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Parents respond in sex-specific and dynamic ways to nestling ectoparasites

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Nest ectoparasites can impose significant costs to altricial nestlings that are confined to the nest and dependent on parental care. These costs are often passed on to parents who may compensate for, or magnify, the direct costs of parasites on their nestlings through adjustments in parental care behaviour. If the effects of ectoparasites on nestlings vary across development, parents would be expected to dynamically adjust their behaviour across time with the possibility that males and females may vary in their responses. Currently, we lack a complete understanding of the potential sex differences and variation in parental care behaviour across the nestling period as a function of offspring parasite infection. Our experimental study compared disinfected and parasitized treatment groups to examine how northern fowl mites, *Ornithonyssus sylviarum*, in nests of the North American barn swallow, *Hirundo rustica erythrogaster*, affect parental care behaviour. Specifically, we addressed how provisioning rates and nest attendance behaviours (time spent at the nest) changed in response to ectoparasite infection early (day 7) and late (day 13) in the nestling period, and between male and female parents. Early in the nestling period, female provisioning rates were lower for parasitized nests than for disinfected nests whereas male provisioning rates did not differ between treatments. However, males of parasitized nests showed higher nest attendance whereas females did not alter their attendance of nestlings as a function of the parasite manipulation. Later in the nestling period, parental care behaviours changed dramatically. Male provisioning rates were higher for parasitized nests than for disinfected nests whereas female provisioning rates did not differ between treatments. Both males and females showed greater nest attendance for parasitized nests compared to disinfected nests on day 13. These findings suggest that parasites do affect provisioning and nest attendance behaviours: parental care responses differ between males and females, and are dynamic across the nestling developmental period.

Parasites exploit host resources and can elicit significant immune and behavioural responses (Lehmann, 1993; Roberts, Janovy, & Schmidt, 2012; Zhong, Pai, & Yan, 2005). Individuals suffering from parasite infections face trade-offs when finite resources are lost to parasites or are used for parasite defence (Owen, Nelson, & Clayton, 2010). This resource loss can have important fitness consequences for hosts, particularly with more virulent parasites, such as haematophagous ectoparasites that feed on offspring, as has been demonstrated for a wide range of avian species (e.g. Bouslama, Lambrechts, Ziane, Djenidi, & Chabi, 2002; Brown, Brown, & Rannala, 1995; Fitze, Clobert, & Richner, 2004; Fitze, Tschirren, & Richner, 2004; Moss & Camin, 1970; Norris & Evans, 2000; Owen et al., 2010). Birds with altricial nestlings are particularly vulnerable to ectoparasites that live in the nest material because nestlings are confined to the nest and are completely dependent on parental care (Tripet & Richner, 1997). During development, nestlings are particularly susceptible to parasites as they have limited defences with relatively immature and weak immune systems and no ability to preen or physically remove parasites (Killpack, Oguchi, & Karasov, 2013; Owen et al., 2010).

The costs of developing in nests with ectoparasites have been documented in altricial nestlings of many different species and include lower mass and body condition (e.g. Moss & Camin, 1970; Saino, Calza, & Møller, 1998; Szép & Møller, 1999), smaller skeletal size (e.g. Christe, Richner, & Oppliger, 1996a; Merino & Potti, 1995; Richner, Oppliger, & Christe, 1993), changes in the immune and stress response (Arriero, Moreno, Merino, & Martínez, 2015; Brinkhof, Heeb, Lliker, & Richner, 1999; Lobato, Moreno, Merino, Sanz, & Arriero, 2005; de Lope, Møller, & de la Cruz, 1998;

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Tschirren & Richner, 2006), development of less attractive sexual traits (e.g. Fitze & Richner, 2002; Tschirren, Fitze, & Richner, 2003), and reduced long- and short-term survival (e.g. Brown & Brown, 1986; Fitze, Clobert et al., 2004; Fitze, Tschirren et al., 2004; Merino & Potti, 1995; Richner et al., 1993). While ectoparasites can impose many important costs for nestlings, a crucial mediator of these costs is determined by how parents respond to the presence of nest parasites.

Changes in parental care in response to ectoparasites varies dramatically across species and even across studies of the same species (Table 1). Parents may provide more care to parasitized nestlings to compensate for the costs associated with parasites (Bańbura, Perret, & Blondel, 2004; Bouslama et al., 2002; Hurtrez-Boussès, Blondel, Perret, Fabreguettes, & Renaud, 1998; Tripet & Richner, 1997). A different evolutionary strategy may lead parents to favour self-preservation over costly parental care because parasitized nestlings may be of lower quality and have reduced chances of survival and reproduction compared to potential future offspring (e.g. Avilés, Pérez-Contreras, Navarro, & Soler, 2009; Darolova, Hoi, & Schleicher, 1997; Møller, 1994). Nest ectoparasites can also feed on adults, so limiting time at the nest can also reduce risk of transmission for parents (e.g. Christe, et al., 1996a; Møller, 1990; Richner & Tripet, 1999).

While there is clear evidence that parental behaviour in some species is influenced by nest ectoparasites, in other species, parents show no change in their parental care if nests are infected (Table 1). A lack of behavioural response from parents could be because some species of parasites, or levels of infection, may not cause large impacts on nestling condition, growth and development (e.g. Thomas & Shutler, 2001). It could also be that feeding rates of these species are inflexible and thus are unresponsive to parasite infestation, even if nestlings are facing resource trade-offs between development and parasite defence (Morrison & Johnson, 2002; Walker & Rotherham, 2011).

While behavioural responses vary across species, there is also evidence that individuals within a species show different strategies for dealing with nest ectoparasites. Several investigators have observed variation in parental care responses of males and females to the presence of parasites in the nest (Avilés et al., 2009; Christe et al., 1996a; Tripet, Glaser, & Richner, 2002; Hurtrez-Boussès & Renaud, 2000). Sex-specific responses to parasites are predicted as males and females often show differences in parental care behaviour without parasites. Theory predicts that the evolutionary interests and breeding opportunities of males and females differ, which causes them to evolve and maintain different parenting strategies (Houston, Székely, & McNamara, 2013; Sheldon, 2002). These underlying sex differences in parental care behaviour may be magnified or changed by the presence of parasites and should be taken into account when trying to assess how parents respond to nestling parasite infections.

While important sex differences in parental care behaviour have been established, we lack information about how such sex-specific differences may vary across the nestling developmental period as a function of ectoparasite infection. Nestlings change dramatically over the course of the nestling period in terms of their growth rate (McCarty, 2001), development of the acquired immune system (Owen et al., 2010), physiological stress response (Sims & Holberton, 2000), regulation of body temperature (Morton & Carey, 1971), growth of flight plumage (Pereyra & Morton, 2001), production of fat stores (Riou & Hamer, 2010) and begging behaviour (Leonard & Horn, 2006). Such developmental changes mean that food and care requirements of nestlings also change across development and that parents have adapted, often in sex-specific ways, to match these needs (García-Navas, Ferrer, & Sanz, 2012; Sonerud et al., 2014; Steen, Sonerud, & Slagsvold, 2012; Wiebe & Slagsvold, 2014). The effects of the parasites themselves are also likely to be inconsistent across development. Parasites can have large impacts early in development (Norris & Evans, 2000; Saino et al., 1998), and these impacts may differ from those experienced by older nestlings (Reed et al., 2012). Susceptibility to parasites may shift across time as older nestlings develop immune systems that can target ectoparasites and shorten feeding time or even reduce parasite fecundity and survival (Killpack et al., 2013; Owen et al., 2010). However, ectoparasites could also further stress nestlings later in development as they rapidly reproduce, increasing the intensity of infection over time (Proctor & Owens, 2000).

While many different patterns across and within species exist for how parents adjust their behaviour in response to nest ectoparasites (Table 1), there are several important questions remaining. First, we know little about whether there are sex differences in parental care as a function of nestling parasites. Specifically, experiments that both remove and add specific numbers of parasites have not been conducted in order to systematically study the effect of parasites on male and female contributions to parental care. Second, to fully understand how parasites influence parental care we must determine whether behavioural changes within each sex are static or dynamic across development. This will allow us to determine whether measuring parental behaviour at one time point, as many studies do, is enough to infer the overall direction and intensity of parasite-induced changes in parental behaviour. To address these questions, we examined the link between the presence of a haematophagous ectoparasite, the northern fowl mite, *Ornithonyssus sylviarum*, and parental care behaviour in the North American barn swallow, *Hirundo rustica erythrogaster*, using an experimental manipulation of parasites and measuring parental care of males and females during standardized time points both early and late in the nestling development period.

METHODS

Study System

Barn swallows are small migratory passerines that form social pairs and exhibit biparental care of altricial nestlings. They nest in loose social groups in human-made structures, most commonly in barns, where they build mud cup nests and raise three to six nestlings per brood and have up to three broods per breeding season (Turner, 2006). Colony size for these birds can range from solitary to up to 50 breeding pairs. Breeding within the colonies is not highly synchronous and fertile females are present throughout the breeding season (Turner, 2006). Extrapair copulations are quite common and up to 40% of nestlings are sired by a male other than their social father (Safran, Neuman, McGraw, & Lovette, 2005). Distances between active nests depend on the structure of the breeding site and colony size, but minimal distance is about 2.5 m. Barn swallows are obligatory aerial insectivores and make frequent trips to the nest to provision nestlings with insects (Turner, 2006). The primary nest ectoparasite of this species in North America is the blood feeding northern fowl mite, which lives in nest material and feeds intermittently on nestlings. These parasites overwinter in nests and can easily be manipulated by disinfecting nests or adding parasites collected from other nests (Hund, Blair, & Hund, 2015; Møller, 1990). The costs of mite infections have been well established in European subspecies (*Hirundo rustica rustica*), where nestlings that were exposed to mites during development had higher mortality, lower body mass, changes in T-cell-mediated immune responses and reduced feather growth (Møller, 1990; Saino, Ferrari, Romano, Ambrosini, & Møller, 2002).