C. Reproductive

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INTRODUCTION

The reproductive anatomy and function of raptors have attracted little attention to date. Basic information, such as the presence and location of sperm-storage tubules and the duration of the fertile period, is still unknown for most species. This paucity of knowledge not only acts as a limiting factor for improved reproductive success in captive breeding programs, but also renders it more difficult to understand the reproductive ecology of wild raptors.

The increasing number of endangered raptor species is being accompanied by a growing interest in their biomedicine and captive propagation. More raptors are coming under the scrutiny of microscopes and modern laboratory techniques, and we hope that this will spark a greater interest in resources and research dedicated to studying reproductive physiology of birds of prey. Meanwhile, readers should consult the limited available studies undertaken in various species used as models, such as the American Kestrel (*Falco sparverius*) (Bird and Buckland 1976, Bakst and Bird 1987), the general review on raptor physiology by Duke (1986), as well as those on the reproductive systems of domestic birds (Johnson 2000, Kirby and Froman 2000) and wild birds (Gee et al. 2004, Samour 2004).

FEMALE REPRODUCTIVE SYSTEM

Reproductive Tract

Ovaries, follicular growth, and ovulation. Unlike the majority of birds, raptors commonly have two functional ovaries (Domm 1939). The phenomenon has been recorded in many species of raptors (Venning 1913, Wood 1932, Boehm 1943, Snyder 1948), but seems more prevalent in accipiters than in Strigiformes (Fitzpatrick 1934).

When growing follicles, females experience a significant increase in body weight. Inability to accomplish this gain may prevent full ovarian growth and egg-laying (Newton 1979, Hardy et al. 1981). Recent studies of Barn Owls (*Tyto alba*) indicate that the onset of reproduction is not triggered by body condition (i.e., an increase in body fat). In fact, the perceived increase in body weight prior to breeding is more likely due to water accumulation as a result of changes in protein metabolism (Durant et al. 2000). Interpretation of the "need" to put on extra body fat as an energy-safe strat-

egy ought to be reconsidered. The rapid growth phase of follicles usually takes 5 to 14 days, during which follicles highest in the growth hierarchy incorporate vitellogenin and low-density lipoprotein in an estrogen-receptor mediated event. In the Golden Eagle (*Aquila chrysaetos*), total fecal estrogen levels progressively increase during the rapid growth phase (Staley 2003), presumably in relation to the increasing activity of the external theca cells of prehierarchal follicles.

Similar to other birds (Wingfield and Farner 1978, Johnson 2000), ovulation of the first egg in Peregrine Falcons (*F. peregrinus*), Golden Eagles, and Asian Imperial Eagles (*A. heliaca*) takes place soon after the estrogen maximum, and coincides with a peak of progesterone and cortisol (J. Blanco, unpubl. data). Both serum luteinizing hormone (LH) and progesterone also peak early in ovulation.

Oviduct. Similar to what has been described for other birds (Gee et al. 2004), the raptor oviduct consists of five distinguishable regions: infundibulum, magnum, isthmus, shell gland, and vagina. The size and mass of the oviduct increase parallel to the ovary early in the breeding season, as regulated by steroid hormones. The presence of sperm storage tubules at the uterovaginal region is poorly documented in raptors. These microscopic structures in the folds of the cervix mucosa have been observed in the American Kestrel (Bakst and Bird 1987; Fig. 1) and in other raptor species (Blanco 2002). These tubules determine the fertile period by maintaining sperm viability and continual release to the site of fertilization.

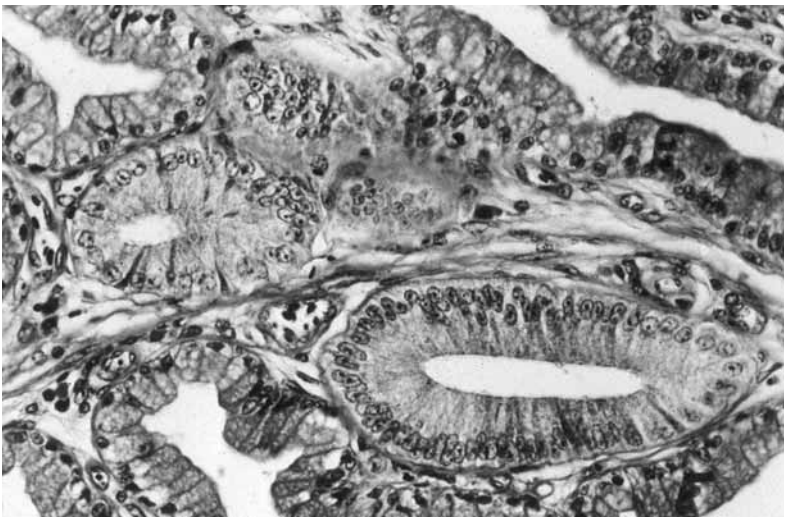

Figure 1. Sperm storage glands were first discovered in American Kestrels (*Falco sparverius*) and are likely found in most other raptors.

Eggs

Egg physiology and variation in eggshell and membrane characteristics. After ovulation the ovum is engulfed by the infundibulum (the site of fertilization), and next descends through the oviduct. The process usually lasts for two or more days, depending on the size of the birds, and involves the addition of numerous layers that conform to the egg. Cuticle, crystallization layers (external, palisade, and mammilary) and eggshell membranes can be differentiated easily in the eggs of raptors. The morphology and size of eggshell pores vary among species (Blanco 2001) and, together with the outer crystallization layer, may be of taxonomic interest.

Falconiformes have been reported to produce more massive eggs than Strigiformes of similar body size (Saunders et al. 1984). Interestingly, body mass is positively correlated with egg width in free-ranging Eleonora's Falcon (*F. eleonorae*) (Wink et al. 1985) and Black Kites (*Milvus migrans*) (Viñuela 1997), but not in captive American Kestrels (Bird and Laguë 1982a). Both inter-annual and intra-seasonal variation in egg-laying dates have been recorded in both captive and free-ranging populations of Peregrine Falcons (Burnham et al. 1984) and Golden Eagles (Blanco 2001), with a significant decrease in length, breadth and initial mass with time.

Certain external factors including stress (Hughes et al. 1986), ambient electromagnetic fields (Fernie et al. 2000a), organochlorine compounds and metabolites (for review see Hickey and Anderson 1968, Ratcliffe 1970, Cooke 1979, Wiemeyer et al. 2001, Chapter 18), heavy metals (Ohlendorf 1989, Blanco 2001), and PCBs (Lowe and Stendell 1991, Fernie et al. 2000b) can induce shifts in eggshell thickness and ultrastructure, as well as in ultrastructure and fiber organization and pattern of the shell membrane.

Clutch size and replacement. Clutch size often is influenced by phylogeny and individual factors including size and age (Brommer et al. 2002). From a global perspective, the number of eggs laid varies latitudinally in some falcons in Australasia (Blanco 2001), as well as longitudinally in several eagles and *Milvus* kites in that region (Olsen and Marples 1993).

The ability to replace clutches has been used as a management tool (see Chapter 23) to augment both captive and wild populations of raptors (Bird and Laguë 1982a). In captive and wild American Kestrels, replacement clutches had fewer eggs than first clutches, but did not differ in fertility, hatchability, and fledging success (Bird and Laguë 1982a,b; Bowman and Bird 1985).

MALE REPRODUCTIVE SYSTEM

Paired reproductive tracts in male birds of prey lie along the dorsal body wall and consist of a testis, epididymis, and a straight ductus deferens, which differs from the highly convoluted version found in some domestic species (J. Blanco, unpubl. data). Spermatogenesis depends on follicle-stimulating hormone (FSH), testosterone, the activity of Sertoli cells and their interaction with the spermatogonial stem cells. Seasonal testicular growth usually takes up to 45 days in the majority of raptor species, a period longer than ovarian growth in the female. FSH and LH, as well as testosterone, are essential for spermatogenesis. The process of spermiogenesis, and the duration of the transport through the excurrent ducts are unknown, but it is clear that fluid is absorbed to concentrate sperm and to become seminal plasma. Seminal plasma differs from blood plasma in electrolyte and protein composition (J. Blanco, unpubl. data). The importance of this process is not well understood, but is likely related to sperm motility more than fertilizing ability, since testicular sperm are able to penetrate the inner periviteline membrane *in vitro*.

Male Gametes

Semen production period, seminal quality, and factors of influence. Semen production period varies among species and individuals, but usually last for nearly three months. Bird and Laguë (1977) described an average period of 74 days for captive American Kestrels with a maximum of 103 days. Longer periods were found for Peregrine Falcons (95 days; Hoolihan and Burnham 1985) and eagles (up to 110 days; Blanco 2002).

Semen production in American Kestrels held in Montreal, Canada begins at about 12 hours and 45 minutes of daylight, and declines considerably at about 15 hours and 45 minutes (Bird and Buckland 1976).

Ejaculate characteristics vary greatly among species and individuals, and with collection method (Bird and Laguë 1976, Boyd et al. 1977, Weaver 1983), male reproductive condition, nutrition (Randal 1994), certain pollutants (Bird et al. 1983) and climate (Bird and Laguë 1977). Concentrations ranging from 31,000 to 40,000 spermatozoa per mm^3 and volumes between 3 and 14.6 µl have been reported for the American Kestrel (Bird and Buckland 1976, Bird and Laguë 1977, Brock 1986). Expectedly, ejaculate volume increases with species size. Semen volume in Peregrine Falcons can be as high as 95 µl (Hoolihan and Burnham 1985), with cell concentrations ranging from 26,000 to 81,000 sperm per µl.

Sperm production varies seasonally; sperm concentration increases early during the breeding season, peaks in mid-season, and declines thereafter. This pattern varies longitudinally. Numbers of spermatogonia, spermatids and abnormal spermatozoa are more likely to be present in the ejaculate both early and late in the season when testes are no longer at their maximum size and when testosterone levels are lower than normal. This is related to the need to ensure maximum sperm quality at the time of maximal frequency of copulation prior to egg laying (Blanco et al. 2002).

Urine contamination of semen and subsequent sperm damage is frequent during collection using forced-massage techniques (Bird and Laguë 1977). Fox (1995) provides a useful description, including an illustration of the various contaminants in raptor semen. The use of modified dilutents may help reduce deleterious effects (Blanco et al. 2002). *Escherichia coli* is the most prevalent bacteria contaminating raptor semen. Samples need to be evaluated with caution before artificial insemination to avoid the risk of ascendant salpingitis (Blanco and Höfle 2004).

Artificial insemination. Artificial insemination with fresh semen has been successful in a variety of non-domestic avian species including raptors. This technique has been used as a management tool in several captive breeding projects using fresh diluted semen (Temple 1974, Samour 1986). In the American Kestrel, fertility rates using artificial insemination are similar to those achieved by natural mating (Bird et al. 1976).

Sperm cryopreservation. Semen collected by massage techniques has been cryopreserved and progeny obtained in several species (Gee 1983, Gee et al. 1985, Brock 1986, Parks et al. 1986, Samour 1988, Gee and Sexton 1990, Brock and Bird 1991, Knowles-Brown and Wishart 2001, Wishart 2001). Comparative studies on sperm tolerance to different osmotic conditions, cryoprotectant concentrations and cooling rates indicate considerable variation, even between closely related raptor species (Blanco et al. 2000). Different freezing rates and protocols are described in Brock et al. (1983) and Knowles-Brown and Wishart (2001).

Glycerol and the alternatives, dimethyl sulphoxide (DMSO) and dimethyl acetamide (DMA), have been used widely in sperm cryopreservation in non-domestic species. Sperm from the falcon type (Brock and Bird 1991, Gee et al. 1993) have been successfully cryopreserved using either 13.6% glycerol; 6%, 8%, or 10%

DMSO; or 13.6% DMA. Evaluation of fertilizing ability has been mostly based on progressive motility and fertility after artificial insemination (Gee et al. 1985, Brock and Bird 1991, Gee et al. 1993). In the American Kestrel, motility after thawing averaged 41% and 13% using glycerol and DMA, respectively (Brock and Bird 1991). Post-thaw fertility rates have been obtained following artificial insemination using glycerol as cryoprotectant in the Peregrine Falcon (33.3%) (Parks et al. 1986) and the American Kestrel (11.8%) (Brock and Bird 1991).

Photoperiodism, Reproductive Hormones, and Endocrine Disruptors

The influence of photoperiodism on levels of gonadal hormones in birds generally is well understood, but most of our knowledge of this phenomenon in raptors is based on the use of artificial lighting to induce reproductive activity in captive pairs (Willoughby and Cade 1964, Bird et al. 1980). We know nothing about natural circadian rhythms in raptors, but data collected on other bird families are likely relevant and applicable.

Nelson (1972) and Swartz (1972) were among the first to elucidate the need for photoperiodic stimulation to induce northern-nesting raptors like Gyrfalcons (*F. rusticolus*) and Peregrine Falcons to breed in captivity (i.e. the farther north they originate from, the longer the photoperiod they require). If extra day-length in the form of artificial lighting is to be used, the changes in day-length should be made as gradually as possible to reduce physiological shocks (Bird 1987). At least one successful attempt using artificial photoperiodic changes has been made to induce American Kestrels to undergo an out-of-season breeding period between two consecutive successful spring breeding periods (Bird et al. 1980). An attempt to hasten sexual maturity in kestrels using photoperiod encountered mixed success (Ditto 1996). Such procedures could be used to increase the output of offspring in endangered species breeding programs or to accelerate the turnover of data in experimental research involving captive raptors.

The vast majority of our knowledge about raptor reproductive endocrinology has relied upon blood sampling and plasma-hormone determinations. In the female, plasma corticosterone, progesterone, estradiol 17β and estrone are highest during courtship and egg laying (Rehder et al. 1984, 1986), whereas high levels of androgens, including testosterone, were associated with aggression, territoriality, courtship, nest-building, testicular development, and spermatogenesis in the male (Temple 1974; see also Rehder et al. 1988). Information on plasma levels of lutenizing hormone in American Kestrels can be found in Ditto (1996). More recently, fecal steroid monitoring, which has been used to study seasonality in hormone levels (Bercovitz et al. 1982), the effects of human disturbance (Wasser et al. 1996), steroid excretion lag time (Wasser et al. 1996), and sex determination (Bercovitz and Sarver 1988), shows potential as a safe non-invasive source of information regarding hormone levels.

Exposure to extreme temperatures can limit avian reproduction (Mirande et al. 1996). Drastic temperature fluctuations often reduce semen production (Kundu and Panda 1990), as well as egg-laying and copulation frequency (Bluhm 1985).

The impacts of organochlorine chemicals on reproduction of birds of prey have been well documented (see Chapter 18). Studies indicate that these chemicals also act as endocrine disruptors. For instance, preliminary data by Bowerman et al. (2003) suggest that hormone disruptors, not necessarily estrogen or androgen mimics and their antagonists, are associated with reproductive and teratogenic effects in Bald Eagle (*Haliaeetus leucocephalus*) populations in the Great Lakes Basin. Alterations in reproductive behavior in captive breeding American Kestrels were induced by exposure to Dicofol, one of the last organochlorine pesticides to be banned from use in the U.S. (MacLellan et al. 1996). Other organochlorine chemicals that impact upon reproduction in birds of prey through hormone disruption come in the form of industrial by-products and include polychlorinated biphenyl ethers (PCBs). Captive American Kestrels exposed to PCBs developed more frequent aggressive courtship interactions and experienced clutch abandonment (Fernie et al. 2003); alterations in brood patches also have been observed in PCB-exposed kestrels (Fisher et al. 2006). Most recently, attention has focused on the alarming increase in residue levels of polybrominated diphenyl ethers (PBDEs) in food chains world-wide, arising from the use of brominated flame retardants applied to many household products (Chapter 18). Using the American Kestrel as a model test species, a number of reproductive effects have been documented thus far (cf. Fernie et al. 2006).

SUMMARY

Captive-propagation programs have been extremely useful in maintaining genetic diversity and restoring

wild populations of endangered raptors. However, captive breeding success requires knowledge of a species' reproductive behavior, physiology and endocrinology. In addition, species-specific differences in anatomy, gamete or physiological parameters may complicate the task of maintaining captive breeding populations of raptors. Further research is needed to unravel some of the major questions including the spatial requirements and factors involved in the control of reproduction in endangered raptors. Finally, an improved knowledge of the reproductive physiology of raptors will help us better understand the impacts of chemicals released into their environment on their reproduction and, ultimately, their survival.

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