

# Nest orientation of the Spotted Barbtail, *Premnoplex brunnescens*, is strongly correlated with stream flow

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**Abstract** The placement and orientation of bird nests may strongly influence reproductive success. For many species, nest orientation is related to the cardinal directions and has to do with prevailing winds or solar exposure. Nest orientation differs among species in different environments, variously cooling or warming nests to maintain a nest microclimate optimal for successful development of eggs and young. The Spotted Barbtail (*Premnoplex brunnescens*) builds mossy, enclosed nests along shaded streams in Neotropical cloud forests. It shows a unique pattern of nest orientation, whereby nests are oriented in relation to the direction of water flowing below the nest entrance, rather than compass bearing. Nests face in one of three directions in relation to the stream: downstream, upstream, or perpendicular to the flow of the water. I discuss the ability of various hypotheses to explain this pattern in the context of factors affecting nest orientation in other species. While the reasons for this pattern of orientation remain unclear, orientation is likely driven by the need to create and maintain an optimal internal nest microclimate.

**Keywords** Andes · Cloud forest · Ecuador · Furnariidae · Nest microclimate · Riparian

## Introduction

Studies of avian nest-site selection have repeatedly shown there to be a great deal of variation in nest orientation, as well as variability in the strength of patterns among species and/or nesting guilds (i.e., open cup, domed nest, primary/secondary cavity nesters). While some studies reveal little or no pattern of nest orientation (e.g., Albano 1992; Rendell and Robertson 1994; Tarvin and Smith 1995), many groups, representing a variety of nest architectures, do show strong preferences in the orientation of their nests (Austin 1974; Balgooyen 1990; Bergin 1991; Hooge et al. 1999; Martin and Roper 1988; Mezquida 2004; Nores and Nores 1994; Walsberg 1981). Typically, nest orientation has been found to be correlated with either prevailing winds (Facemire et al. 1990; Mezquida 2004; Norment 1993) or sun exposure (Burton 2006; Hartman and Oring 2003; With and Webb 1993; Yanes et al. 1996), both of which may have a direct effect on the microclimate of the nest (Ardia et al. 2006; Hartman and Oring 2003). Thus, nest orientation and placement are important aspects of avian reproduction and may affect embryonic development, hatching success, and nestling growth (Austin 1974; Burton 2006; Cook et al. 2003; Lloyd and Martin 2004; Viñuela and Sunyer 1992), the energetics of attending adults (Vleck 1981; White and Kinney 1974), and overall nesting success (Filliater et al. 1994; Martin and Roper 1988; Rauter et al. 2002).

The Spotted Barbtail (*Premnoplex brunnescens*: Passeriformes: Furnariidae) is a small bird inhabiting the interiors of montane forests from Costa Rica to Bolivia (Hilty 2003; Hilty and Brown 1986; Remsen 2003). Nests are thick mossy balls with a downward-facing tubular entrance, built in dark, humid environments (Areta 2007; Greeney 2008b). While there appears to be some

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geographic variation in the details of nest architecture (Greeney 2008b), nests are almost exclusively built directly over shaded streams (Areta 2007; Greeney 2008a, b; Marín and Carrión 1994; Skutch 1967). This uniformity in nesting habitat notwithstanding, nest placement is extremely variable, even within populations (Greeney 2008b). Nests may be built partially or entirely into various natural cavities, completely pendant, or attached in various manners to logs, banks, and epiphyte tangles. This extreme flexibility in nest substrate and mode of attachment allows nests to potentially be oriented in any direction. Here I describe the unique, non-random pattern of nest orientation shown by Spotted Barbtail in northeastern Ecuador.

## Materials and methods

I recorded the orientation of the nest entrance (hereafter nest orientation) at 196 Spotted Barbtail nests, from May 2001 to September 2007, in the vicinity of the Yanayacu Biological Station and Center for Creative Studies (00°36'S, 77°53'W, 1,900–2,400 m) and Cabañas San Isidro (1,900–2,200 m), 3–5 km west of Cosanga, Napo Province, northeastern Ecuador. At each nest, I recorded the compass orientation of the nest, as well as the direction of stream flow, to the nearest 5°. I took orientation readings by holding a compass directly below the nest and orienting with the nest entrance or with the flow of water directly below. Thus, the direction recorded for water flow did not always correspond to the overall direction of the stream, as it was often affected by a bend in the stream or large boulders upstream from the nest.

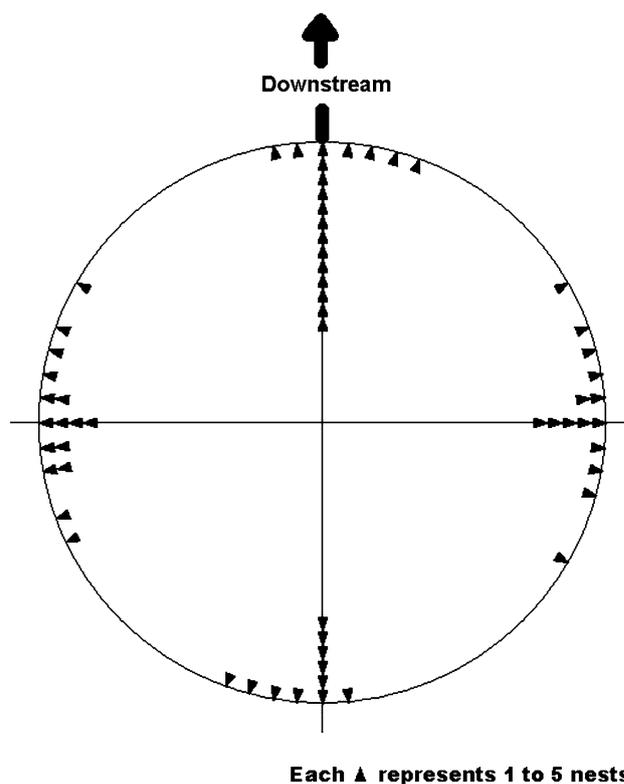
A wide variety of both circular and linear statistics have been used in previous studies of nest orientation (e.g., Ardia et al. 2006; Austin 1974; Burger and Gochfeld 2005; Norment 1993; Ricklefs and Hainsworth 1969). As circular distributions do not usually conform to the assumptions of many of these tests (Cain 1989; Zar 1999), most recent studies of circular data rely on one of several analyses. The three most widely used circular statistics show marked differences in their abilities to detect non-uniform dispersions with varying sample sizes, vector dispersions, and directional modality (Bergin 1991). Therefore, I tested uniformity of direction around 360° using three separate tests. Raleigh's test ( $Z$ ; Batschelet 1981; Zar 1999) and Watson's test ( $U^2$ ; Batschelet 1981; Zar 1999) are frequently used statistics for analyzing patterns of nest orientation (Ardia et al. 2006; Burton 2006; Rafael 1985). Both of these tests, however, were designed to test unimodal patterns, whereas Rao's test ( $U$ ; Batschelet 1981; Rao 1976) performs much better with polymodal distributions (Bergin 1991).

Because nest orientation in relation to the cardinal directions showed a weak unimodal distribution with high

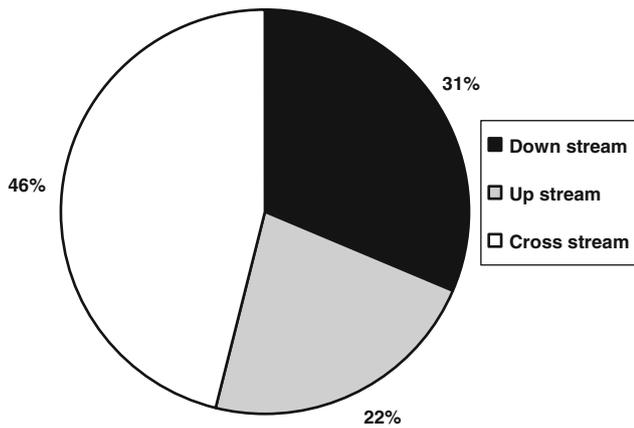
vector dispersion, while nests showed strong polymodality in relation to stream flow, I feel it is appropriate to report all three tests. For each analysis, I present mean vector length ( $r$ ). Mean vector length is a unitless measure (0–1) of the dispersion of the data, with a value of 0 being widely dispersed (uniform) and 1 being tightly concentrated. I used Oriana 2.0 (Kovach, Wales, UK) for calculating all circular statistics.

## Results

Spotted Barbtail nest orientation was strongly correlated with stream flow, such that nests were oriented in one of three ways in relation to the direction of water movement (Fig. 1,  $r = 0.16$ ,  $n = 196$ ; Raleigh's test:  $Z = 5.401$ ,  $P = 0.005$ ; Rao's test:  $U = 303.43$ ,  $P < 0.01$ ; Watson's test:  $U^2 = 1.121$ ,  $P < 0.005$ ). Of the three categories (upstream  $\pm 20^\circ$ , downstream  $\pm 20^\circ$ , across-stream  $\pm 30^\circ$ ), most were oriented either with, or against, the flow of water (Fig. 2), but showed no significant preference for parallel or perpendicular ( $\chi^2 = 1.1$ ,  $P \gg 0.05$ ,  $df = 1$ ). Nests oriented perpendicular to the stream showed no relationship



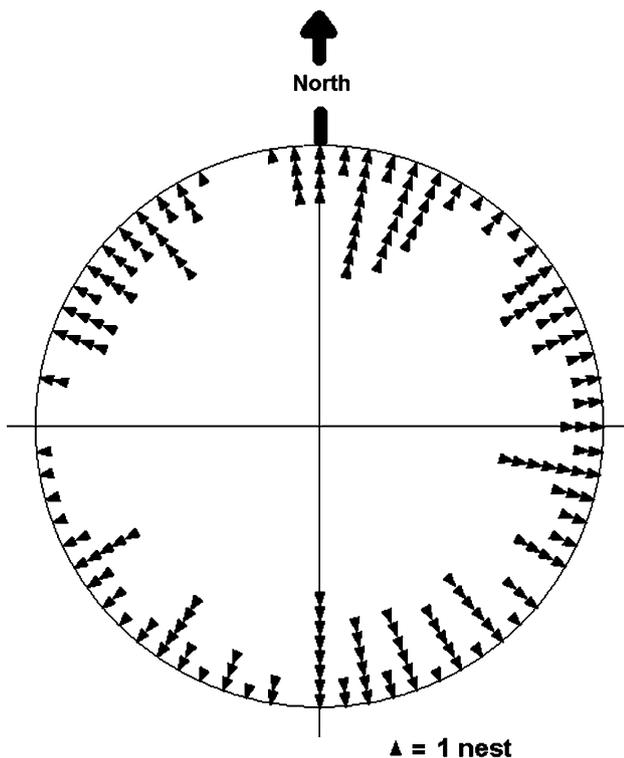
**Fig. 1** Nest orientation of Spotted Barbtails (*Premnoplex brunne-cens*) in relation to the direction of water flowing directly below the nest. Nests oriented right ( $90^\circ$ ) are those opening towards the far side of the stream and nests oriented left ( $270^\circ$ ) are those opening towards the closest bank



**Fig. 2** The relative percentages of nests of Spotted Barbtails (*Premnoplex brunnescens*) oriented in each of three directions in relation to stream flow: upstream, downstream, and across-stream (perpendicular)

with regards to the closest bank, sometimes opening across the stream and sometimes opening towards the nearest bank ( $X^2 = 0.2$ ,  $P \gg 0.05$ ,  $df = 1$ ).

Nest orientation showed only a weak relationship to compass bearing (Fig. 3,  $r = 0.113$ ,  $n = 196$ ; Raleigh's test:  $Z = 2.503$ ,  $P = 0.082$ ; Rao's test:  $U = 240.61$ ,  $P < 0.01$ ; Watson's test:  $U^2 = 0.187$ ,  $P > 0.05$ ). As Rao's test is more sensitive to patterns with high levels of



**Fig. 3** Nest orientation of Spotted Barbtails (*Premnoplex brunnescens*) in relation to the four cardinal directions

dispersion (indicated by low  $r$  value; Bergin 1991), it is understandable that it was the only one of the three tests to yield a significant result. This propensity to be oriented east is most likely a reflection of the study areas streams' significantly ESE direction ( $r = 0.437$ ,  $n = 196$ ; Raleigh's  $z = 37.423$ ,  $P \ll 0.001$ ; Rao's  $U = 253.469$ ,  $P < 0.01$ ; Watson's  $U^2 = 1.992$ ,  $P < 0.005$ ), in combination with 78% of nests showing either a downstream or across-stream orientation (Fig. 2).

## Discussion

Nest orientation within a species may vary through the breeding season (i.e., nests built later in the season may be oriented differently), presumably optimizing nest microclimates by tracking shifting weather patterns (Burton 2006; Finch 1983; Ricklefs and Hainsworth 1969). Recently, nest orientation has also been shown to vary intraspecifically, in a predictable manner, with latitude (Burton 2007). Most species, however, show a preference for one direction, generally that which exposes them to, or protects them from, wind and solar radiation (Ardia et al. 2006; Burton 2006; Facemire et al. 1990; Mezquida 2004; Norment 1993). The barbtails studied here nest in a cool, dark, humid environment, and rear their young in thick, enclosed nests with a downward-opening entrance tube (Greeney 2008a, 2008b). Thus, we would not expect thermal radiation to be a concern for this species. Similarly, they are nesting in sheltered locations where they would be unlikely to experience extreme wind conditions.

Nestlings are provisioned by both adults, and nestling development is comparable to related species of similar size (Skutch 1996; Greeney 2008c; Greeney and Zyskowski unpublished data; Greeney unpublished data). Incubation is carried out by both adults, yet barbtails leave their eggs unattended for over 6 h during the middle of each day (Greeney unpublished data). Presumably, because this may allow eggs to drop below a temperature at which they can maintain development (Webb 1987; White and Kinney 1974), this results in an extended incubation period of 27–31 days (Greeney 2008a). While the reasons for these unusual incubation rhythms remain unclear (Greeney unpublished data), the very specific manner in which nests are oriented in relation to their environment may shed some light on the means by which they can maintain such levels of neglect without deleterious effects on their developing embryos.

Successful rearing of a brood in any given nest depends on a complex interaction of biotic and abiotic variables that may, to varying degrees, limit success. It is the interaction between adult behavior (i.e., time budgets for caring for the young) and nest characteristics (i.e., architecture,

materials) that optimizes the microclimate within the nest and facilitates successful reproduction (Ar and Sedis 2002). This “bird-nest unit” (Deeming 2002; Hansell and Deeming 2002) involves a myriad of conflicting selective pressures. For example, while the proper and timely development of eggs requires them to be maintained within a specific range of temperatures (Webb 1987), adults must balance their own energetic needs and the risks of predation while maintaining this thermal regime (Conway and Martin 2000a; Vleck 1981; White and Kinney 1974). Reduced visits to the nest in response to predation pressures (Conway and Martin 2000b; Ghalambor and Martin 2001) may reduce the egg temperatures, which, in turn, may extend the incubation period (Haftorn 1988; Williams 1991) and result in longer periods of exposure to predation. Thus, in the face of trade-offs that keep adults away from their eggs for extended periods, a species would be expected to build nests that maintain a specific microclimate and that prevent excessive heat loss or gain during parental absences (Ar and Sedis 2002).

In addition to temperature, the relative humidity around the eggs may have an impact on their development (Ar and Sedis 2002). As avian embryos develop, they rely on pores in the egg shell for maintaining balanced gas exchange, allowing them to consume oxygen from the outside while dissipating CO<sub>2</sub> build-up inside (Ar 1991a, b). The resulting diffusion gradient presents a problem whereby the water balance of the egg must be sufficiently maintained such that the eggs do not desiccate during passive movement of water vapor across the shell membrane during the egress of CO<sub>2</sub>, thus interfering with normal embryonic development (Ar and Rahn 1980; Meir and Ar 1986). Excessive humidity or desiccation of the nest, therefore, can negatively impact embryonic development (Ar and Sedis 2002).

Air currents move along slopes and riparian areas in a predictable manner during the day, generally flowing upstream (anabatic winds) as ambient air temperatures increase and warm air moves upwards along drainages, and then downstream (katabatic winds) as temperatures drop and cold air sinks from surrounding slopes (e.g., Gazzilli et al. 2001; Hunt et al. 2003). Movement of air across the opening of enclosed bird nests has been suggested to create a small vacuum that circulates air and creates cooler internal temperatures beneficial to a desert nesting species (Facemire et al. 1990). It is possible, therefore, that nest entrances are oriented in specific directions to take advantage of predictable air currents to help regulate internal nest temperature and humidity. In the case of barbtails, we might predict that nests are oriented in a manner opposite that of species nesting in heat-stressed environments, instead oriented so as to minimize air movement and heat loss from inside the nest.

Conversely, unattended eggs in cool, humid microclimates are thought to be more susceptible to invasion by pathogenic bacteria (Cook et al. 2003, 2005a), and air currents may help to prevent the buildup of pathogens. The risk of trans-shell infection may be an understudied factor influencing avian life-history strategies (Cook et al. 2005b), and barbtail nests may be oriented so as to minimize this risk. Creating a nest microclimate that deters the build-up of pathogens may be particularly important for barbtails because of their extended periods of nest reuse (Greeney 2008a), as fungal pathogens have been shown to build up in repeatedly used nests (Hubalek 1978; Hubalek and Balat 1974). As barbtail nest orientations are related to the direction of water flowing below the nest, rather than with the overall direction of the drainage, however, these explanations seem unlikely. While the effect of Spotted Barbtail nest orientation on the nests’ internal microclimate is unknown, comparisons of incubation period, rates of egg water loss, pathogen levels, and egg hatchability, in relation to nest orientation, might provide useful insights into the degree to which orientation affects egg development.

If predation is a factor in determining nest orientation, it is possible that a specific orientation may provide adults with the least obstructed means of escape. This seems unlikely, however, as regardless of the orientation of the opening in relation to the nest, adults must first exit downward and are then not limited in the direction they may fly. The orientation of nests can be related to the location of nearby objects for some species, as illustrated by woodpeckers choosing to excavate nests in cacti such that none of the arms obstruct their rapid entrance or exit (Korol and Hutto 1984; Zwartjes and Nordell 1998). As the flow of water below the nest is not necessarily correlated with the least obstructed path to or from the nest, however, this explanation also seems unlikely for barbtails.

Mennill and Ratcliffe (2004) proposed a biotic factor, other than predation, that may affect the orientation of bird nests. Their study showed that chickadee nest cavities differed in their acoustic properties, and that chickadees showed a preference for nests oriented towards conspecific territories, possibly facilitating intraspecific communication. If the orientation of barbtail nests affects their acoustic properties, it is possible that, in the noisy environment of the stream, certain orientations favor the reception of sound for the adult inside the nest. This may either facilitate conspecific communication or, perhaps, increase the detectability of approaching predators. As barbtail nest entrances open downward through a narrow tube (Greeney 2008b), the field of vision of adults in the nest is extremely restricted. The detection of predators via acoustic cues, therefore, may be of more importance to barbtails, as adults would be easily trapped within the nest by a predator that has approached close enough to be

detected visually. In particular, if nest orientation facilitates adults' correct detection of the directionality of sound, adults emerging blindly out of a narrow entrance would have an advantage if the location of the predator was known prior to exiting.

Most studies on nest orientation focus on compass orientation rather than physical characteristics of the nest site (but see Korol and Hutto 1984; Zwartjes and Nordell 1998). Although there are few studies that relate nest orientation to physical habitat characteristics such as stream flow, the strongly polymodal pattern of orientation shown by barbtail nests appears to be fairly unique. While I lack the data to strongly support or reject most of the above hypotheses, it seems most likely that nest orientation in barbtails is related to controlling the internal nest microclimate. Nests of Spotted Barbtails are fairly permanent structures, taking up to 1.5 years to build, and being reused for over 7 years and for up to five attempts per year (Greeney 2008a, b). Thus, there is a fair degree of permanence to the birds' original choice of orientation, which could potentially face in any direction. Thus, although the factors driving this pattern of nest orientation in barbtails remain unclear, the highly conserved pattern shown here suggests that there are strong selective pressures acting on nest orientation in this species.

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