



Phenotypic plasticity in nest departure calls: weighing costs and benefits



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In birds, male song has been extensively studied, but female vocalizations have received little attention. Females of several North American species produce a unique vocalization, the nest departure call (NDC), upon leaving nests. Producing NDCs has costs due to acoustical properties that make nests easy to locate by predators. Thus, NDCs must also have benefits that balance or outweigh costs, and females should modulate call production as costs and benefits change. We explored whether female song sparrows, *Melospiza melodia*, adjust calling rate to reflect differential costs and benefits of calling induced by male presence, male quality (measured by body mass and song complexity), nest predator presence and nest height. Results suggest that calls benefit females by promoting male nest guarding and that females display adaptive plasticity in call production. Specifically, calling rate increased when the male was present, and male nest guarding increased when females gave an NDC. Females called less in the presence of a model nest predator, probably because the perceived costs of predator attraction outweighed the benefits of male recruitment. Conversely, females with heavier mates called more, perhaps because the efficacy of male nest guarding increases with mass. In addition, females called more from elevated nests in the presence of the predator and decreased calling later in the day. Male song complexity failed to predict calling rate, suggesting that this sexually selected trait does not reflect direct benefits gained by producing an NDC. Plasticity in calling probably exists because context-appropriate communication elevates fitness, whereas contextual mistakes in the decision to communicate result in fitness declines.

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The complex and prominent vocalizations of male songbirds are the focus of extensive study (Nowicki & Searcy, 2004; Searcy & Andersson, 1986). However, the subtler vocalizations of females have received little attention (Gorissen & Eens, 2005; McDonald & Greenberg, 1991). One unique type of female vocalization that has been recorded in at least 15 species of North American passerines is the nest departure call (NDC). NDCs are initiated upon leaving the nest and have a characteristic acoustical structure (broadband frequency, short note duration and repetitiveness) that makes nests easy to localize and also acts to project flight trajectory (McDonald & Greenberg, 1991; Fig. 1).

Passerine nests are vulnerable to predation, and nest depredation has played a pivotal role in driving the evolution of species-level differences in incubation behaviour (Conway & Martin, 2000; Martin, 1995; Martin, Scott, & Menge, 2000; Ricklefs, 1969).

Thus, the adaptive function of highly conspicuous calls, given from nests and open to exploitation by predators, evades easy explanation. Indeed, empirical research has demonstrated that giving NDCs can increase nest predation rates (McDonald & Greenberg, 1991; Yasukawa, 1989) as well as parasitism by brown-headed cowbirds, *Molothrus ater* (Clotfelter, 1998). Thus, NDCs must have benefits that override these costs. Previously hypothesized benefits of calling include recruiting male vigilance for nest guarding during female absence (McDonald & Greenberg, 1991; Yasukawa, 1989), decreasing harassment of females by males that may mistake them for territorial intruders (Beletsky & Orians, 1985; Edwards, 1987; McDonald & Greenberg, 1991), advertising female receptivity, discouraging settlement of other females on the territory, distracting predators (McDonald & Greenberg, 1991) and recruiting males to mate-guard during incubation off-bouts (Fedy & Martin, 2009; McDonald & Greenberg, 1991).

However, due to the paucity of work on this behaviour, the actual functions of these calls and the associated costs and benefits remain poorly understood (McDonald & Greenberg, 1991). Moreover, communication systems have evolved to elevate fitness, but signalling in the wrong context may result in fitness declines (Zuk &

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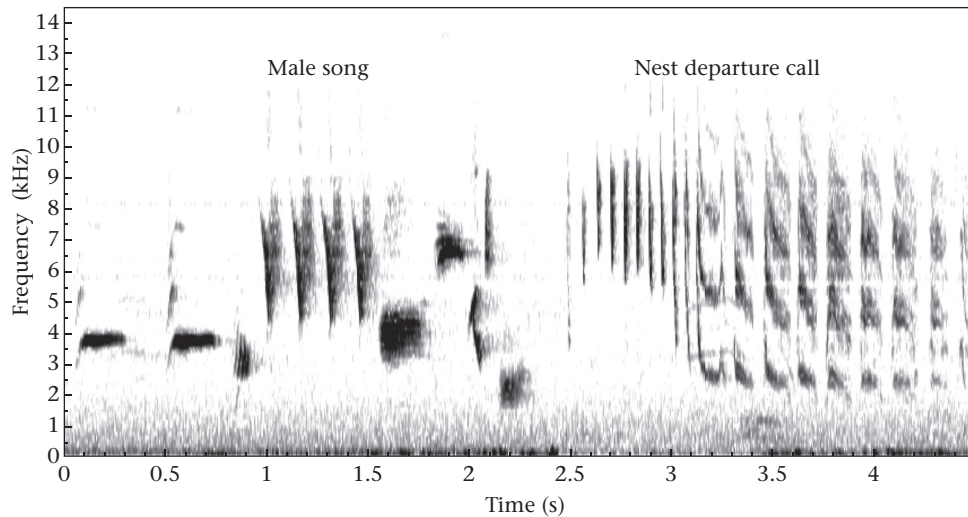


Figure 1. Nest departure call of a female song sparrow, shortly following a male song. Note the characteristic broadband frequency, short note duration and repetitiveness of the call. Nest departure calls and nest departures are often associated with the male singing in close proximity to the nest.

Kolluru, 1998; Zuk, Simmons, & Rotenberry, 1995). Thus, individuals should exhibit phenotypic plasticity in calling behaviour (Lima & Dill, 1990; McNamara & Houston, 1996; Stearns, 1989). However, no study has comprehensively investigated whether females adjust calling behaviour in a context-dependent fashion to maximize benefits and minimize costs. We address these gaps in understanding by addressing novel questions about the function and context dependency of NDCs in female song sparrows, *Melospiza melodia*. Our study had five primary objectives, which we outline below.

First, we explored whether females plastically adjust NDC production in a fashion consistent with the hypothesis that these calls function as a signal to increase male vigilance during incubation off-bouts. Given a male recruitment function, benefits of calling should be high when the male is near and available to nest-guard, but calling should have little adaptive benefit in absence of the male, such that calling rate increases in the presence of the male. The benefit of calling should also be manifest by an increase in male nest-guarding behaviour during incubation off-bouts following an NDC. Although the efficacy of nest guarding is unclear in the song sparrow, the behaviour is well documented (Hatch, 1997; Weatherhead, 1989), and as pointed out by Hatch (1997), it is unclear why the behaviour would persist if it has no potential to deter predators.

Second, we sought to determine whether the presence of a nest predator affects female call production. Avian nest predators have highly developed auditory systems and may thus use NDCs to locate nests (Eggers, Griesser, Nystrand, & Ekman, 2006; Martin, 1987a; Peluc, Sillett, Rotenberry, & Ghalambor, 2008). Thus, we predicted that females would reduce call production in the presence of perceived corvid nest predation risk as an adaptive means of reducing the likelihood of nest predation.

Third, we examined whether male quality modifies female calling behaviour. Specifically, we considered effects of two indicators of male quality on NDC production: body mass and song complexity. More massive males may be larger or may be in better body condition and have higher energy reserves. Thus, heavier males may be more effective at nest defence either due to larger size, or because they need to devote less time to foraging and self-maintenance (Martin & Horn, 1993; Sproat & Ritchison, 1993; Wallin, 1987; Winkler, 1992). In addition, greater mass may reflect high territory quality, which may increase both foraging

efficiency and time available for vigilance (van de Crommenaker, Komdeur, Burke, & Richardson, 2011; Drent & Daan, 1980; Komdeur, 1992; Martin, 1987b; Svensson & Nilsson, 1995). Thus, we predicted that benefits of calling and NDC production increase with male body mass. Song complexity is the basis for female choice in many species, including *M. melodia* (Nolan & Hill, 2004; Nowicki & Searcy, 2004; Searcy, 1984; Searcy & Andersson, 1986; Searcy & Yasukawa, 1996), and female choice of males with complex songs may be motivated by direct benefits gained in the form of paternal assistance. Thus, we predicted that benefits of calling and NDC production would increase with male song complexity (Buchanan & Catchpole, 2000; Hill, 1991; Hoelzer, 1989). However, an alternative hypothesis is that females choose males with complex songs primarily for indirect benefits, and males with more complex songs trade off mating effort against paternal effort (Burley, 1988; Møller & Thornhill, 1998; Qvarnström, Pärt, & Sheldon, 2000). In this case, nest-guarding services and NDC production might decline with song complexity. Furthermore, with respect to male quality in general, we predicted that female call production would decline less in the presence of the predator when the male was of higher quality, since benefits of male recruitment and guarding might offset costs of predator attraction in this case.

Fourth, we explored the effect of nest site location on calling behaviour (Eggers et al., 2006; Martin, 1987a; Martin, 1995; Martin et al., 2000; Peluc et al., 2008). More concealed nests may be more difficult to locate, lowering costs of calling. Indeed, across avian taxa, NDCs are given almost exclusively by species occupying marshland or grassland habitat, where dense cover may provide a buffer against nest detection (McDonald & Greenberg, 1991). Furthermore, among open-cup passerines, ground nests are subject to the lowest predation rates, with nests elevated in the canopy or shrubs experiencing higher depredation (Martin, 1993, 1995; Peluc et al., 2008). In song sparrows at our study site, nests on the ground tend to be more concealed than elevated nests (M. L. Grunst, A. S. Grunst, & J. T. Rotenberry, personal observations). Moreover, elevated nests are more exposed to attack from above by visually oriented corvid predators (Martin, 1987a; Peluc et al., 2008). Thus, we predicted that costs of calling at elevated nests would outweigh benefits, resulting in higher calling rates at ground nests than at elevated nests, and that this effect would be magnified in the presence of the predator.

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