz, Kreutzer, & Nagle, 1998; Bentley et al., 2000; Maney, Goode, Lake, Lange, & O'Brien, 2007). By contrast, little work has been done on the effects of song on testicular function of other males. In one of the few studies on this subject, exposure of rufous-winged sparrows to conspecific song increased the effects of long-day exposure on testicular growth (Small et al., 2008c). No such effect has, however, been observed in the canary (Boseret, Carere, Ball, & Balthazart, 2006).

Testicular function, particularly in monogamous species, is influenced by the presence of a mate. Captive male European starlings, Japanese quail, and brown-headed cowbirds that are kept without or with only limited exposure to a female exhibit a decreased capacity to develop their testes, and/or regress them sooner than males held with a female (Dawson & Goldsmith, 1984; Delville, Sulon, Hendrick, & Balthazart, 1984; Dufty & Wingfield, 1986b; Gwinner, Van't Hof, & Zeman, 2002). The importance of the pair bond is also demonstrated in crossbills, which can develop their testes and breed in winter provided that they receive proper food and are exposed to mates (Hahn et al., 2005). Similarly, captive male ptarmigans (*Lagopus* sp.) show a truncated breeding season relative to free-ranging conspecifics (Stokkan et al., 1988) and this difference may result from lack of exposure to social factors. The role of such factors should be considered during studies, particularly those using captive birds from wild populations, on the environmental control of reproduction.

7. ECOLOGY OF TESTICULAR FUNCTIONS

Birds have become model organisms for addressing questions related to the evolution of breeding systems, costs of reproduction, and sexual selection of ornamental traits. Work on this subject largely stems from three basic characteristics of birds:

(1) The dependence of measurable behaviors on numerous physiology-based processes such as territoriality and courtship displays;

(2) Breeding structures and behaviors that are easily quantifiable as potential costs of reproduction;

(3) Highly variable and flexible breeding strategies resulting from numerous physiological adaptations (Section 6).

The two main functions of testes—androgen synthesis and sperm production—are under intensive natural and sexual selection pressures and are considered to be energetically costly. Detailed understanding of these functions has led researchers to examine broad-scale patterns related to testicular size, plasma T, and androgen-dependent behaviors, leading to free-ranging birds becoming one of the best-studied taxa for investigating this topic.

7.1. Linking Testosterone (T) and Sperm Quality

Testosterone in vertebrates is essential for spermatogenesis, but the negative feedback effect of T on the hypothalamus and pituitary gland can also lead to suppressed testicular functions. The degree to which plasma T levels reflects spermatogenetic activity or sperm quality is controversial, but a few studies have attempted to clarify this link. An early study on turkeys found no relationship between serum T and ejaculate volume (Cecil & Bakst, 1986). Similarly, T administration either does not alter or in some cases decreases the ejaculate volume of free-ranging male dark-eyed juncos, but this effect depends on the breeding stage (Kast, Ketterson, & Nolan, 1998). An inverse relation between plasma T and ejaculate volume in T-treated birds may reflect a treatment-mediated increase in copulation rate that in turn results in reduced residual ejaculate volumes (Kast et al., 1998). Alternately or in addition, the negative action of T on the hypothalamo—pituitary gland axis may decrease testicular function, resulting in smaller ejaculate volume. In contrast to the above studies, Penfold et al. (2000) reported that circulating T levels in breeding northern pintail (*Anas acuta*) are correlated to both the total number of sperm and the percentage of sperm exhibiting normal morphological characteristics, and T administration in some circumstances stimulates testicular functions (e.g., Deviche et al., 2006). Future studies should aim at elucidating the mechanisms mediating this increase and address the relation between T and sperm quality and/or production, particularly by comparing taxa with varying seasonal T profiles and male fertility rates.

7.2. Correlates of Testicular Size

7.2.1. Body size and age

Most testicular tissue is devoted to spermatogenesis and testis size is, therefore, often used to estimate sperm production (Section 3) (Moller, 1988). Large testes produce more sperm than small testes in the house sparrow (Birkhead et al., 1994) and the zebra finch (Birkhead, Pellatt, & Fletcher, 1993). However, little empirical information concerning sperm production in wild birds is available with which to assess whether these data can be generalized, especially as sperm production estimates can be highly variable (Briskie & Montgomerie, 2007). Inter- and intra-specific comparisons suggest allometric associations between testis and body sizes, but the strength of this association varies (Rising, 1987a; Moller & Erritzoe, 1988; Moller, 1988; 1991; Olsen, 1991; Moller, 1994; Moller &

Briskie, 1995; Rising, 1996; Merilä & Sheldon, 1999; Coker, McKinney, Hays, Briggs, & Cheng, 2002; Pochron & Wright, 2002; Garamszegi et al., 2005; Pitcher et al., 2005; Calhim & Birkhead, 2007; Gunn et al., 2008). These observations have prompted researchers to correct testis sizes for variations in body mass, most often by using regression residual methods.

Several studies have documented age-related variation in testis size, with older adults generally having larger testes than younger adults (Selander & Hauser, 1965; Morton, Peterson, Burns, & Allan, 1990; Hill, 1994; Deviche, Wingfield, & Sharp, 2000b; Graves, 2004; Laskemoen, Fossoy, Rudolfsen, & Lifjeld, 2008). These studies have primarily compared after-hatch-year males with older males (two or more years of age), as it is often difficult to age birds, especially passerines, that are older than two years. Age-related differences in testis size may result from younger birds secreting less GTHs than older birds (Ketterson & Nolan, 1992; Silverin et al., 1997; but see Morton et al., 1990), but whether testicular sensitivity to these hormones is also age-dependent has not been investigated. Age-dependent differences in mean and maximal testis size may account for lower plasma T in younger adult males compared with older males (Sorenson, Nolan, Brown, Derrickson, & Monfort, 1997; Deviche et al., 2000b; Deviche & Sharp, 2001). Age-related variation in other sexual characteristics, such as the size of the seminal glomerula and cloacal protuberance, has been documented in the bluethroat (*Luscinia svecica*) (Laskemoen et al., 2008). Superb fairy-wrens (*Malurus cyaneus*) are thought to endure intensive sexual selection. In adult males of this species, the size of the cloacal tip, which likely serves as an intromittent organ (Rowe, Bakst, & Pruett-Jones, 2008), also increases with age (Mulder & Cockburn, 1993). Collectively, these results are consistent with evidence for age-related variation in male reproductive success, particularly in reference to the number of extrapair matings (Richardson & Burke, 1999; Gonzalez-Solis & Becker, 2002; Westneat & Stewart, 2003; Laskemoen et al., 2008). However, specific associations between age-related variation in testicular functions and fitness are few, and this topic warrants further investigation.

7.2.2. Testosterone (T), mating systems, and geography

Testosterone in male birds influences the expression of various behaviors, particularly in relation to the establishment of territories, the pursuit of extrapair mating opportunities, the defense of females against their extrapair forays, and the allocation of energy towards paternal care of offspring (Ketterson et al., 1991; De Ridder, Pinxten, & Eens, 2000; Van Roo, 2004; Garamszegi et al., 2005; Schwabl, Flinks, & Gwinner, 2005; Soma, 2006).

Reviewing the effects of T on male bird behavior is beyond the scope of this chapter (see Chapters 7 and 8, this volume), but collectively these studies suggest a link between testis size and T profiles, particularly through comparative studies in avian taxa whose life-history traits differ. Seasonally maximal plasma T levels are thought to be higher in birds exhibiting polygynous mating systems than in monogamous species, which is considered to reflect the intensity of sexual selection (Wingfield, Hegner, Dufty, & Ball, 1990). Further, polygynous species tend to have larger testicular volumes than size-matched monogamous birds (Garamszegi et al., 2005). Interspecific studies on this subject have provided largely consistent results, but intra-specific comparisons attempting to relate plasma T to testicular size have generated mixed results. For example, a positive relation between these variables was reported for mallards (Denk & Kempenaers, 2006) but not red-winged blackbirds (Weatherhead, Metz, Bennett, & Irwin, 1993).

A further complication is illustrated by a study comparing 116 bird species in which positive associations between testicular size and circulating T concentrations were confounded by strong latitudinal variation, with tropical species having lower plasma T and smaller testes than temperate or high-latitude breeders (Section 6.2.2) (Garamszegi et al., 2005). Similar latitudinal trends of increasing testicular size have been reported in other comparative studies (Merilä & Sheldon, 1999; Moore, Perfito, Wada, Sperry, & Wingfield, 2002; Pitcher et al., 2005). The length of the breeding season and, therefore, potentially the period during which plasma T is elevated, often decrease as latitude increases (Wingfield & Hunt, 2002; Hau, Gill, & Goymann, 2008). At high latitudes, reproduction within a species often is more synchronous than at low latitudes, where relatively constant environmental conditions may enable longer reproductive periods (Wingfield & Hunt, 2002; Goymann et al., 2004; Moore, Wingfield, & Brenowitz, 2004; Hau et al., 2008). As a result, extrapair paternity is thought to be less frequent in tropical than temperate or high-latitude-region species (Stutchbury, Morton, & Piper, 1998; Spottiswoode & Moller, 2004). This hypothesis is supported by intraspecific observations showing that testicular size increases with latitude (house finch (*Carpodacus mexicanus*), red-eyed vireo (*Vireo olivaceus*), and greenfinch (*Carduelis chloris*) (Merilä & Sheldon, 1999)). However, no such increase was found in black-throated blue warblers (*Dendroica caerulescens*) (Graves, 2004) and the opposite situation was described in savannah sparrows (*Passerculus sandwichensis*) (Rising, 1987b; Pitcher & Stutchbury, 1998). It is currently unclear whether positive correlations between testicular size and latitude reflect genetic differences between populations or species, or are induced by environmental effects on the phenotype. In support of the latter, Silverin et al. (2008) compared the testicular development

of photostimulated great tits obtained from different latitudes (45 to 70°N) and held in identical captive conditions. It was found in this species that the time course of photo-induced changes in testicular size depends on the latitude of origin, but populations do not differ with respect to their maximal testicular size.

7.3. Evolutionary Explanations for Testicular Size Asymmetry

Variation in size between the left and right testes has also drawn the attention of researchers. Moller (1994) proposed that, in some species with asymmetric testes, such as the house sparrow and the barn swallow (*Hirundo rustica*), the normally smaller testis develops only when the other testis fails to grow normally ('compensation hypothesis'). This hypothesis is supported by studies showing that hemi-castration causes compensatory growth of the remaining testis, regardless of which testis is removed (Farner, Morton, & Follett, 1968; Driot, De Reviers, & Williams, 1979), and increased FSH secretion (Wilson & Follett, 1978). Thus, the normally less developed testis in a species with asymmetric testicular sizes presumably is sensitive to gonadostimulatory factors, such as GTHs. Within an individual, however, the two testes may be differentially sensitive to GTHs, but the cellular basis of this potential difference has not been researched. The compensation hypothesis predicts that males in poor body condition have a lower capacity to engage in this compensatory growth. Accordingly, within a population the degree of testicular asymmetry should reflect overall male quality, with lower quality males having less symmetric testes. This was the case in some studies (house sparrow and barn swallow (Moller, 1994)) but not others (tree swallow (Kempenaers et al., 2002); black-throated blue warbler (Graves, 2004)) and the generality of the compensation hypothesis remains to be established.

The degree of adult testicular size asymmetry is also thought to be associated with survival (Birkhead et al., 1997). The observation in black-throated blue warblers that adult testicular size asymmetry increases with age is consistent with this view (Graves, 2004). However, there is no identified mechanism linking the degree of testicular size asymmetry to adult survival, and a causal relation between these variables remains speculative. Finally, testicular asymmetry may be advantageous in increasing flight efficiency by reducing paired testicular mass and, therefore, wing loading. However, why the same increase in flight efficiency could not be attained by developing symmetric testes of same paired mass as that of asymmetric testes is unclear. Further, some predominantly terrestrial birds (chicken (Hocking, 1992)), but also highly aerial species (e.g., tree swallows (Kempenaers et al., 2002)), show no testicular size asymmetry. New descriptive and experimental work investigating testicular asymmetry in species belonging to various phylogenetic groups and exhibiting diverse lifestyles (e.g., aerial vs. terrestrial) is needed to address these issues. Age and reproductive condition (Dang & Guraya, 1978) are also thought to influence avian testicular asymmetry and studies would benefit from incorporating these factors into the data analysis and interpretation.

7.4. Theories of Sperm Competition

Two seminal papers (Parker, 1970a, b; no pun intended) introduced the concept of 'sperm competition.' Accordingly, in situations where females mate with multiple males during a given reproductive cycle, fertilization and thus paternity of offspring would be determined by the outcome of competition between the sperm of the mated males. This hypothesis, initially developed based on insect studies, has become a predominant theme in avian research. Sperm competition may be especially prominent in birds. Females of many species can store sperm for several days or weeks in specialized sperm storage tubules (SSTs), which may result in competition between several males with which they mated (Briskie & Montgomerie, 1993). In situations of sperm competition, males can gain more fertilizations by (1) producing greater quantities of sperm per ejaculate (often inferred from studies of testicular size—see Section 7.2) or (2) altering sperm morphology to increase sperm mobility or longevity in the female reproductive tract. Few data exist on whether an increase in testicular size is associated with increased sperm production. Further, this relation does not need to be linear because large increases in testicular size may be associated with a proportionally small increase in sperm production (Calhim & Birkhead, 2007).

Sperm morphology varies considerably among species (for reviews see Briskie & Montgomerie, 2007; Jamieson, 2007). Sperm length, in particular, may be an important determinant of mobility, but the limited experimental data available on this subject do not support this assertion (Denk, Holzmann, Peters, Vermeirssen, & Kempenaers, 2005). Sperm length is highly consistent within individuals but varies among individuals (Laskemoen, Kleven, Fossoy, & Lifjeld, 2007), and a study on zebra finches suggests that individual variation in sperm size is heritable (Birkhead, Pellatt, Brekke, Yeates, & Castillo-Juarez, 2005). A comparative study of 16 shorebird species revealed that longer sperm are produced in polyandrous and polygynous than in monogamous species (Johnson & Briskie, 1999). However, an earlier study on passerines found no relation between sperm length and mating system, but rather a positive and a negative correlation between sperm length and the length of female SSTs and the number of SSTs, respectively (Briskie & Montgomerie, 1992). These

authors reasoned that longer sperm may swim faster, which would be advantageous when there is little opportunity for sperm storage (i.e., fewer SSTs). Testes may also be sites of a physiological tradeoff between energetic investment into individual sperm size and the number of sperm produced or the volume of the ejaculate, as suggested by studies in other diverse taxa (mammals (Gomendio & Roldan, 1991); snails (Oppliger, Hosken, & Ribi, 1998)). In birds, intense sperm competition appears to be more closely associated with variation in sperm size than ejaculate volume, but few direct comparisons of these parameters are available (Briskie, Montgomerie, & Birkhead, 1997).

Evolutionary theory suggests that, for a given trait under intense stabilizing or directional selection, additive genetic variance in a heritable trait should decrease. A recent study (Kleven, Laskemoen, Fossoy, Robertson, & Lifjeld, 2008) demonstrates decreased variance in sperm length with increasing frequency of extrapair paternity for 22 passerine species, suggesting that sperm length is under strong selection pressure via sperm competition (Figure 2.2). Postcopulatory sexual selection may account for the evolution of sperm morphology, but little empirical research exists in birds concerning how variation in sperm morphological characteristics relates to increased fertilization success.

A current topic of research on sperm competition is sperm precedence, where copulation may result in disproportionate fertilization success simply due to the sequence by which mating occurred. Several models have been proposed to explain situations of sperm precedence, but one in particular—the passive sperm loss model—has received the most attention (Lessells & Birkhead, 1990; Birkhead & Biggins, 1998). Accordingly, sperm are lost from a female at a constant rate and, thus, the longer the time between two matings, all else being equal, the greater the proportion of offspring fathered by the second mating (Birkhead & Biggins, 1998). This model is supported by studies in chickens, turkeys (Birkhead & Biggins, 1998), and zebra finches (Birkhead & Fletcher, 1998). The study of sperm competition in birds is a fruitful area of research that has contributed substantially to our understanding of the flexibility of avian reproductive systems. However, much of this work has focused on describing large-scale patterns in free-living birds and includes relatively little experimental research. We have few empirical data regarding how sperm characteristics influence their mobility and have largely relied on the assumption that greater sperm length translates to increased speed (although see Humphries, Evans, & Simmons, 2008).

7.5. Negative Consequences of Large Testes

Large testes may impart benefits but also physiological costs. One such cost is the increased energetic investment
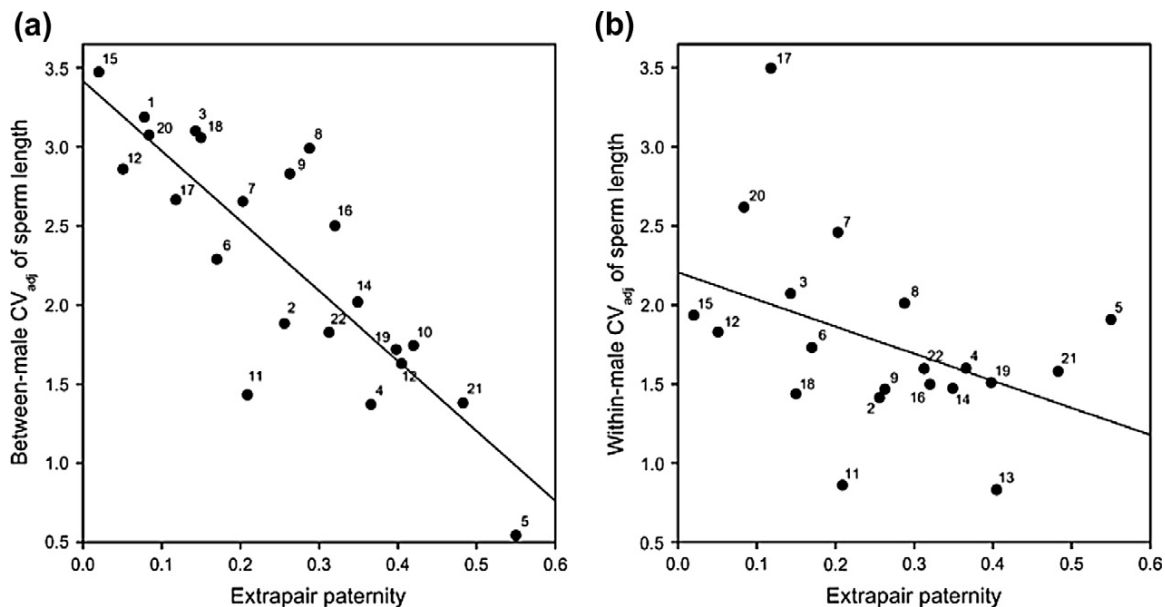

FIGURE 2.2   Relationship between extrapair paternity (proportion of young sired by extrapair males) and (**a**) intraspecific (22 species) and (b) individual (20 species) variation (coefficient of variation (CV)) in total sperm length in passerines. Each point represents the mean value per species. Data are presented as untransformed values and are not corrected for phylogeny. Labels refer to the following species: 1, *Acrocephalus schoenobaenus*; 2, *Agelaius phoeniceus*; 3, *Carduelis tristis*; 4, *Dendroica petechia*; 5, *Emberiza schoeniclus*; 6, *Fringilla coelebs*; 7, *Geothlypis trichas*; 8, *Hirundo rustica*; 9, *Luscinia svecica*; 10, *Malurus splendens*; 11, *Melospiza georgiana*; 12, *Melospiza melodia*; 13, *Passerculus sandwichensis*; 14, *Passerina cyanea*; 15, *Phoenicurus phoenicurus*; 16, *Phylloscopus trochilus*; 17, *Poecile atricapilla*; 18, *Riparia riparia*; 19, *Setophaga ruticilla*; 20, *Sialia sialis*; 21, *Tachycineta bicolor*; 22, *Vermivora chrysoptera*. Adapted from Kleven, Laskemoen, Fossoy, Robertson, and Lifjeld (2008), with permission.

involved in maintaining testicular tissue. This may be the case particularly in seasonally breeding birds in which testicular mass fluctuates dramatically throughout the year. The added mass of larger testes during breeding may also increase wing loading, thus increasing flight cost. Little empirical data on this topic exists, but, in one study on European starlings, addition of weights comparable to fully developed testes decreased the nest visitation rate, possibly as a result of decreased flight efficiency (Wright & Cuthill, 1989).

Increased sperm production by larger testes may be associated with greater androgen production (Garamszegi et al., 2005; Denk & Kempenaers, 2006). As with many steroids, chronically high T levels can be immunosuppressive (Muehlenbein & Bribiescas, 2005; Singh & Haldar, 2005; Deviche & Parris, 2006; Mougeot, Redpath, & Piertney, 2006; Boonekamp, Ros, & Verhulst, 2008). Females may asses the quality of males on the basis of characteristics that are androgen-dependent, and it is suggested that better-quality males are in a better condition to cope with the immunosuppressive effects of higher androgen levels (Moller, 1990; Folstad & Karter, 1992; Day, McBroom, & Schlinger, 2006; Fusani, 2008; Mcglothlin et al., 2008). The suppressive action of T remains paradoxical, but an interesting hypothesis suggests that this hormone, which concentrates in the seminiferous tubules during spermatogenesis, may act locally to deter autoimmune responses (i.e., antibody production) to antigenic sperm (Folstad & Skarstein, 1997; Hillgarth, Ramenofsky, & Wingfield, 1997). Reproductive 'lower-quality' males that are combating infectious organisms may have difficulty regulating this localized immunosuppression, which may interfere with sperm production (Folstad & Skarstein, 1997; Hillgarth et al., 1997). Thus, increased T production by larger testes may increase susceptibility to infection and ultimately interfere with sperm production. Future studies aimed at testing this hypothesis may lead to further insights into the costs of maintaining large testes.

8. TESTICULAR DYSFUNCTION

The exocrine and endocrine functions of avian testes normally are carefully regulated at multiple levels ranging from the brain to locally produced chemicals. A myriad of conditions may, however, interfere with normal testicular function. This topic is of great interest to reproductive biologists, conservationists, evolutionists, veterinarians, and those interested in the artificial propagation of game and poultry species. A complete analysis of avian testicular dysfunction and its ultimate causes is beyond the scope of this chapter. Instead, we will discuss some findings on naturally occurring and anthropogenically induced conditions in birds, particularly with reference to the endocrine function of the testes (see also Chapter 9, this volume).

8.1. Phytoestrogens

One proposed form of testicular dysfunction results from effects of natural plant compounds termed endocrine-active phytochemicals (Vajda & Norris, 2006) ingested by birds. Some plants produce phytoestrogenic compounds (substances with natural chemical properties similar to estrogens) that can act as endocrine disruptors in insects (Lafont, 1997), mammals (Shackell, Kelly, & Johnstone, 1993; Saloniemi, Wahala, Nykanenkurki, Kallela, & Saastamoinen, 1995; Santti, Makela, Strauss, Korkman, & Kostian, 1998; Odum et al., 2001; Dixon, 2004; see Volume 5, Chapter 14), fishes (Ishibashi et al., 2004; see Volume 1, Chapter 13), and birds (Berry, Zhang, & MacDaniel, 1999; Millam et al., 2002; Corbitt, Satre, Adamson, Cobbs, & Bentley, 2007; Rochester et al., 2008b; see Chapter 9, this volume). These phytoestrogenic compounds are thought to have evolved as a defense against herbivory (Labov, 1977; Hughes, 1988; Wynne-Edwards, 2001) and can vary in potency depending on factors such as the part and age of the plant and whether the plant is under stress (e.g., drought or constant herbivory) (Leopold, Erwin, Oh, & Browning, 1976; McMurray, Laidlaw, & McElroy, 1986; Tsao, Papadopoulos, Yang, Young, & McRae, 2006; Rochester et al., 2008b). Exposure to phytoestrogens decreases testicular weight relative to body size in developing Japanese quail (Rochester et al., 2008b) and can inhibit T production in cultured avian Leydig cells from chickens and geese (Opalka, Kaminska, Ciereszko, & Dusza, 2004; Opalka, Kaminska, Puchajda-Skowronska, & Dusza, 2006), but the mechanism involved is unclear. These effects may explain the decrease in fertility and reproductive success as well as differential breeding responses observed in birds that consume phytoestrogenic plants or plant-based diets (Leopold et al., 1976; Beck, Unterrieder, Krenn, Kubelka, & Jungbauer, 2003; Corbitt et al., 2007). Effects of phytoestrogens are not always pronounced (Opalka et al., 2008) but, when apparent, seem to affect male more than female reproductive functions (Wilhelms, Scanes, & Anderson, 2006; Rochester et al., 2008b). As the suppressive actions of phytoestrogens on the reproductive system are being unraveled, it will be important to research interactions between these effects and those of endocrine disruptors (Section 9.3).

8.2. Hybridization and Infertility

Hybridization between closely related taxa has long fascinated biologists due to the nature of the outcome, implications for the biological species concept, and the possibility of a rapid mechanism for genetic evolution via introgression. Hybridization has been recorded in wild birds more commonly than in other vertebrate taxa and incidences of hybrids have been reported in numerous

orders (P. Grant & B. Grant, 1992). We have long known that hybrid offspring often exhibit lower fertility and in some cases complete sterility, and studies of free-ranging avian populations have documented declines in the reproductive success of hybrids relative to parental species (Bell, 1997; Baker & Boylan, 1999; Solberg, Jensen, Ringsby, & Saether, 2006; Svedin, Wiley, Veen, Gustafsson, & Qvarnstrom, 2008). However, little research has been conducted to investigate physiological consequences of hybridization, particularly in male birds. Crossbreeding of Muscovy duck drakes (*Cairina moschata*) and Pekin duck females produces hybrids with testes of intermediate size relative to those of the parents (Snapir et al., 1998). Hybrids produce normal quantities of T, at levels intermediate to those of males of the two parent species, and they exhibit normal testicular growth and organization of the seminiferous tubules. However, they do not produce mature spermatids, indicating an inability to successfully complete spermatogenesis (Snapir et al., 1998). This deficiency likely results from genetic incompatibility at the chromosomal level (Snapir et al., 1998). Hybrids between hermit warblers (*Dendroica occidentalis*) and Townsend's warblers (*Dendroica townsendi*) likewise have plasma T levels intermediate relative to those of males of the parent species (Owen-Ashley & Butler, 2004). These levels are positively associated with the degree of backcrossing (hybrid score) to the parent phenotypes and possibly reflect genetic divergence in aggressiveness between males of the species (Owen-Ashley & Butler, 2004). Although most hybridizations result in sterile offspring, they can in some cases increase fitness by increasing heterozygosity (i.e., hybrid vigor (P. Grant & B. Grant, 1992)). This outcome is of particular interest to researchers concerned with adaptations at the microgeographic level. In particular, hybrid zones where the ranges of two species overlap, thus resulting in higher frequencies of hybridization, are thought to be especially prominent in 'edge' habitats (Hayes, 2001; Adamik & Bures, 2007). Anthropogenic disturbance increases these types of transitional habitats, which in turn may influence the frequency of hybridization. This may become especially important for vulnerable or threatened species, in which hybridization with a more common species can influence population status. The degree to which hybridization may impact free-ranging avian populations is poorly explored. Understanding the reproductive consequences of hybridization requires an appreciation of its effects on steroidogenesis and spermatogenesis.

8.3. Testicular Pathology

Several conditions, many of which are associated with epididymal abnormalities, can negatively affect fertility in domestic poultry. In turkeys, yellow semen syndrome (YSS), which results from overaccumulation of lipid droplets in the efferent duct epithelia, is associated with an increase in seminal proteins (Thurston, 1979; Thurston, Hess, Froman, & Biellier, 1982) and cholesterol (Hess & Thurston, 1982), as well as with increased frequency of abnormal sperm and spermatids (Thurston & Korn, 1997). Turkeys exhibiting YSS also show elevated plasma levels of the androgen 5α-dihydrotestosterone (DHT) and increased capacity to bind DHT in semen, but the mechanism that accounts for this increased binding capacity remains unresolved (Hess, Birrenkott, & Thurston, 1984). In one study androgen treatment of turkeys failed to induce YSS (Froman & Thurston, 1983), suggesting that androgen dysfunction was not responsible for the condition. The cause of YSS in turkeys is unknown, but most of the existing evidence points to a viral origin (Boltz et al., 2006; C. Boltz, D. Boltz, Bunick, Scherba, & Bahr, 2007; Villarreal et al., 2007).

Another condition affecting the epididymis of male birds is the formation of calcium stones, known as epididymal lithiasis, which can impair T and sperm production primarily by limiting testicular size (Janssen et al., 2000). These stones are thought to block the passage of sperm, leading to increased pressure in dilated seminiferous tubules and impaired spermatogenesis. The factors that cause calcium stones have not been identified. Birds with such stones exhibit reduced fertility even after artificial insemination using equal amounts of sperm from birds with and without stones. Thus, epididymal stones may impair specifically sperm maturation (Janssen et al., 2000). The formation of stones has been linked to the avian infectious bronchitis virus (Boltz et al., 2006; 2007; Villarreal et al., 2007).

In a couple of captive species, testicular tumors have been reported as neoplasms of the Sertoli cells (Gorham & Ottinger, 1986; Rossi, Ceccherelli, Piersigilli, & Tarantino, 2003), which likely impairs male fertility. The occurrence of Sertoli cell tumors in birds is thought to be rare, but has been documented in Passeriformes (Rossi et al., 2003), Galliformes (Gorham & Ottinger, 1986), Psittaciformes (Beach, 1962), and Columbiformes (Turk, Kim, & Gallina, 1981). In the Gouldian finch (*Erythrura gouldiae*), testicular neoplastic tissue was associated with a polyomavirus (Rossi et al., 2003), but in most cases the cause was unknown. Little research has been done that addresses how specific diseases impact testicular function in captive or wild species, even though this topic is of considerable importance to the poultry industry and to investigators interested in the captive breeding of rare species.

9. ANTHROPOGENIC EFFECTS ON TESTICULAR FUNCTION

9.1. Introduced Species

Some successful invasive/introduced species, such as the European starling (Dawson & Goldsmith, 1982; Dawson,

1983; Young et al., 2001; Dawson & Sharp, 2007) and house sparrow (Hegner & Wingfield, 1986; Anderson, 2006; Trivedi, Rani, & Kumar, 2006), are also among the best-studied species in avian physiology. Other species, such as the rock pigeon, have been less studied, but have been noted to breed year-round, despite some evidence for photoperiodic influence on testicular function (Johnston, 1992; Ramachandran, Patel, & Patel, 1996). Overall, little research has been done on differences in testicular cycles that may exist between the invasive, introduced, and native ranges of any species. Indirectly, based on captive studies on birds from both native and introduced populations, there is little evidence for drastic differences in annual testicular development (Dawson & Goldsmith, 1982; Dawson, 1983; Young et al., 2001). Whether introduced species alter their testicular cycle to adapt to local environmental conditions or whether only species with cycles similar to those of local native species adapt successfully is not known and warrants new studies.

A major question of interest to wildlife managers is why some species are more successful colonizers than others. For example, house sparrows have spread throughout the world following multiple introductions, whereas congeneric Eurasian tree sparrows (*Passer montanus*) have not spread far beyond their North American initial release area (St. Louis & Barlow, 1988; Lang & Barlow, 1997). Factors other than the flexibility of the testicular cycle, the number of birds released, the number of releases, and the ability to exploit urban resources (see Section 9.3) may contribute to determining the success of introduced species. New studies are warranted to compare species that differ with regard to their capacity for invasiveness and their ability to breed in human-modified environments. Research on this subject may provide valuable information on how to manage the potentially damaging effects of invasive species on native wildlife and may improve our understanding of how reproductive flexibility influences adaption to novel environmental conditions.

9.2. Climate Change

Global climate change has the potential to profoundly affect factors that birds utilize to time their reproductive development. However, to our knowledge, no research on the direct effects of climate change on testicular function has been conducted. In the recent past, the average breeding dates of many bird species have advanced by a few days to over a week from historic breeding dates (generally established by long-term studies of species populations), presumably as a result of ambient temperature increases (Jarvinen, 1989; Crick, Dudley, Glue, & Thomson, 1997; Both, Bijlsma, & Visser, 2005; Pearce-Higgins, Yalden, & Whittingham, 2005; Torti & Dunn, 2005) and the subsequent earlier availability of insect

food sources (e.g., Visser, Holleman, & Gienapp, 2006). As global climate changes continue, the degree to which birds will be able to adapt the phenology of their annual cycle to new environmental conditions is not known. The long-term effects of changes in ambient conditions also are hypothetical. Intraspecific variation in the timing of testicular development in captive-bred (Bentley et al., 2003; Hurley et al., 2008) and free-ranging birds originating from different areas of their range have been observed (Figure 2.3). These findings suggest that within species some flexibility exists with respect to the cues used to regulate reproduction. However, the evolutionary time course for these adaptations is unclear and may be insufficient to cope with the drastic pace of current and
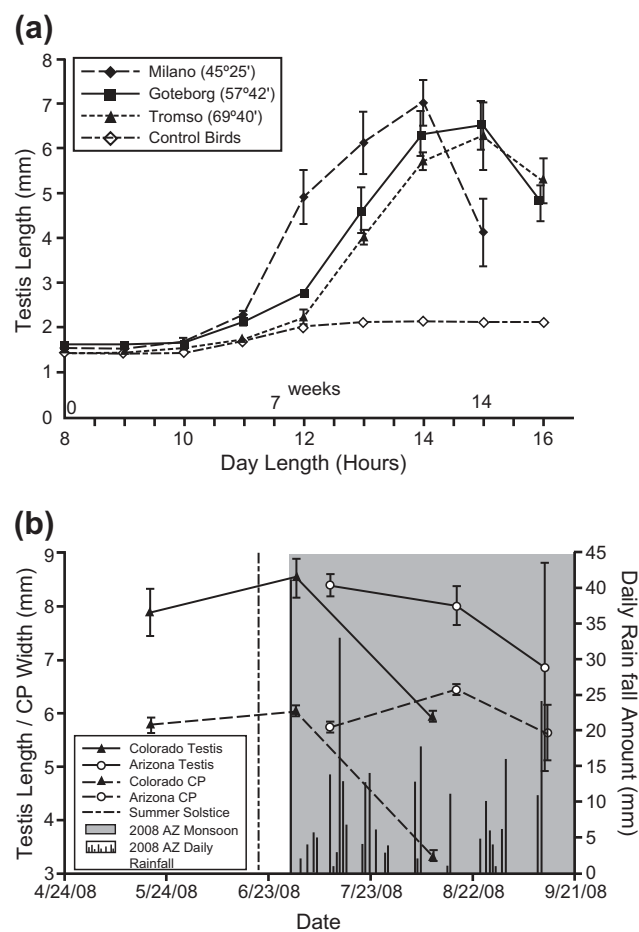

FIGURE 2.3   Intraspecific variation in photoinduced testicular development. (a) Testicular development in captive great tits (*Parus major*) from three sedentary populations at varying latitudes as a function of photophase. Birds were photostimulated by increasing day length 30 minutes weekly for 16 weeks, starting at 8L : 16D. Control birds remained exposed to 8L : 16D and all birds were maintained at 20°C. *Adapted with permission from Silverin et al., 1993.* (b) Development of testes and cloacal protuberance (CP) (mm) in two geographically separate populations of free-ranging Cassin's sparrows (*Aimophila cassinii*) during the 2008 breeding season. *From L.L. Hurley, unpublished observations.* Values are means ± standard error (SE).

projected climate change (Dawson, 2008; Gienapp, Teplitsky, Alho, Mills, & Merilä, 2008). Research on the impact of climate change on reproductive physiology is urgently needed to answer these questions.

9.3. Direct Human Impact—Endocrine Disruption and Urbanization

In many regions of the earth, the natural landscape has been heavily impacted by humans in terms of land use (e.g., farming and urbanization) and as a result of the release of pollutants (e.g., chemicals or light) into the environment. A plethora of studies have investigated how these impacts influence avian reproduction. One major area of this research is the influence of xenobiotic (man-made) substances introduced into the environment through agriculture and industry and that mimic the actions of phytoestrogens or endogenous hormones (endocrine-disrupting chemicals). Most work on this topic has involved administering these chemicals *in ovo* or after hatching and then determining the effects of the treatments on reproductive development, behavior, fertility, and nesting success (Adkins, 1975, 1978; Adkins-Regan & Ascenzi, 1987; Millam et al., 2001). In male zebra finches, early post-hatch treatment with estradiol benzoate can reduce fertility due to lowered sperm aggregation, decreased sperm density, and alterations in seminiferous tubule organization (Figure 2.4). This treatment can also lead to oviduct formation in males during development (Wade, Gong, & Arnold, 1997). Males exposed to low doses of xenobiotic compounds still display stereotypical courting and mating behaviors, but those given higher doses exhibit female parental behavior and hatch fewer young than control birds (Millam et al., 2001; Rochester, Heiblum, Rozenboim, & Millam, 2008). These findings suggest that xenobiotic chemicals mimic endogenous hormones and are capable of disrupting normal endocrine function, resulting in decreased male fertility (Millam, 2005). If the same applies to free-ranging avian populations, these populations could be affected negatively. A broader discussion of endocrine-disrupting chemicals in birds is found in Chapter 9 of this volume.

Urbanization also has the potential to have a major impact on avian populations. As urban landscapes expand and encroach on native habitats, they alter many components of the environment, resulting, in a decrease in native vegetation, an increase in exotic plant and animal species, an alteration of food types and their availability, exposure to a great variety of anthropogenic chemicals, and exposure to artificial lights and increased ambient temperatures (Schoech, Bowman, Bridge, & Boughton, 2007; Schoech & Hahn, 2007; Robb, McDonald, Chamberlain, & Bearhop, 2008; Fokidis, Orchinik, & Deviche, 2009). Changes

in native landscapes also impact parasite and disease risks (Ruiz, Rosenmann, Novoa, & Sabat, 2002; Fokidis, Greiner, & Deviche, 2008) and physiological responses to acute stress (Ruiz et al., 2002; Schoech et al., 2007; Fokidis et al., 2009; see also Chapter 5, this volume). Several studies have demonstrated that urbanization is associated with a seasonal shift of breeding dates (European blackbirds (*Turdus merula*) (Partecke, Van't Hof, & Gwinner, 2004; 2005); Florida scrub jays (*Aphelocoma coerulescens*) (Schoech et al., 2007); curve-billed thrasher (*Toxostoma curvirostre*) (Fokidis, unpublished data)) and gonadal development (Figure 2.5). The drastic environmental changes outlined above have great potential to alter the specific cues that birds use to time their testicular development. Research on this topic may help us understand how birds adapt to urbanization by changing their use of environmental factors that control reproductive cycles.

10. CONCLUSIONS AND FUTURE DIRECTIONS

Investigations conducted in the past half-century have informed us about many aspects of avian testicular functions. As a result, considerable information is available on the environmental control of testicular function, including the influence of day length and other abiotic factors such as temperature and food availability; the mechanisms by which photic information, in particular, is integrated by the brain and used to regulate seasonal testicular cycles; the regulation of sperm formation and testicular steroidogenesis; and the mode of action of a wide and ever-expanding variety of paracrine and other chemical mediators on testes. In addition, birds have become choice experimental models for research related to sperm competition, effects of acute and chronic stress on the male reproductive system, and the influence of intraspecific social interactions on the secretion of testicular androgens.

Despite this progress, large gaps remain in our understanding of avian testicular function and its regulation. This is partly due to the fact that most work on this topic has used either captive or domesticated species. Thus, large groups of birds, in particular those inhabiting tropical and equatorial regions, where most of the global diversity in avian species is present, remain essentially unstudied. This situation may, however, improve in the near future as an increasing number of physiologists focus their attention on the control of reproduction in birds inhabiting these regions.

A particularly promising area for future research concerns the effects of global climate changes and urbanization on testicular function. Global climate changes are already impacting avian populations, and the rapid
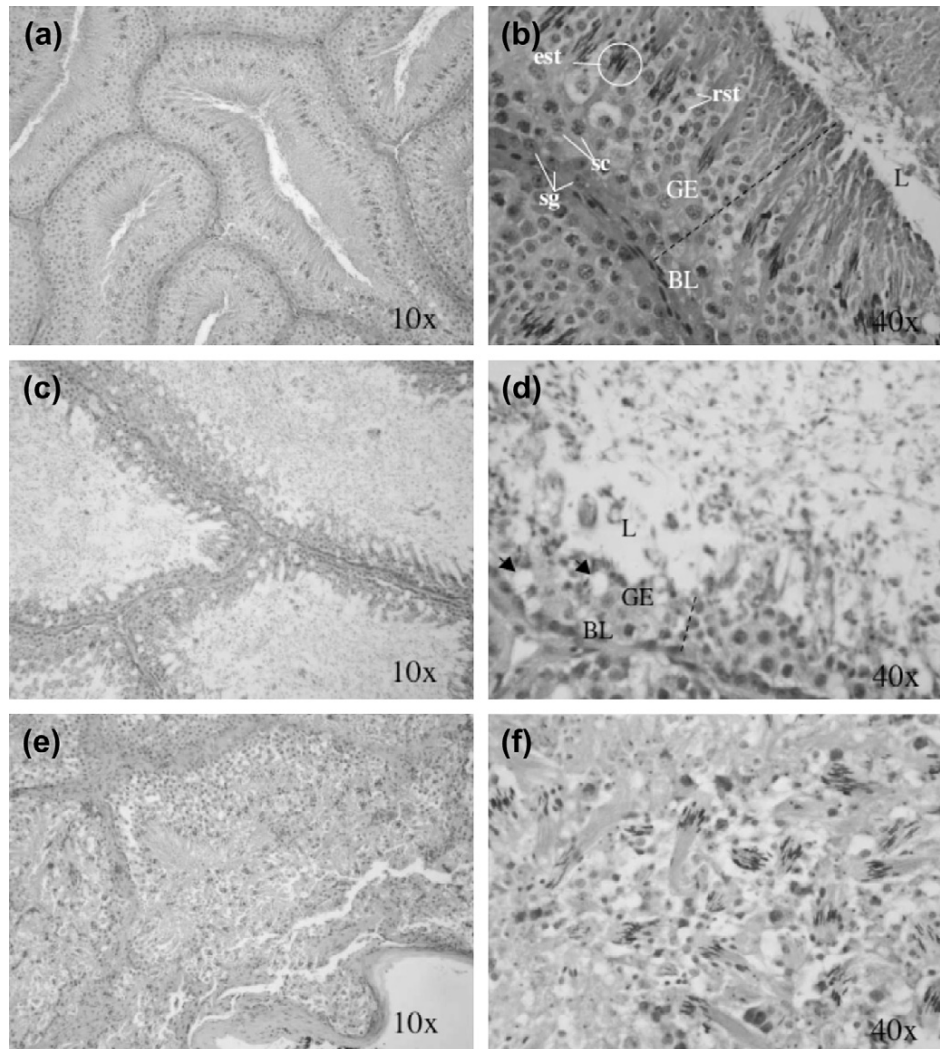
FIGURE 2.4   Testicular disruption resulting from postnatal estradiol benzoate treatment in the zebra finch. The figure shows representative photomicrographs of testicular sections from adult male zebra finches treated from post-hatch days 5 to 11 with 10 (EB10) or 100 (EB100) nmol/g body weight estradiol benzoate or control canola oil. (a and b) Testicular morphology in a control male. Note the orderly progression of spermatogenesis development through the germinal epithelium (GE), from spermatogonia (sg) near the basal lamina (BL) to primary spermatocytes (sc); the spermatids (est, elongated spermatids; rst, rounded spermatids) near the lumen (L); and the normal thickness of the germinal epithelium (dotted line). (c and d) Testicular morphology in an EB100 male. Note the thinner germinal epithelium and lumen containing a large matrix of developing sperm cells. Black arrows denote vacuoles. (e and f) Testicular morphology in an EB10 male. Note the absence of laminarity and lumen. *Reprinted from Rochester, Forstmeier, and Millam (2010), with permission.*

urbanization that is taking place in many regions of the world is having severe detrimental effects on natural ecosystems. These effects are thought to result from many factors including direct habitat alterations; the release into the environment of endocrine disruptors and pollutants; and, in some cases, the development of urban microclimates It is likely that at least some of these factors—in particular endocrine disruptors, pollutants, and locally altered enviroments—influence testicular function directly or indirectly, but whether and the extent to which this is the case is not well known. We also have a poor understanding of the specific mechanisms involved and the relative

sensitivity of various avian species to these factors. Short- and long-term studies that address these questions are consequential because they may shed light on the resiliency of bird communities to anthropogenic disturbances and, thus, also on the extent to which these communities will be affected by future climate change and urbanization.

Research on the above and related topics will likely be most beneficial if it combines work on some already well-studied domesticated and free-ranging species with new studies, using a primarily comparative perspective. Along with our already vast knowledge on the subject, this research has the potential to serve as a focus point for work
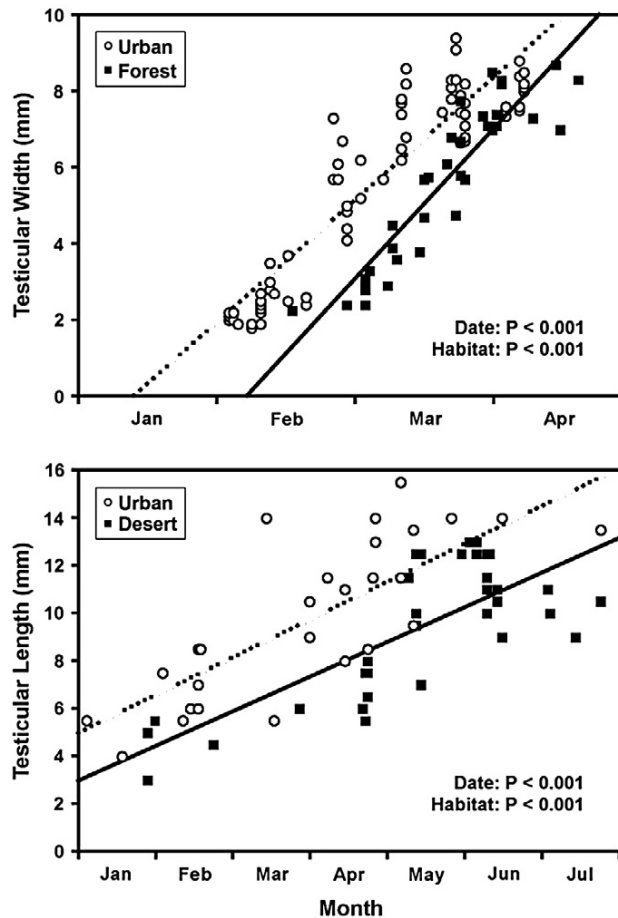
FIGURE 2.5 (upper panel) Seasonal change in testicular width of free-ranging European blackbirds (*Turdus merula*) sampled in an urban (open circles) and forest (filled squares) environment in Germany. *Adapted from Partecke, Van't Hof, and Gwinner (2005), with permission.* (lower panel) Seasonal change in testicular length of free-ranging curve-billed thrashers (*Toxostoma curvirostre*) sampled in Phoenix, Arizona (urban, open circles) and in the surrounding Sonoran Desert (rural, filled squares). *From H.B. Fokidis, unpublished data.* Each panel shows linear regression lines for each sampled population and each point represents one individual.

at multiple levels of organization—from molecular to the whole organism in its environment—and that integrates concepts drawn, among others, from population biology, ecology, ethology, physiology, genetics, immunology, and neuroscience.

ABBREVIATIONS

17β-HSD	17β-hydroxysteroid dehydrogenase
3β-HSD	3β-hydroxysteroid dehydrogenase
ABP	Androgen-binding glycoprotein
AMH	Anti-Müllerian hormone
AND	Androstenedione
cAMP	Cyclic adenosine 3',5'-monophosphate

CBG	Corticosteroid-binding globulin
CORT	Corticosterone
D-Asp	D-aspartate
DHT	5α-dihydrotestosterone
FSH	Follicle-stimulating hormone
GH	Growth hormone
GnIH	Gonadotropin-inhibiting hormone
GnRH	Gonadotropin-releasing hormone
GTH	Gonadotropin
IGF	Insulin-like growth factor
LH	Luteinizing hormone
MEL	Melatonin
NAD⁺	Nicotinamide adenine dinucleotide
NADH	Reduced nicotinamide dinucleotide
NO	Nitric oxide
P450$_{aro}$	Aromatase enzyme
PRL	Prolactin
PRL-R	Prolactin receptor
SHBG	Sex hormone-binding globulin
SST	Sperm storage tubule
T	Testosterone
T$_3$	Triiodothyronine
T$_4$	Thyroxine
TSH	Thyrotropin
VIP	Vasoactive intestinal peptide
YSS	Yellow semen syndrome

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