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THE EFFECTS OF ELECTROMAGNETIC FIELDS FROM POWER LINES ON AVIAN REPRODUCTIVE BIOLOGY AND PHYSIOLOGY: A REVIEW

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Electrical power lines are ubiquitous in the developed world and in urban areas of the developing world. All electrical currents, including those running through power lines, generate electric and magnetic fields (EMFs). Electrical power lines, towers, and distribution poles are used by birds for perching, hunting, and nesting. Therefore, many bird species, like humans, are exposed to EMFs throughout their lives. EMFs have been implicated in adversely affecting multiple facets of human health, including increasing the risks of life-threatening illnesses such as leukemia, brain cancer, amyotrophic lateral sclerosis, clinical depression, suicide, and Alzheimer's disease. A great deal of research and controversy exists as to whether or not exposure to EMFs affects the cellular, endocrine, immune, and reproductive systems of vertebrates. Laboratory work has used mice, rats, and chickens as models for this EMF research in an effort to understand better the possible implications of EMF exposure for humans. However, EMF exposure of wild birds may also provide insight into the impacts of EMFs on human health. This review focuses on research examining the effects of EMFs on birds; most studies indicate that EMF exposure of birds generally changes, but not always consistently in effect or in direction, their behavior, reproductive success, growth and development, physiology and endocrinology, and oxidative stress under EMF conditions. Some of this work has involved birds under aviary conditions, while other research has focused on free-ranging birds exposed to EMFs. Finally, a number of future research directions are discussed that may help to provide a better understanding of EMF effects on vertebrate health and conservation.

Power lines carrying high-voltage electricity are ubiquitous in the developed world and in urban areas of many developing countries. For example, as of 1999, Sweden had 220,000 km of power lines covering 450,000 km^2 while South Africa, the most developed African country, possessed 255,745 km of lines carrying electricity over 1,185,000 km^2 (Ferrer & Janss, 1999). Many kilometers of power lines will be established in the world over the next few decades, and the majority will run overhead, with underground installation being prohibitively expensive (£500,000 per km vs. £10 million per km respectively; National Grid web site, http://www.nationalgrid.com). In England and Wales, the relatively high costs of underground power-line installation are reflected in the paucity of underground lines constituting the transmission system (Table 1).

Similar to every device that carries an electric current, power lines generate electric and magnetic fields that are collectively called electromagnetic fields (EMFs). Electric fields are measured in kilovolts per meter (kV/m) and magnetic fields in microteslas (μT). Studies by Hydro-Québec, a Canadian power company, found that the ambient magnetic field produced by all electric currents flowing inside and outside a Canadian home ranges from 0.01 to 1 μT, while household appliances alone may generate magnetic fields of up to 4 μT (Hydro-Québec, 1989). The strength of the electric and magnetic fields depends upon the current intensity carried through a conductor and the distance of exposure from the source. Both fields are highest immediately around a power line and diminish

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TABLE 1. Electricity Transmission Network in England and Wales as of the End of 2003, Defined by Lengths of Power Lines (km) of Different Voltage and Underground Versus Overhead Installation

Voltage (kV)	Overhead	Underground
400	10,223	132
275	3,484	425
≤132	199	70
Total coverage (km)	13,906	627

Note. Data from National Grid web site: http://www.nationalgrid.com/uk/library/documents.

rapidly with distance away from the source. In North America, the maximum voltage of alternating current power lines is 735 kV and their respective electric and magnetic fields are 10 kV/m and 60 μT at 0 m; 6 kV/m and 35 μT at 20 m; and 2 kV/m and 14 μT at 40 m from the power line. However, direct-current power lines in North America are much larger with stronger EMFs; the Pacific Northwest Intertie, a power line of critical importance in distributing power throughout the western United States, carries hydroelectric power at 1150 kV DC. Currently, in Canada an 80-m-wide exclusion zone exists around each power line, within which residential homes are not built (Hydro-Québec, 1989).

The debate rages about potential risks of EMFs to public health (NIEHS, 1999). Among more than 7,000 scientific publications about the potential effects of EMF exposure, an extensive number of reviews have been written relating to EMF exposure and human health (Brainard et al., 1999; NIEHS, 1999; Preece et al., 2000). Controversy exists about studies that have found that EMFs increase the risks of life-threatening illnesses such as childhood (London et al., 1991) and adult (Bastuji-Garin & Zittoun, 1990) leukemia, adult brain cancer (Harrington et al., 1997), and amyotrophic lateral sclerosis (Johansen & Olsen, 1998), a neurodegenerative disease also known as Lou Gehrig's disease, as well as clinical depression (Verkasalo et al., 1997), suicide (Reichmanis et al., 1979), and Alzheimer's disease (Sobel et al., 1996). The findings of recent studies are also indicative of indirect effects of power lines, further adding to the concern about power lines and mammalian health. Corona ions generated by the electric fields of power lines may increase the concentrations and deposition of particles and other environmental pollutants (Fews et al., 1999; Henshaw, 2002). Exposure to static magnetic fields altered a number of functional parameters of immune cells, particularly macrophages, spleen lymphocytes, and increased apoptosis of thymic cells (Flipo et al., 1998).These studies, along with other recent findings, have sharpened the focus even more on the potential dangers of EMFs to public health, and they may result in considerable pressure on governments to ban the building of new homes within prescribed distances of high-voltage power lines.

Studies showed that EMFs influence the development, reproduction, and physiology of insects (Greenberg et al., 1981) and mammals (Burchard et al., 1996), but the purpose of this review is to consider the breeding biology of a taxon (i.e., birds) that lives most intimately with power lines and therefore exposed to EMFs. There are numerous examples of the detrimental effects of power lines (Bevanger, 1998) in terms of birds that die through collision (Bevanger, 1990; Savereno et al., 1996) or electrocution (Ledger & Annegarn, 1981; Ferrer et al., 1991). Birds can seriously disrupt the supply of electricity through (1) short-circuits caused by electrocutions, (2) the accumulation of droppings, and (3) material delivered to nests. Successful measures have been taken to reduce the frequency of outages and the concurrent mortality of birds at those sites where electricity pylons pose the most risk (Manosa, 2001). Such measures include the reconfiguration of cross-arms, conductors, and power lines (Olendorff et al., 1981), and deterring birds from approaching wires using colored plastic spirals and balls (Alonso et al., 1994) and raptor models (Janss et al., 1999). Birds can be kept away from conducting wires at transmission towers by employing plastic sheaths and by providing platforms above wires where birds can perch and nest (Bayle, 1999).

Despite the risks to birds posed by transmission towers carrying power lines, they are also beneficial to birds by providing substrate on which birds can perch, roost, and nest (Steenhof et al., 1993) and

TABLE 2. Bird Species Nesting on Electricity Transmission Towers

Latin name	Common name	Reference
Aquila chrysaetos	Golden eagle	Steenhof et al. (1993)
Aquila verreauxii	Verreaux's eagle	Ledger et al. (1987)
Bubo virginianus	Great-horned owl	Steenhof et al. (1993)
Buteo jamaicensis	Red-tailed hawk	Steenhof et al. (1993)
Buteo regalis	Ferruginous hawk	Gilmer and Wiehe (1977)
Ciconia ciconia	White stork	Navazo and Roig (1997)
Corvus corax	Raven	Steenhof et al. (1993)
Falco biarmicus	Lanner falcon	Kemp (1993)
Falco mexicanus	Prairie falcon	Roppe et al. (1989)
Falco peregrinus	Peregrine falcon	Emison et al. (1997)
Falco sparverius	American kestrel	Fernie et al. (2000a)
Gyps africanus	African white-backed vulture	Ledger and Hobbs (1985)
Myiopsitta monachus	Monk parakeet	Hyman and Pruett-Jones (1995)
Pandion haliaetus	Osprey	Castellanos et al. (1999)
Polemaetus bellicosus	Martial eagle	Dean (1975)

from which birds can hunt. For the most part, birds that are only transiently associated with power lines sustain limited exposure to EMFs. Yet many birds that nest on transmission towers in close proximity to power lines may be exposed to EMFs for protracted periods throughout a breeding season (e.g., over 3 mo) and over repeated breeding seasons (e.g., over 3 yr). Table 2 lists the bird species that are associated with power lines during breeding. Next, the effects of EMFs on various aspects of avian breeding biology are considered, specifically whether EMF exposure alters birds' behavior, reproductive success, growth and development, physiology, endocrine and immune systems, and oxidative stress. Oxidative stress has been implicated in cancer, neurodegenerative disease, and aging in humans. The directions in which future research should proceed are also discussed if studies of avian species nesting in close proximity to power lines are to contribute to our understanding of how EMFs affect physiological systems and the breeding biology of organisms. There is little doubt that such studies will also have direct implications for human health.

BEHAVIOR

The length of time to which birds are exposed to EMFs, and resulting behavioral changes, may have repercussions for the reproductive success, health, and survival of the individual bird, and, in turn, for the population. EMF exposure may be transient during the day or season, but may have more serious implications when birds are exposed to EMFs for extended periods like the breeding season. Changes in courtship or incubation behavior may adversely affect egg laying and/or hatching success. Only one study has examined bird behavior under EMF conditions, and changes in behavior were observed (Fernie et al., 2000a).

Fernie et al. (2000a) studied free-living American kestrels (*Falco sparverius* L.) in Québec, Canada, to estimate their exposure to EMFs during reproduction. Commonly, raptors in North America nest on platforms or in nest boxes on transmission towers and distribution poles that have been provided by electricity companies (Olendorff et al., 1981). For example, Steenhof et al. (1993) found that, within 11 yr of its construction, 133 pairs of raptors and ravens (*Corvus corax* L.) nested along a 500-kV transmission line in Idaho and 82% of pairs nested on the power line in successive years. Fernie et al. (2000a) determined that free-living reproductive kestrels were exposed to EMFs for 75–86% (minimum-maximum: females) and 71–91% (males) of daylight hours. Fernie et al. (2000a) also examined the behavior of captive kestrels that were exposed to EMFs of strength similar to those experienced by free-living birds when nesting within 1 m of a 735-kV power line. Captive birds were exposed to EMFs for 95 d from pairing to the fledging of young. Males and females were more active during courtship than control (low EMF exposure) birds, and the authors invoke an endocrinological explanation: They propose that EMFs influence corticosterone titers and these, in turn, stimulate locomotor activity (Dufty & Beltoff, 1997; see later discussion). Although males under EMF exposure were more alert during incubation, the behavior of incubating females was unaffected. Females exposed to EMFs spent less time preening and resting during brood-rearing than did control females. Behavioral modification resulting from EMF exposure under captive conditions probably also occurs in free-living birds nesting close to power lines.

Changes in courtship behavior as a result of EMF exposure did not disrupt egg laying or reduce clutch size, and, therefore, why should such modification of behaviour patterns raise concerns? EMFs increase levels of activity in mice (Moos, 1964) and rats (Persinger et al., 1973), and it requires further investigation in birds breeding near power lines to determine whether EMFs result in wholesale elevation in prebreeding activity levels. Investigations of prelaying female birds revealed reductions of activity in the immediate prelaying period (Ettinger & King, 1979), a strategy that Fogden and Fogden (1979) attributed to protection of the developing egg from breakage. However, energetic savings might provide a more plausible explanation for such reduced activity; Houston et al. (1995) found that food intake did not change during egg production in the zebra finch (*Taeniopygia guttata* Vieillot) but females reduced activity by 65% in the immediate prelaying period and while the first egg was laid, allowing significant energetic savings at a time when nutrient and energetic demands are high. Elevations, rather than reductions, in activity just prior to egg laying might seriously compromise egg-laying performance of females nesting near power lines and exposed to persistent EMFs.

REPRODUCTIVE SUCCESS

Reproductive success of birds comprises measures of fertility, hatching success, and fledging success. In turn, hatching success is a function of egg properties as well as chick growth and development (see next section) that also contribute to fledging success at the postnatal development stage. Four studies have examined the reproductive success of birds under EMF conditions, three of which reported adverse effects on reproduction in several species.

Steenhof et al. (1993) studied ravens and raptors that nested on a transmission line in an area of Idaho where a lack of natural nesting sites was clearly limiting the size of the breeding population. They found that nesting success (defined as successful if young reached 80% of the average age when the young normally fledge) of birds nesting on transmission towers was significantly higher for ferruginous hawks (*Buteo regalis* Gray) and similar for ravens, golden eagles (*Aquila chrysaetos* L.), and red-tailed hawks (*Buteo jamaicensis* Gmelin) compared with conspecifics nesting on natural substrates. This increased nesting success of ferruginous hawks is an obvious benefit to the species, which is listed as threatened on the IUCN Red List (IUCN, 2002). Towers often provided more secure nesting places where chicks were more protected against range fires and mammalian predators than at natural nest sites. Furthermore, nesting raptors on towers were less susceptible to heat stress compared with birds at natural sites, where wind and air circulation were much reduced.

Gilmer and Wiehe (1977) found no significant decline in reproductive success of ferruginous hawks nesting on transmission-line towers compared with conspecifics nesting on other substrates. Similarly, Doherty and Grubb (1996) found no significant effects of EMFs from power lines on the reproductive success of eastern bluebirds (*Sialia sialis* L.) and house wrens (*Troglodytes aedon* Vieillot) nesting in nest boxes placed directly below the midline of 765- and 69-kV power lines. However, in the same study, fewer fledglings and declines in fledging success (percent of nestlings that fledged) and in overall reproductive success (percent of eggs that fledged) were found for tree swallows (*Tachycineta bicolor* Vieillot) nesting immediately below power lines compared with conspecifics exposed to low EMFs.

Hamann et al. (1998) studied the breeding performance of four hole-nesting passerine species breeding in close proximity to transmission lines (100 kV, 50 Hz) in Germany. Over 6 yr, they found consistent but differential inter-specific differences in reproductive parameters in response to EMF exposure. For example, egg size was (1) not significantly different between control and EMF sites in nuthatches (*Sitta europaea* L.) and coal tits (*P. ater* L.), (2) significantly reduced in great tits (*P. major* L.), and (3) significantly increased in blue tits (*P. caeruleus* L.). Furthermore, EMF exposure appeared

TABLE 3. Reproductive and Egg Traits of American Kestrels Exposed to Control Conditions (Low Electromagnetic Fields [EMFs]) or EMFs for One Breeding Season in 1995

Variable	Control	EMF
Reproductive		
Pairs, one clutch laid (%)	96	79
Fertility/total eggs (%)	46.8 ± 7.1	50.9 ± 6.5^a
Hatch/fertile eggs (%)	13.6 ± 4.2	11.1 ± 4.3
Fledging/hatched (%)	57.1 ± 4.7	71.4 ± 6.2^a
Egg		
Number of eggs	25	19
Not corrected for volume:		
Volume (cm^3)	13.99 ± 2.00	14.65 ± 1.83^a
Shell thickness (mm)	0.145 ± 0.002	0.138 ± 0.004
Yolk (g)	1.54 ± 0.02	1.65 ± 0.04^a
Albumen (g)	0.40 ± 0.02	0.47 ± 0.02^a
Water (g)	8.14 ± 0.16	8.61 ± 0.15^a
Corrected for volume:		
Shell thickness (mm mm^{-3})	$1.00 \pm 0.02 \times 10^{-5}$	$0.90 \pm 0.03 \times 10^{-5a}$
Albumen (g mm^{-3})	$0.29 \pm 0.10 \times 10^{-5}$	$0.32 \pm 0.01 \times 10^{-5}$

Note. Adapted from Fernie et al. (2000b).
[a]Significant at $p < .05$.

not to influence clutch initiation date of any of the species but depressed clutch size of great tits. Finally, nuthatches were the only species in which total brood loss was more common at EMF-exposed nest boxes than control sites.

Of the studies of the effects of EMFs on the overall reproductive success of birds, Fernie et al. (2000b) studied the most constituent components of overall breeding success (Table 3). These authors found that, while EMF exposure significantly increased fertility, egg size and fledging success, and enhanced embryonic development (see following section) of captive kestrels compared with low EMF exposure controls, it significantly reduced eggshell thickness and hatching success. In a recent laboratory experiment in which domestic chicken (*Gallus domesticus* L.) embryos were exposed to EMFs from computers and televisions, at levels much lower than would be experienced by free-ranging birds, fetal mortality was significantly greater than sham-exposed embryos (Youbicier-Simo et al., 1997).

GROWTH AND DEVELOPMENT

For species that routinely nest in close proximity to power lines, some individuals are exposed to EMFs repeatedly throughout their entire lives. As adults, they use power lines and associated structures as roost sites, hunting perches, and nest substrate; as young, they are exposed to EMFs as embryos within incubated eggs and as chicks when they remain in the nest before fledging. For larger species, young birds may be exposed for 3 mo or more. EMF exposure for an extended time period may adversely affect the growth and physiology of the developing embryo and nestling, thereby potentially altering reproductive success. Several studies have addressed teratology and growth of young birds when exposed to EMFs, and, while contradictory results occurred, most studies (88%) found adverse effects.

Contradictory results in the 1980s from studies (Delgado et al., 1982; Maffeo et al., 1984) of embryogenesis of chickens exposed to pulsed EMFs resulted in “the hen house project” in which identical equipment, protocols, and embryonic assessments were employed by six different laboratories in four different countries (Berman et al., 1990). Overall, the study concluded that exposure to a 10-mG pulsed magnetic field, of strength similar to that experienced by free-living species nesting near power lines, increased the incidence of abnormal embryogenesis. While it should be noted that there were confounding genetic factors involved with part of "the hen house project," nevertheless the increased incidence of abnormal embryogenesis has also been observed in more recent studies involving EMFs from 50-Hz and 60-Hz currents (Farrell et al., 1997; Lahijani & Ghafoori, 2000). Typical abnormalities include malformation of the neural tube and abnormal twisting of the chicken embryo (Juutilainen & Saali, 1986). However, EMF-exposed embryos of captive American kestrels exposed to a 60-Hz current with 30 μT and 10 kV/m (Fernie et al., 2000b), EMFs typically experienced by free-living conspecifics and their offspring, and that had died within 5 d of hatching, showed no signs of physical abnormalities. Still, these EMF-exposed embryos were larger than the control embryos that died.

When EMF exposure was continued until postfledging, exposure influenced the growth of both male and female kestrel nestlings (Fernie & Bird, 2000). Nestlings were heavier and had longer tarsal bones than controls at 21 d of age and also after fledging. EMF-exposed males began their maximal growth (antebrachial bone, body mass) later than controls. Yet other growth parameters were unaffected by the EMF exposure (i.e., antebrachial bone and feather lengths, growth rates). While these growth differences were identified by comparing EMF-exposed and control birds of the same gender, unusual differential growth patterns were also evident when EMF-exposed females were compared with exposed males. Instead of the maximal growth periods beginning earlier in males than females, as happened with the control nestlings, there were no differences in the initiation of maximal growth between the two genders in the EMF-exposed group. Given the reverse sexual size dimorphism in nestling and adult raptors, the lack of earlier initiation in growth by the males versus the females may render the males less successful in competing with their larger siblings during periods of low prey availability or poor weather.

In sum, EMF exposure of kestrel chicks resulted in depressed hatching success but elevated fledging success (Fernie et al., 2000b). At first glance, therefore, the detrimental effects of EMFs on early chick development (i.e., hatching success) appear to be easily counterbalanced by their beneficial effects in later developmental stages (i.e., fledging success; Table 3). However, recent evidence suggests that disruption of the programme of development in birds can have dire consequences for life history traits (Metcalfe & Monaghan, 2001), despite little effect on proximate measures of development. For example, Buchanan et al. (2003) demonstrated that European starlings (*Sturnus vulgaris* L.) that were nutritionally stressed for 3 mo following independence delayed singing and sang shorter and fewer song bouts during the following spring than controls that received ad libitum food as independent young. Depressed quality and quantity of song as a result of developmental stress could impact dramatically on lifetime reproductive success in species, such as the European starling, where females prefer males with larger vocal repertoires (Eens et al., 1993).

PHYSIOLOGY

Changes in the reproductive biology of adult birds and in the growth and maturation of chicks that are exposed to EMFs are mediated through effects on physiology. For example, hatching success, growth, and long-term survival of nestlings are dependent on egg size and composition (e.g., Reynolds et al., 2003). Physiological effects of EMFs may be closely related to the type of EMF exposure experienced, specifically whether the exposure is intermittent or continuous. Depending on the phase of the breeding season, adult birds are intermittently exposed to EMFs from power lines on a daily basis. This intermittent exposure is particularly true of males, which are the primary provisioners of incubating females and nestlings (in some species, the adult female may be the main provider). In contrast, young birds are exposed continuously from the egg through the nestling stages. Recent research indicates that intermittent exposure has more profound effects than continuous exposure in eliciting cellular mechanisms relating to cellular differentiation, proliferation, and survival, particularly of B lymphoid cells, cultured bone samples, and osteoblast cell lines (Adey, 2003). Hormonal and enzymatic responses occurred in osteoblast cell lines at the onset or immediately after termination of field exposures involving 76-Hz magnetic field generators (Adey, 2004). These cellular responses may explain some of the changes observed in captive kestrels exposed to EMFs.

At a gross level, EMF exposure promotes food intake and mass gain in adult mammals such as domestic cattle (Burchard et al., 1996) and birds (Fernie & Bird, 1999). Breeding male birds exposed to EMFs responded as if photoperiod was lengthening, advancing moult and, therefore, increasing body mass (Fernie, 1998). Female kestrels did not gain weight during EMF exposure because moult occurred earlier than in males and females lost approximately 40 g during incubation.

EMFs also influence more subtle aspects of reproductive biology. For example, EMF-exposed kestrels were more fertile. This is difficult to explain, especially since there was no observed difference in copulatory rates between exposed and control groups (Fernie et al., 2000a). Sikov et al. (1984) found that fertility of rats was unaffected by exposure to an electric field that was 10-fold the magnitude of that used by Fernie et al. (2000b). McGivern et al. (1990) found that, while adult rat testis size increased after exposure to low frequency EMFs during hypothalamic development, sperm count did not differ between exposed and control testes. There is no empirical evidence to suggest that EMFs impact avian fertility through disruption of the structure or function of germ cells.

EMF exposure also resulted in increased egg volume despite Fernie et al. (2000b) keeping most factors known to affect egg size, such as female age (Sæther, 1990), clutch size (Nager et al., 2000), laying date (Viñuela, 1997), food availability (Meijer & Drent, 1999), laying sequence and ambient temperature (Ojanen, 1983), constant for high- and low-EMF exposure groups. Table 3 presents egg traits for EMF-exposed and control kestrels.

Intrinsic (e.g., age, mass, and size of female) and extrinsic (e.g., food availability, temperature) factors explain little of the observed variation in avian egg size (Christians, 2002), and, because many of these factors do not act independently of one another, Christians (2002) suggests that it is unlikely that the cumulative effect of these influences will be equivalent to the sum of their individual effects. Data suggest that EMFs probably act at the level of the individual physiological systems that are responsible for egg formation. For example, Williams (2001) administered the anti-estrogen tamoxifen to laying zebra finches. They laid smaller eggs than controls, and this was associated with a 50% reduction in the plasma concentrations of vitellogenin and very-low-density lipoprotein, two yolk precursors. EMF-exposed kestrels deposited significantly more yolk in eggs than controls (Table 3; Fernie et al., 2000b), and this might suggest that endocrine disruption by EMFs (see later discussion) may result in alteration of egg size through direct effects on yolk precursor pools (Christians & Williams, 2001).

EMF-exposed female kestrels laid eggs with thinner eggshells than controls (Table 3). Eggshell thickness usually increases proportionately as egg volume increases under conditions of ad libitum calcium (Reynolds, 2001), and the thinning of eggshells of larger eggs laid by exposed females suggests that EMFs may have been the direct cause of incomplete calcification. Initial studies on the biological effects of EMFs focused on ionic mechanism disruption in brain tissues (see Adey, in press), but interest has broadened to include EMF sensitivity of cells of other tissues. Adey (2003) discussed how cells “whisper together” when exposed to EMFs and how metabolic and growth processes can be affected as a result. Of relevance to the findings of Fernie et al. (2000b) is the sensitivity of intercellular calcium ion movements to EMFs (Adey, in press) and the apparent modulation of calcium transport into cells by EMFs (Walleczek, 1994). Calcium is deposited as eggshell across the wall of the shell gland by the action of prostaglandins and further research is needed to investigate the sensitivity of the shell gland cellular calcium movements to EMF exposure. Eggshell thinning as a result of DDT exposure is mediated through disruption of prostaglandin production by mucosa of the shell gland and the subsequent reduction in uptake of calcium (Lundholm, 1997). EMFs may similarly disrupt uptake of calcium ions across the shell gland but the mechanism is as yet unknown.

Nestlings raised under continuous EMF exposure show elevated bone length compared with nestlings exposed to low EMFs (Fernie & Bird, 2000). Animals exhibit electrically induced osteogenesis (Bassett et al., 1964). Landry et al. (1997) described osteogenesis at an injury site in tibiae of rats during EMF exposure as resulting from a transient increase in osteoblasts due not to cellular proliferation, but to increased differentiation of osteoprogenitor cells near the injury site. Enhancement of skeletal development of EMF-exposed chicks may operate at earlier growth stages than post-hatch. Fernie et al. (2000b) found that kestrel embryos exposed to EMFs were larger than controls. Further work is needed to investigate the timing of osteogenic events in young birds in both pre- and posthatching stages of development. EMFs may increase overall structural size of chicks independently of other influential factors such as egg size and genetics.

ENDOCRINE AND IMMUNE FUNCTION

EMFs have altered the endocrine and immune systems of birds, although research in this area with birds is in its infancy. Circulating levels of corticosterone and anti-thyroglobulin antibodies were markedly suppressed in young chickens continuously exposed to EMFs that would be lower than those experienced by wild birds (Youbicier-Simo et al., 1997). Much more research has focused on the effects of EMFs on melatonin, which is produced by the pineal gland, elevated under dark conditions but suppressed by light.

The nocturnal synthesis, release, and amplitude of melatonin have been suppressed in some mammalian species by ultraviolet wavelengths (Reiter, 1992, 1993), changes in the direction of the earth's geomagnetic field (Olcese et al., 1985; Reiter, 1992), pulsed magnetic fields (Kato et al., 1993, 1994a, 1994b; Yellon, 1994), and alternating electric and magnetic fields (Reiter, 1985). Melatonin has also been suppressed in birds exposed to EMFs. The seasonal melatonin pattern of reproducing adult male American kestrels was suppressed then elevated under EMF conditions, and likely indicated a seasonal phase shift or compression during the breeding season. Melatonin concentrations were also suppressed in fledgling kestrels raised by parent birds exposed for two breeding seasons to EMF conditions (Fernie et al., 1999) and in embryonic chickens exposed to lower EMFs than those experienced by wild birds (Youbicier-Simo et al., 1997). The nocturnal synthesis of melatonin was reduced in migrating pied flycatchers (*Ficedula hypoleuca* L.) experiencing changes in artificial magnetic fields (Schneider et al., 1994a).

The suppression and seasonal phase shift of melatonin in birds suggests that they may perceive EMFs as light, as do some mammals (Reiter, 1992, 1993). Birds see in ranges of the light spectrum that are invisible to humans (Bennett et al., 1996), and kestrels use ultraviolet light for hunting (Viitala et al., 1995). Photoperiod and melatonin rhythms are closely synchronized in birds (Doi et al., 1995; Miché et al., 1991), with longer photoperiods advancing photorefractoriness and moult (Maitra & Dey, 1996; Dawson, 1998). Melatonin is also involved with moult in birds (Gupta et al., 1987). Captive adult male kestrels responded to EMF exposure as if it was a longer photoperiod, becoming photorefractory by mid-season and beginning to moult in advance of the control birds (Fernie & Bird, 1999). Further research is required to determine specifically if, and how, birds perceive EMFs as light.

For birds, the suppression of melatonin through EMF exposure may alter other circannual (e.g., reproduction, migration, seasonal metabolism) (Schneider et al., 1994a, 1994b; Schneider, 1995) and circadian rhythms (e.g., physiology, locomotor activity, feeding, sleeping) critical to survival (Zeman et al., 1993). Furthermore, melatonin also (1) is associated with plumage color changes (Gupta et al., 1987), (2) is important in mate selection in birds (Hill, 1990; Sundberg, 1995), (3) plays a key role in the growth and development of young birds (Lamašová et al., 1997), and (4) acts as an antioxidant and free radical scavenger (Reiter et al., 1999) relating to oxidative stress.

OXIDATIVE STRESS

From metabolic activity and immune defence, oxidative metabolites and free radicals are generated as highly reactive by-products (von Schantz et al., 1999). Accumulation of such by-products results in oxidative stress that can damage DNA, cell membranes, protein, and lipids, and impact upon lymphocyte immune reactions. Oxidative stress has been implicated in cancer, neurodegenerative disease, and aging in humans, and has also been reported in birds (Surai et al., 1996). Excessive generation of free radicals occurs as a result of activity in the immune system, biotransformation systems and cellular respiration. The accumulation of free radicals, and the subsequent damage to tissues, is avoided in mammals and birds through antioxidant defence mechanisms such as melatonin (Surai et al., 1996; Reiter et al., 1998).

There is growing evidence that EMFs can induce oxidative stress in exposed organisms and this may be the result of free radical mechanisms (Adey, in press). Adey (in press) argues that, traditionally, the infrastructure of biological tissues has been considered in relation to the chemical reactions between constituent biomolecules, whereas studying the physical events at the atomic level, and how they contribute to system integrity, may be a fruitful research approach in future. Although free radicals are ephemeral (i.e., lifetime <1 ns), their production might be sensitive to EMFs even at very low magnitude (Adey, 2003).

American kestrel males exposed to EMFs showed evidence of oxidative stress (Fernie & Bird, 2001). Short-term EMF exposure for one breeding season resulted in a suite of responses including depressed total proteins, erythrocytes, lymphocytes, hematocrits, carotenoids and melatonin (Fernie et al., 1999). Taken together, results suggested that birds mounted an immune response to EMF exposure and that they were experiencing higher levels of oxidative stress than were low exposure controls. No adverse health consequences were apparent during the short-term study of Fernie et al. (1999). Nevertheless, our concerns lie with the continuous exposure of some avian species that live in intimate contact with power lines throughout their lives (Table 2). Such birds probably experience protracted elevated immune responses and oxidative stress as a result of EMF exposure and their susceptibilities to infectious agents, immune system malfunction and premature aging might increase as a result.

DISCUSSION AND CONCLUSIONS

A great deal of uncertainty surrounds the findings on the effects of EMF exposure on birds. Most of the uncertainty exists because there has been a limited number of studies involving birds. Despite the limited numbers, much of the research has found that EMF exposure has generally affected birds, and most of the effects have been adverse. EMF exposure, either in the field or at environmentally relevant levels in laboratories, has altered the behavior, physiology, endocrine system, and the immune function of birds, which generally resulted in negative repercussions on their reproduction or development. Such effects were observed in multiple species, including passerines, birds of prey, and chickens in laboratory and field situations, and in North America and Europe. Given the paucity of research concerning EMF exposure and birds, given that birds are frequently exposed to EMFs for extended periods and given that birds may provide a better understanding of how EMF exposure affects higher level vertebrates than any other taxon, many research questions remain unanswered. Several research gaps are next identified and discussed.

A number of different EMF intensities occur when transporting electricity via power lines. Humans and free-ranging birds are subsequently exposed to these multiple-EMF power lines, and also have comparative physiological and reproductive systems that may be disrupted by these EMFs in similar ways. Future research needs to address multiple research questions and directions relating to EMF exposure and the health of vertebrates; each question may also be examined in light of the multiple EMF intensities that occur with power lines.

As with many contaminants (e.g., polychlorinated biphenyls), vertebrate species appear to be diverse in their sensitivities to EMF exposure. Chickens are considered to be one of the most sensitive species to environmental contaminants, and this is likely to be true for EMFs. Yet American kestrels and tree swallows are also sensitive to EMF exposure, with both species showing reduced reproductive success under environmentally relevant EMF conditions. In contrast, wild eastern bluebirds, ferruginous hawks, ravens, golden eagles, and red-tailed hawks do not appear to be reproductively sensitive to EMFs from power lines. However, it remains unknown whether these latter species (and others besides) show differential physiological, endocrine and immune sensitivities to EMFs.

A number of behavioral modifications in captive birds occur as a result of EMF exposure. Prebreeding activity levels of captive kestrels were elevated under EMF conditions at a time when such activity is normally reduced, possibly to conserve energy. Research is required to determine if this elevated prebreeding activity occurs in wild birds, and whether such a response compromises egg-laying performance in females nesting near power lines and exposed continuously to EMFs. Research may also be directed toward determining the possible behavioural and physiological disadvantages to smaller (male) nestlings when they fail to initiate maximal growth before their larger siblings, particularly during periods of low prey availability or adverse weather conditions when sibling competition may be particularly fierce.

Generally, the reproductive success of some wild bird species does not appear to be compromised by EMF conditions, at least not in the short term. Numerous raptors, particularly ospreys (*Pandion haliaetus* L.), are breeding on pylons and towers under EMF conditions. Over 75% of the ospreys in Germany are now breeding on power-line structures and demonstrate significantly higher breeding success (1.65 fledged young per pair) than birds breeding on natural substrate (1.32 fledglings per pair) (R. Prinzinger, personal communication). During the past decade, approximately 25 new nesting pairs of ospreys have been reported annually along the Willamette River in the Pacific Northwest of the United States, with 74% of these occupied nests built at power-pole sites in 2001 (Henny et al., 2003). Ospreys also nest extensively in the Maritime provinces of Canada and eastern parts of the United Sates (e.g., Maine, Florida). Ospreys live up to a maximum of 25 yr for free-ranging birds. Osprey populations nesting under elevated EMF conditions represent an excellent opportunity to investigate whether the developmental stresses observed in captive kestrels will translate into depressed lifetime reproductive success of birds exposed to such EMF conditions for much of their reproductive lives.

It is necessary to know whether elevated EMF exposure results in similar impoverished song development of passerines as that mediated through nutritional stress during their growth. It is likely that EMF-mediated depressed song quality and quantity may impact dramatically on lifetime reproductive success in passerines breeding under conditions of high EMF exposure. These research questions obviously require the long-term monitoring of individuals and populations, but may be readily incorporated into existing long-term monitoring and research programs.

Changes in egg size and growth occur in a number of captive and free-living birds under EMF conditions. Egg size was significantly reduced in great tits but significantly increased in blue tits in one 6-yr study. Kestrels also laid larger eggs but with thinner eggshells; in addition, the kestrel embryos and nestlings were likely to be larger, with longer bones. Research would be particularly valuable in identifying the mechanisms involved in these changes in egg size, eggshell thickness, and overall growth and elongation of specific bones of nestlings. Certainly, it is possible that disruption of calcium uptake mechanisms across the shell gland by EMFs results in disruption of eggshell structure and formation. Research should also focus on calcium transport during growth of nestlings; intercellular calcium ion movements are sensitive to EMFs (Adey, in press), and calcium transport into cells is apparently modulated by EMFs (Walleczek, 1994).

Further research needs to determine whether EMF exposure alters the multifaceted endocrine and immune systems of birds and, in so doing, needs to identify the mechanisms related to these possible changes. The changes in plasma corticosterone levels are likely to indicate further changes in the adrenocorticotropin system that governs the “stress response” of an individual (Hontela, 1997). This “stress response” has been suppressed in various bird species when exposed to organochlorine contaminants (e.g., Love et al., 2003).

Given the multiple roles that melatonin plays in the body, and the circadian and circannual rhythms of birds, some of which are critical to survival, research needs to identify the ramifications of suppressed melatonin concentration and altered seasonal patterns as a result of EMF exposure. For birds, the timing of reproduction, multiple aspects of migration, seasonal metabolism, circadian physiology, feeding and sleeping patterns, plumage color changes that relate to mate selection, growth and development, and the oxidative stress status of an individual may all be expected to change when melatonin is altered under EMF conditions. Changes in melatonin and moult seen in the captive kestrels raise interesting questions regarding how birds perceive EMFs from power lines. Are they seeing the EMFs as light? What other wavelengths in the light spectrum are detectable by birds and do they influence their biology and physiology? What physiological mechanisms do birds use to detect EMFs?

Finally, more research is required in relation to the protracted and continuous exposure of some avian species to EMF-producing power lines throughout their lives (Table 2), and the probability that they experience persistent elevated immune responses and oxidative stress. Are these birds more susceptible to infectious agents, immune system malfunction, and premature aging as a result compared with conspecifics exposed to low levels of background EMFs?

Currently, there are ample research opportunities relating to how multiple EMF intensities from power lines affect the physiological and reproductive systems of free-living birds. Changes in the breeding success of birds, particularly threatened or endangered species, under EMF conditions may have important long-term implications for populations and conservation. Given the similarity in the functioning of these systems between birds and humans, understanding EMF effects on birds may provide a better understanding of how EMF exposure affects the health of other vertebrates.

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