



# Environmental regulation of the reproductive system in a flexibly breeding Sonoran Desert bird, the Rufous-winged Sparrow, *Aimophila carpalis*

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## Abstract

We investigated reproductive regulation in male Rufous-winged Sparrows, *Aimophila carpalis*, a Sonoran Desert passerine that

breeds after irregular summer rains. Field and captive data demonstrate that increased photoperiod stimulates testicular development in March and maintains it until early September. Free-living birds caught in July and placed on captive long days (16L: 8D) maintained developed testes for up to 7 months, and free-living birds caught in September, during testicular regression, redeveloped testes when placed on captive long days, indicating that these birds were still photosensitive. Captive birds on long days maintained testicular development when exposed to temperatures mimicking those occurring during regression in free-living birds. In free-living birds, testicular development was observed during spring and summer, but unless this was associated with rainfall, breeding (indicated by juveniles) did not occur. Large increases in plasma luteinizing hormone (LH) in free-living males were correlated with heavy rainfall in July/August, when the birds bred, and in November, when they did not breed. In captive birds, plasma LH concentrations were unresponsive to photoperiodic changes, but may have responded to social cues. Plasma prolactin concentrations were directly correlated with photoperiod in free-living birds, but an effect of photoperiod on prolactin secretion was not seen in captive birds. It is concluded that male Rufous-winged Sparrows use long photoperiods to stimulate and maintain testicular development, but exposure to long photoperiods does not terminate breeding by inducing absolute photorefractoriness. The specific timing of reproductive behaviors is apparently determined by elevated plasma LH coinciding with long day stimulated gonad development.

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# Introduction

In many species of birds, environmental information initiates reproductive development prior to the onset of optimal conditions for raising offspring while other environmental information regulates the specific timing of reproductive behaviors and the eventual termination of reproduction (Wingfield et al., 2000). In many seasonally breeding, temperate zone birds, the annual increase in day length (photoperiod) is the primary proximate factor used to initiate reproductive development (Dawson et al., 2001, Follett and Maung, 1978, Hamner, 1968, Mishra and Tewary, 1999, Silverin et al., 1999, Wingfield et al., 1993). Long days maintain reproductive function throughout the breeding period and if photoperiod is reduced below the threshold duration, the reproductive system regresses (Hamner, 1968, Wingfield et al., 1993). For most photoperiodic birds studied, prolonged exposure to long days (approximately eight weeks) causes a total loss of sensitivity to photoperiod as a reproductive stimulus and breeding is terminated (Dawson, 1991, Silverin et al., 1999, Wingfield et al., 1993). This phenomenon is called absolute photorefractoriness (Hamner, 1968). Japanese Quail, *Coturnix coturnix japonica*, exhibit a second form of photorefractoriness, termed relative photorefractoriness, in which prolonged exposure to long days results in reduced sensitivity to photoperiod, but never a total loss of sensitivity to photoperiod as a reproductive stimulus (Robinson and Follett, 1982). Consequently, in Japanese Quail longer photoperiods are necessary to maintain reproductive development at the end of the breeding season than are needed to induce

development at the beginning of the breeding season. Relative photorefractoriness may also precede the onset of absolute photorefractoriness in Turkey breeder hens, *Meleagris gallopavo* (Siopes and Proudman, 2003) and Song Sparrows, *Melospiza melodia* (Wingfield, 1993), but this phenomenon has not been identified in other species (Dawson, 1998).

Non-photoperiodic environmental signals also influence the timing of reproduction in birds. These signals include temperature (Perfito et al., 2005, Wada, 1993, Wingfield et al., 2003), food availability (Deviche and Sharp, 2001, Hahn, 1998, Hau et al., 2000, Ligon, 1974), increased green vegetation (Priedkalns et al., 1984), humidity (Cynx, 2001, Vleck and Priedkalns, 1985), water availability (Vleck and Priedkalns, 1985), rain (Ohmart, 1969, Zann et al., 1995), and presence of mates (Eda-Fujiwara et al., 2003, Moore, 1982, Wingfield and Monk, 1994). Non-photoperiodic cues are thought to accelerate or inhibit the effect of photoperiod on reproductive development and behaviors, thus ensuring that the timing of breeding is synchronized with optimal local environmental conditions (Wingfield et al., 2000). In some environments such as the tropics, deserts, and near Arctic, birds may breed at different times in different years (Deviche and Sharp, 2001, Hahn et al., 1997, Ohmart, 1969, Stutchbury and Morton, 2001), and in these environments the timing of reproductive behaviors appears to be predominantly controlled by non-photoperiodic stimuli (Hahn et al., 1997, Hau, 2001, Zann et al., 1995) such as increased rainfall (Grant et al., 2000, Lloyd, 1999, Marshall, 1963, Ohmart, 1969, Zann et al., 1995).

Both photoperiodic and non-photoperiodic environmental information may be conveyed through neuroendocrine pathways that influence luteinizing hormone (LH), follicle stimulating hormone (FSH), and prolactin secretion. Elevated plasma prolactin inhibits LH secretion and promotes testicular regression in some birds (Buntin et al., 1988, Camper and Burke, 1977, You et al., 1995) and thus, this hormone may play a role in fine-tuning the timing of breeding (Dawson and Sharp, 1998, Sharp and Blache, 2003). In photoperiodic birds, experimental studies show that prolactin, LH, and FSH secretion responds to changes in photoperiod (Ebling et al., 1982, Gahali et al., 2001, Maney et al., 1999a, Stokkan et al., 1988, Tong et al., 1997) and increase in association with photoinduced gonadal growth (Deviche and Sharp, 2001, Haase et al., 1985, Silverin, 1991). The development of absolute photorefractoriness is associated with decreased plasma LH while plasma prolactin decreases after absolute photorefractoriness is established (Dawson et al., 2001, Sharp et al., 1998, Sharp, 2005). Non-photoperiodic information influencing reproduction can increase plasma LH and/or sex steroids, as demonstrated in the Houbara bustard, *Chlamydotis undulata* (Saint Jalme et al., 1996), Spotted Antbird, *Hylophylax naevioides* (Wikelski et al., 2000), Canary, *Serinus canaria* (Leitner et al., 2003), and Darwin's Finch, *Geospiza fuliginosa* (Hau et al., 2004). Prolactin secretion has also been shown to be regulated by non-photoperiodic factors associated with reproductive function, such as the expression of parental behaviors (Ketterson et al., 1990, Seiler et al., 1992, Sharp et al., 1998), or with environmental factors which might affect reproductive function including temperature (Maney et al., 1999a)

and hydration level (Arad and Skadhauge, 1984, Arnason et al., 1986, Harvey et al., 1984).

The present study investigates the environmental control of reproduction in the Rufous-winged Sparrow, *Aimophila carpalis*, a year-round resident of the Sonoran Desert (Lowther et al., 1999). This species normally reproduces during the summer monsoon season (July–September), but can also breed between March and June in years with a wet winter or spring (Lowther et al., 1999, Ohmart, 1969, Phillips, 1968, Wolf, 1977). It has been hypothesized that many birds living in the deserts of Mexico and the American Southwest use a combination of photoperiod and cues associated with rain to time reproduction (Delesantro, 1978, Miller, 1958, Vleck, 1993). In male Rufous-winged Sparrows, testes consistently develop in March/April, concurrent with increasing photoperiod and temperature. Testicular regression normally occurs in September after breeding and during decreasing photoperiod (Deviche and Small, 2005, Ohmart, 1969, Phillips, 1968, Wolf, 1977).

Based on this information, we hypothesized that the annual testicular cycle of Rufous-winged Sparrows is regulated by photoperiod and is terminated by decreasing photoperiod rather than by the development of absolute photorefractoriness. This hypothesis predicts that Rufous-winged Sparrows will increase testis size in response to long photoperiods but will not undergo spontaneous testicular regression in response to chronic exposure to a long, stimulatory photoperiod. This hypothesis also predicts that Rufous-winged Sparrows will always be photosensitive, and

consequently, testicular regression in the fall will be reversed if the birds are exposed to long days.

Based on data from other species that breed during periods of rain (Balthazart et al., 2004, Cornil et al., 2006, Hegner and Wingfield, 1987, Hill et al., 2005, Ketterson et al., 1992, Wingfield, 1984, Wingfield et al., 1990), we hypothesized that the absence of breeding in the spring and early summer of most years is due to low plasma LH and sex steroids and we predicted that LH would increase during the monsoon season. Furthermore, because prolactin may inhibit reproductive function in birds (Sharp and Blache, 2003), we hypothesized that the predicted increase in plasma LH during the monsoon season is facilitated by a decrease in plasma prolactin and we predicted that plasma prolactin would increase in the spring, while testes are developing, but decrease during the monsoon season.

Ohmart (1969) postulated that in Rufous-winged Sparrows temperature is “the main factor involved in terminating the northern [population's] breeding season”. We tested the hypothesis that temperature is the main factor controlling seasonal testicular regression by exposing captive birds held on long days to a daily temperature cycle that was similar to, or cooler than, temperatures experienced by free-living birds during reproductive regression. If temperature is the primary regulator of gonadal development, we predicted that testicular regression would occur in birds exposed to cooler temperatures, despite long day exposure.

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#### Materials and methods

Birds were caught at the University of Arizona's Santa Rita Experimental Range and on public lands in and around Green Valley, Arizona (31°46'N/110°50'W, elevation approximately 900m). Palo Verde, *Cercidium* sp., Mesquite, *Prosopis* sp., Hackberry, *Celtis* sp., Acacia, *Acacia* sp., Dalea, *Dalea* sp., Cholla, *Opuntia* sp., and other cacti are the dominant woody vegetation in this Sonoran Desert grassland.

The Arizona State University Institutional Animal Care and Use Committee approved all techniques...

#### Field study

Testis size changed seasonally ( $F_{16, 107}=201.1, P<0.001$ ; Fig. 1A). In 2000, testicular regression began between August 10 and September 6 ( $P=0.003$ ) when photoperiod declined from 13.45 to 12.65h/day. Testes were completely regressed by October 7



(September 6 to October 7,  $P < 0.001$ ) and remained small through the winter. In 2001, testis diameter increased between February 15 and March 14 ( $P < 0.001$ ) when photoperiod increased from 11.03 to 11.93 h/day, and testes reached maximal observed size by...

## Regulation of the seasonal testicular cycle

These data demonstrate that free-living male Rufous-winged Sparrows develop gonads in the spring when photoperiod increases and regress gonads in the fall when photoperiod is decreasing. Similar to previous experiments (Deviche and Small, 2005), the photoperiodic manipulation studies presented here show that long photoperiods stimulate and maintain testicular growth, indicating that seasonal testicular function is photoperiodically regulated. However, unlike most photoperiodic passerines,...

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