



Short communication

Absence of protandry in a population of Gray Catbirds *Dumetella carolinensis*

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Sex-based differential arrival on the breeding grounds at the completion of migration has been poorly studied in monochromatic and monomorphic species because individuals are difficult to sex without recapture or molecular tests. We examined sex-based arrival timing to the breeding grounds of the Gray Catbird *Dumetella carolinensis*, a monochromatic species. We also examined differences in size and arrival by age as these are well documented to affect arrival timing. Older birds were larger than younger birds, and older males were larger than older females. Older birds arrived back on the breeding grounds earlier than younger birds, as documented in many species, but males did not precede females. Our results provide evidence of sexual size dimorphism in Catbirds and add to a growing body of information on arrival timing in monochromatic species.

Differences in intensity of sex-based competition for breeding resources are hypothesized as the primary selective force for one sex to precede the other to the breeding grounds (Kokko 1999, Kokko *et al.* 2006). Typically, males arrive at the breeding grounds in advance of females (Morbey & Ydenberg 2001), a phenomenon known as protandry (Rubolini *et al.* 2004). This is because males are thought to experience more intensive selective pressure for acquiring territories or other resources for attracting a mate than females (but see Kokko *et al.* 2006 for a discussion of why females may also be under selection pressure for earlier arrival to compete for resources or mates). Furthermore, comparative studies suggest that the extent of sexual selection

experienced by males, as evidenced by the degree of sexual dichromatism (Møller & Birkhead 1994, Owens & Hartley 1998), sexual size dimorphism (Owens & Hartley 1998, Dunn *et al.* 2001), polygyny or rate of extra-pair paternity (Coppack *et al.* 2006), affects the degree of protandry.

While protandry is well documented in dimorphic species (Rubolini *et al.* 2004), little is known about arrival dates by sex in monomorphic or monochromatic species (Rubolini *et al.* 2004, Edwards & Forbes 2007, Newton 2008). The primary reason for this is the difficulty in sexing individuals upon arrival at the migratory destination. Moreover, the limited studies to date have produced equivocal results. For example, male Spotted Flycatchers *Muscicapa striata* preceded females during passage on the island of Ventotene, Italy, (Mabey 2002), and male White-throated Sparrows *Zonotrichia albicollis* and Least Flycatchers *Empidonax minimus* preceded females during spring migration at Long Point Observatory, Ontario, Canada (Mills 2005). In contrast, Edwards and Forbes (2007) presented evidence that Song Sparrows *Melospiza melodia* did not exhibit protandry upon arrival at breeding grounds in Ontario.

Our research on arrival and breeding in the Gray Catbird afforded us the opportunity to assess arrival timing by sex and age in a songbird migrant described as monochromatic and monomorphic (Cimprich & Moore 1995). One advantage of our study is that we captured birds both during the arrival period and throughout the breeding season, permitting us to determine an individual's sex and relate it back to when it arrived at breeding grounds in northeastern Pennsylvania. Although there are several hypotheses regarding differences (or lack of differences) in arrival timing between the sexes (Morbey & Ydenberg 2001) here we focus on assessing whether catbirds are indeed monomorphic and whether they exhibit protandry.

METHODS

Study species and study site

Fieldwork took place in Lackawanna County, northeastern Pennsylvania, within Lackawanna State Park (41°34'30"N, 75°42'54"W) and private lands immediately adjacent to the Park (41°33'45"N, 75°43'18"W). Birds were captured during spring migration in 2005–2007 in forested and shrubland habitats. For a detailed description of the habitat, see Smith and Hatch (2008). We captured birds using mist-nets checked at 30-min intervals. For each individual we recorded the following: capture date and time, age and sex where possible (Pyle 1997), mass and tarsus length. All captured birds were banded with a US Geological Service aluminium leg band and were individually colour-banded. We limited our analyses to first captures of Catbirds during the

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month of May, which encompasses the bulk of the arrival period at our study site (R.J. Smith & M.I. Hatch unpubl. data).

Individuals were classified as breeders and assigned to sex based on a combination of netting, nest monitoring and daily searches of both the study site and adjacent areas (up to 2 km distant) during the breeding season. We used several types of evidence to identify local breeders and individual sex, including morphological evidence on recapture [presence of a brood patch (female) or an enlarged cloacal protuberance (male)], and observation of reproductive behaviours [including nest construction/attendance, incubation, brooding (female), or repeated evidence of territoriality (male)]. Because birds were individually colour-banded we were able to back-assign sex to when the bird was first captured. We only include verified breeders of known age and sex in the subsequent analyses.

Statistical analyses

The first principal component extracted from field measurements of wing, tail and tarsus length was used as a body size estimate (Freeman & Jackson 1990). We then ran a general linear model (GLM) with body size as the dependent variable and age, sex and year as factors and included all possible interaction terms. We then re-ran the model with the main effects and significant interactions only. Finally, a generalized linear model on ranked data was used to examine factors that may have affected arrival timing. Arrival day was used as the dependent variable, and age, sex, year and all possible interaction terms as independent variables. We then re-ran the model with the main effects and significant interactions, if any. All statistical tests were run using SPSS 15.0 (SPSS Institute 2006).

RESULTS

The first principal component explained 56.8% of the variance in body size parameters and had the following loadings: wing 0.919, tail 0.866 and tarsus 0.332. Although tarsus loading was low, analyses with a principal components analysis (PCA) score derived without tarsus produced similar results. We therefore chose to keep tarsus in the analysis because it is used in other studies (e.g. Freeman & Jackson 1990, Bergstrom & Sherry 2008). A GLM with body size (PCA scores) as the dependent variable indicated a significant relationship between body size and age ($F_{1,76} = 7.6$, $P = 0.007$), sex ($F_{1,76} = 8.0$, $P = 0.006$), year ($F_{2,76} = 7.4$, $P = 0.001$) and a marginally significant interaction between year and age ($F_{2,76} = 3.1$, $P = 0.050$). No other possible interaction terms were significant (all $P > 0.4$). Overall, older birds were larger than younger birds, older males larger than older females, and younger males and females were of similar size (Fig. 1). A

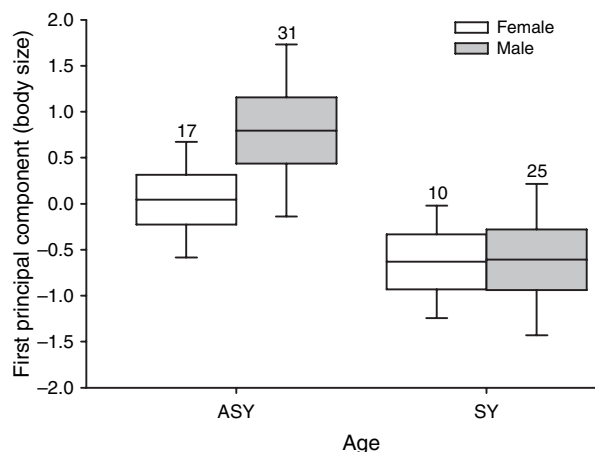


Figure 1. Size variation by sex and age of Gray Catbirds arriving in northeastern Pennsylvania, 2005–2007. Lines represent means, boxes encompass ± 1 se, and the whiskers encompass ± 1 sd. Numbers above indicate sample sizes. Ages are 'After Second Year' (ASY) and 'Second Year' (SY).

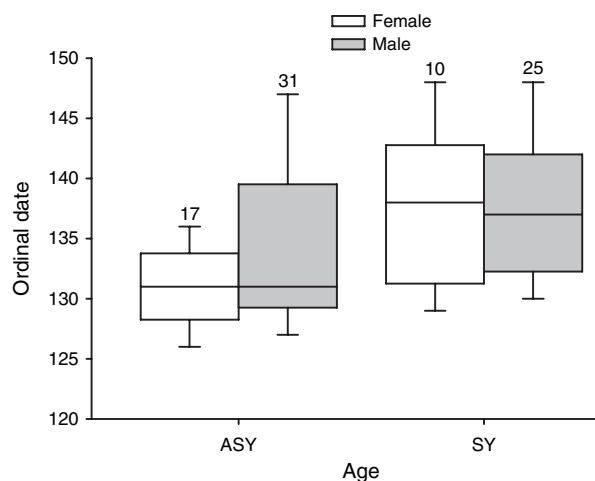


Figure 2. Arrival timing by sex and age in Gray Catbirds breeding in northeastern Pennsylvania, 2005–2007. Lines represent medians, boxes encompass the interquartile range, which contains 50% of the values, and whiskers represent maximum and minimum values. Numbers indicate sample sizes. Ages are 'After Second Year' (ASY) and 'Second Year' (SY).

generalized linear model of arrival day indicated a significant age effect (older birds arrive earlier: Wald $\chi^2 = 15.0$, $df = 1$, $P < 0.001$; Fig. 2) with no effect of year (Wald $\chi^2 = 0.3$, $df = 2$, $P = 0.86$) or sex (Wald $\chi^2 = 0.93$, $df = 1$, $P = 0.34$; Fig. 2) on when birds arrived at the breeding grounds. All two-way and three-way interactions were non-significant (all $P > 0.1$).

DISCUSSION

Our results suggest the existence of sexual size dimorphism in our population of Catbirds, at least in older birds. A high degree of sexual size dimorphism has been associated with mating system variation, such that polygamous species show greater dimorphism (Owens & Hartley 1998, Dunn *et al.* 2001). However, although polygyny has been reported in Gray Catbirds (Johnson & Best 1980, Hanley *et al.* 2007), it appears to be relatively rare (Hanley *et al.* 2007). In support of this, at our site we have observed nesting behaviour of individually colour-banded Catbirds for 5 years and have not documented polygyny. Furthermore, sexual size dimorphism associated with mating system variation has been linked to protandry (Weatherhead & Clark 1994, Kissner *et al.* 2003), which is not evident in our population. Finally, the fact that only older males were significantly larger than females argues against polygyny as a reason for the observed size differences because if polygyny were prevalent in this mating system we would expect to see males of both age classes being larger than females.

The degree of sexual dichromatism, as one measure of the intensity of sexual selection, is related to protandry (Rubolini *et al.* 2004). Our findings support this idea as we demonstrated an apparent lack of protandry in a monochromatic species. Edwards and Forbes (2007) similarly found no evidence of protandry in monochromatic Song Sparrows, although other studies of monochromatic species (including Song Sparrows) have presented evidence for protandry (Nice 1937, Bédard & LaPointe 1984) or earlier passage by males during spring migration (Mills 2005). This suggests that while degree of dichromatism may be related to sexual selection, there are other manifestations of sexual selection such as body size, song rate or repertoire size (Andersson 1994) which may affect the degree of protandry. Monochromatism is not the only possible explanation for the apparent lack of protandry in our population of Gray Catbirds, and we emphasize that our goal was to examine arrival timing in an apparently monochromatic species rather than to provide a comprehensive or multi-species test of the causes of protandry. We also acknowledge that while Gray Catbirds are described as monochromatic, their visual system may see sex differences we cannot perceive, as has been demonstrated for a large number of other 'monochromatic' passerines (Eaton 2005).

Our results differ from those of Zimmerman (1963) and Darley *et al.* (1971), who reported that male catbirds arrived at breeding grounds before females. However, both studies focused principally on breeding parameters, and hence neither rigorously collected data as birds were arriving at the breeding grounds. Furthermore, both studies relied heavily on observational data to indicate the presence of individuals. Because males

make themselves conspicuous by singing and females tend to remain relatively concealed (R.J. Smith & M.I. Hatch pers. obs.) the timing of female arrival may have been less accurately determined (see also Darley *et al.* 1971). By combining daily netting with a high density of nets in a relatively small area, our methodology is more robust to assumptions regarding detectability. Indeed, other studies have employed passive netting to estimate protandry (Lozano *et al.* 1996, Kissner *et al.* 2003, Edwards & Forbes 2007). This study adds to the limited information available about presumably monochromatic species and arrival timing, but further investigation of the fitness costs and benefits of early arrival and how they might differ between the sexes is warranted.

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