General and Comparative Endocrinology xxx (2015) xxx–xxx

Contents lists available at ScienceDirect

General and Comparative Endocrinology

journal homepage: www.elsevier.com/locate/ygcen

Advanced seasonal reproductive development in a male urban bird is reflected in earlier plasma luteinizing hormone rise but not energetic status

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ARTICLE INFO

Article history:
Received 28 January 2015
Revised 2 May 2015
Accepted 9 May 2015
Available online xxxx

Keywords:
Energetic status
Innate immunity
Luteinizing hormone
Reproductive development
Testosterone
Urbanization

ABSTRACT

Urban animals inhabit an environment considerably different than do their non-urban conspecifics, and to persist urban animals must adjust to these novel environments. The timing of seasonal reproductive development (i.e., growth of gonads and secondary sex organs) is a fundamental determinant of the breeding period and is frequently advanced in urban bird populations. However, the underlying mechanism(s) by which birds adjust the timing of reproductive development to urban areas remain(s) largely unknown. Here, we compared the timing of vernal reproductive development in free-ranging urban and non-urban male Abert's Towhees, *Melozone aberti*, in Phoenix, Arizona, USA, and tested the non-mutually exclusive hypotheses that earlier reproductive development is due to improved energetic status and/or earlier increase in endocrine activity of the reproductive system. We found that urban birds initiated testicular development earlier than non-urban birds, but this disparity was not associated with differences in body condition, fat stores, or innate immune performance. These results provide no support for the hypothesis that energetic constraints are responsible for delayed reproductive development of non-urban relative to urban male Abert's Towhees. Urban birds did, however, increase their plasma luteinizing hormone, but not plasma testosterone, earlier than non-urban birds. These findings suggest that adjustment to urban areas by Abert's Towhees involves increases in the endocrine activity of the anterior pituitary gland and/or hypothalamus earlier than non-urban towhees.

1. Introduction

Urbanization profoundly alters ecosystems and produces environments that differ considerably from non-urban areas. Urban areas are characterized by a high proportion of impervious surface (i.e., buildings, roads, etc.), high human density (Nakwa et al., 2008), elevated levels of noise (Halfwerk and Slabbekoorn, 2013) and artificial light (Gaston et al., 2013). Furthermore, urbanization modifies primary productivity (Buyantuyev and Wu, 2009; Imhoff et al., 2004), food abundance (Cook and Faeth, 2006), and ambient temperature (Imhoff et al., 2010). For urban animal populations to persist, they must adjust to these modified environmental conditions. As urban spaces are the most rapidly expanding habitat type worldwide (Grimm et al., 2008), the potential impact of urbanization on biodiversity is considerable. There is, therefore, an urgent need to understand the mechanisms responsible for adjustment to these new habitats.

A consistent effect of urbanization on bird populations is an advancement of the timing of seasonal gonadal development (Deviche et al., 2010; reviewed by Deviche and Davies, 2014; Partecke et al., 2005). Although this phenomenon appears to be widespread, a lack of mechanistic studies means that the underlying mechanism(s) remain(s) largely unknown. Most animals have distinct seasonal breeding periods that are synchronized with optimal environmental conditions to maximize fitness (Visser et al., 2006; Williams, 2012). For many vertebrates, including most birds, the transition from the non-breeding to the breeding life history stage is associated with extensive physiological and morphological

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http://dx.doi.org/10.1016/j.ygcen.2015.05.005
0016-6480/

changes, such as increases in the plasma concentrations of reproductive hormones and gonad size, respectively (Murton and Westwood, 1977; Williams, 2012). Reproductive development, in particular growth of the gonads and secondary sex organs, is a fundamental determinant of the breeding period. Hence, it may be advantageous for urban birds to adjust the timing of reproductive development to local environmental conditions.

The timing and/or rate of reproductive development have the potential to be modulated by the activity of the hypothalamo–pituitary–gonadal (HPG) axis through changes in hormone secretion, hormone carrier protein concentrations, and hormone receptor densities. The HPG axis begins with the hypothalamus, the site of production of gonadotropin-releasing hormone-I (GnRH-I; Sharp and Ciccone, 2005). Gonadotropin-releasing hormone-I stimulates the release of the gonadotropins luteinizing hormone (LH) and follicle-stimulating hormone (FSH) from the anterior pituitary gland (Kuenzel, 2000). Gonadotropins initiate gonad development, gametogenesis, secretion of the sex steroids (testosterone (T) and estradiol (E_2) in males and females, respectively), and expression of reproductive behaviors (Deviche et al., 2010; Murton and Westwood, 1977). The activity of the HPG axis is determined by information provided by a suite of environmental cues that can predict future conditions (Dawson, 2008). In seasonally breeding birds, the annual change in day length (photoperiod) is the initial predictive cue used to begin reproductive development. As changes in day length at a given latitude are constant from year to year, birds use a host of supplementary cues, such as ambient temperature (Schaper et al., 2012b) and food availability (Davies and Deviche, 2014; Hahn et al., 2005), to fine-tune development to a given year's conditions. Urbanization potentially modifies some or all of these non-photic cues. In particular, urbanization potentially creates differences in food availability between urban and non-urban areas. For example, in Phoenix (Arizona, USA), where the present study was conducted, urbanization is associated with an earlier seasonal growth of plants (Buyantuyev and Wu, 2009, 2010), as well as increased arthropod abundance (Cook and Faeth, 2006).

Understanding the mechanism by which food availability influences seasonal reproductive development is complicated by the fact that food may provide both environmental information (i.e., an abundance of food could signal optimal conditions via physiological pathways independent of energetics; O'Brien and Hau, 2005; Watts and Hahn, 2012) as well as influence energetic status (via effects on food consumption; Davies et al., 2015; Hahn et al., 2005). Within the window of opportunity for reproductive development governed by day length, a bird's energetic status, defined as the amount of available energy stores, is thought to constrain the timing of reproductive development (Hahn et al., 2005; Meijer and Drent, 1999). Life history theory posits that when resources are limited there is a resource allocation trade-off between reproduction and self-maintenance, in which allocation into reproduction comes at a cost to somatic processes, such as immune function (Stearns, 1989; Zera and Harshman, 2001). If urbanization affects food availability (see above), this may lead to differences in energetic status between urban birds and their non-urban conspecifics, and, in turn, a disparity in reproductive development, energy stores, and investment into somatic processes, such as innate immunity, between urban and non-urban populations.

We compared the timing of reproductive development in urban and non-urban male Abert's Towhees, *Melozone aberti*, in Phoenix, Arizona and tested the non-mutually exclusive hypotheses that (1) earlier reproductive development is due to improved energetic status and/or (2) earlier increase in endocrine activity of the reproductive system. We predicted that urban towhees would develop their testes and cloacal protuberance (CP, an androgen-dependent secondary sexual characteristic) earlier than non-urban conspecifics. Furthermore, we compared endocrine activity of the HPG axis between these populations and predicted that plasma LH and T, hormones essential for reproductive development and male reproductive function (Deviche et al., 2010), would rise earlier in urban than non-urban birds. If urbanization increases food availability, we also predicted that urban male towhees would have greater endogenous fat stores, be in better body condition (i.e., body mass corrected for body size), and have higher innate immune function compared to non-urban birds.

2. Methods

2.1. Study species

Abert's Towhees, *M. aberti*, are common in riparian woods and marshes of the Sonoran Desert and also throughout the Phoenix Metropolitan area, particularly in urban yards (Rosenberg et al., 1991). They consume a variety of foods including arthropods and seeds, but arthropods are thought to dominate the diet in all seasons (winter: 73%; summer: 96%; Rosenberg et al., 1991). In urban areas, this species will also consume a wide variety of human-provided food (S. Davies, pers. obs.). Abert's Towhees are sedentary, form life-long pair bonds, and hold a permanent territory (1.5–2 ha; Rosenberg et al., 1991). Captive studies indicate that males are photoperiodic and develop their reproductive system in response to increasing day length (S. Davies, unpublished data). Free-ranging towhees can have multiple broods in a given breeding season and active nests have been found from February to September (Tweit and Finch, 1994). Most brood attempts occur during spring and the number of active nests and CP width increase substantially during March and peak in April (Tweit and Finch, 1994). Breeding during the summer is dependent on monsoon rainfall (Tweit and Finch, 1994), suggesting that, in addition to day length, this species modulates its reproductive activity based on the use of supplementary environmental cues.

2.2. Study sites

To investigate the effect of urban areas on vernal development of the reproductive system, we compared adult male Abert's Towhees from six urban and four Sonoran Desert localities in Maricopa County, Arizona (Davies et al., 2013; Fig. 1; Table 1). Urban localities were distributed throughout the Phoenix metropolitan area: in the cities of Phoenix (320 m above sea level [m.a.s.l.]; latitude: 33°25′N; longitude: 112°04′W), Gilbert (242 m.a.s.l.; latitude: 33°21′N; longitude: 111°44′W), and Tempe (357 m.a.s.l.; latitude: 33°26′N; longitude: 111°56′W), and include the Arizona State University Tempe campus, residential housing, city parks, and riparian areas adjacent to the Salt River. Desert localities were Robbins Butte Wildlife Area (247 m.a.s.l.; latitude: 33°19′N; longitude: 112°38′W), Powers Butte Wildlife Area (242 m.a.s.l.; latitude: 33°18′N; longitude: 112°43′W), and the confluence of the Agua Fria and Gila Rivers (278 m.a.s.l.; latitude: 33°23′N; longitude: 112°21′W). On average, desert study sites were 9 km from the nearest urban area (i.e., Buckeye, AZ) and 61 km from urban study sites. These desert locations border the Gila River and the vegetation is characteristic of the Sonoran Desert, including mesquite (*Prosopis* spp.), palo verde (*Parkinsonia* spp.), saltbush (*Atriplex* spp.), creosote (*Larrea tridentata*), white bursage (*Ambrosia dumosa*), and willows (*Salix* spp.). These areas also contain dense thickets of invasive salt cedar (*Tamarix* spp.) and, in the case of the Robbins Butte and Powers Butte areas, retired agricultural lands.

Please cite this article in press as: Davies, S., et al. Advanced seasonal reproductive development in a male urban bird is reflected in earlier plasma luteinizing hormone rise but not energetic status. Gen. Comp. Endocrinol. (2015), http://dx.doi.org/10.1016/j.ygcen.2015.05.005