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SHORT COMMUNICATION

Bimodal breeding seasonality of an understorey bird, *Premnoplex brunnescens*, in an Ecuadorian cloud forest

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Despite the aseasonality of temperature and day length of many tropical regions, especially when compared with temperate latitudes, most tropical animals show fairly pronounced seasonal shifts in foraging, movement patterns and reproduction (Flecker & Feifarek 1994, Saul 1975, Wolda & Fisk 1981). Understanding reproductive seasonality in tropical avian communities involves distinguishing among complex interactions between weather, resource abundance, hormones, behaviour and other life-history traits (Wikelski *et al.* 2003). While there is a great deal of evidence that many tropical bird species breed seasonally (Hau 2001, Marchant 1959, Miller 1963, Snow & Snow 1964), we still understand little of the causes which drive observed patterns (Wikelski *et al.* 2003). Most studies which address the seasonality of reproduction in tropical birds have focused on locations with fairly extreme temporal changes in rainfall (Cruz & Andrews 1989, Lack 1950, Marchant 1959, Poulin *et al.* 1992, Voous 1950), and comparatively few have looked at relatively aseasonal low-latitude locations (Miller 1963, Moreau 1950). Similarly, though a few studies have pointed out slight variation in the within-species initiation of breeding based on microhabitat (Wikelski *et al.* 2003), we know very little about how micro-habitat choice for nesting may affect (or be affected by) breeding seasonality. In this study I describe the nesting cycle of the spotted barbtail (*Premnoplex brunnescens*), from the Ecuadorian Andes to better understand how reproduction may be seasonal when climatic cues are subtle or absent.

The spotted barbtail inhabits the interiors of montane forests from Costa Rica to Bolivia and nests above flowing water along streams (Greeney 2008a). From March 2001 to March 2008, spotted barbtail nests were searched for in the vicinity of the private reserve of Cabañas San Isidro, adjacent to the Yanayacu Biological Station & Center for Creative Studies (00°36′S, 77°53′W, 1900–2400 m). Yanayacu lies 5 km west of Cosanga, Napo Province, Ecuador. Few data are available from the immediate area, but Ecuadorian government rainfall data from Baeza (*c.* 20 km away) shows that rainfall in the area ranges from 100 to 600 mm mo^{-1}, with a drier season lasting roughly from August to February (Figure 1). Total annual rainfall ranges from 2300 to 3500 mm, and mean monthly temperatures range from 15 °C to 17 °C. Combined with extensive experience at ageing eggs and nestlings of this and other tropical birds, an incubation period of 28 d (plus 3 d of laying) and a nestling period of 20 d (Greeney 2008b) were used to estimate clutch initiation for all nests found after incubation had begun. Seasonality was evaluated by quantifying the dispersion of nesting across the year using Rao's test (Batschelet 1981, Rao 1976). This test performs well when testing for polymodal non-uniformity (Bergin 1991). Tests were performed using Oriana 2.0 (Kovach, Wales, UK).

Spotted barbtail breeding was significantly non-uniform ($U = 291$, $r = 0.322$. $n = 166$, $P < 0.01$) and, with 64% of clutches initiated from August to November, was significantly biased towards the drier months ($\chi^2 = 8.36$, $df = 1$, $P < 0.05$). Clutch initiation coincided with both the onset of the rainy season, and the beginning of the drier period (Figure 1), resulting in most fledglings leaving the nest during both the rainiest and driest months of the year.

Riparian zones are among the most dynamic terrestrial habitats (Naiman & Decamps 1997). Thus, the nesting

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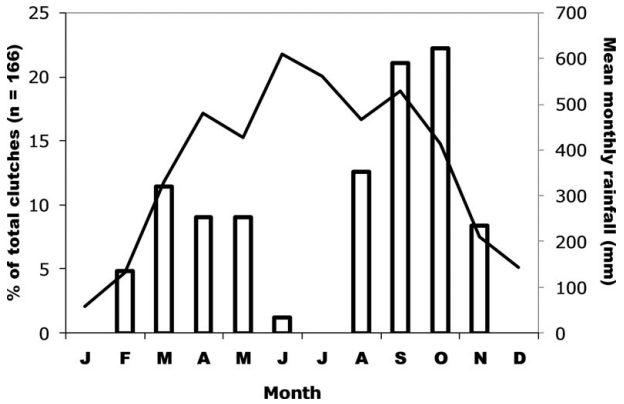

Figure 1. Seasonal patterns of egg-laying of spotted barbtail (*Premnoplex brunnescens*) in northeastern Ecuador. Bars represent the percentage of clutches initiated each month. The line illustrates mean monthly rainfall.

sites of spotted barbtails, always above streams (Greeney 2008a), are subject to rapidly rising water levels after wet season rainstorms and one would predict them to breed during drier periods as do other riparian-nesting species in the area (Dobbs & Greeney 2006, Greeney 2007, 2008c; Greeney *et al.* 2004, 2006). These dry-season breeders, however, are also generally specialized feeders, taking predominantly aerial prey (e.g. swifts, flycatchers), nectar (hummingbirds), or aquatic insect larvae (white-capped dipper). Thus, while most species avoid rainy-season habitat disturbance, diet is likely an important constraint for these species as well.

As most leaf production in tropical plants occurs during rainier periods (Fogden 1972, Janzen 1967, pers. obs.), we would expect the abundance of herbivorous arthropods to increase during this period. Conversely, studies of tropical aquatic insects suggest that emergence occurs during drier periods (Dudgeon & Watt 1986, Wolda & Flowers 1985), and thus flying aquatic insects (adults) would be most prevalent during drier periods in my area. As food abundance is thought to have a strong effect on the seasonality of avian breeding (Poulin *et al.* 1992, Skutch 1950, Young 1994), it makes sense that a riparian-nesting, generalist insectivore such as spotted barbtail, would time its breeding in relation to these two peaks in insect abundance. Two other riparian specialists in the area show preferences for the drier season, but also nest year-round (*Dysithamnus occidentalis*; Greeney 2004, Harris *et al.* 2008: *Chlorospingus parvirostris*; Greeney 2005). What little is known of their foraging and diet suggest that they too may be generalist insectivores (Hilty & Brown 1986, Ridgely & Greenfield 2001). Thus it appears that only more generalized insectivores, able to capitalize on multiple peaks of a variety of insect types, are breeding year round. It should be noted, however, that the riparian-nesting community is biased towards aerial insectivores and nectarivores, and it may have been these aspects of their ecology which allowed them to specialize on highly dynamic, montane riparian habitats.

While it is apparent that empirical data are lacking in order to properly access the factors determining seasonality in my area, the relationship between seasonality and microhabitat use may be an important, yet under-explored factor in this and other avian communities. For example, it appears that a taxonomically diverse assemblage of species nesting in fast-growing, dynamic patches of montane *Chusquea* bamboo, may also restrict breeding to the drier months in the area (Greeney & Miller 2008). In the case of riparian-nesting species in my area, habitat instability may be a factor in both seasonality of breeding and community composition.

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