



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.

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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 (Triplet & 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 (Bañbura, 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).

Table 1
Previous research findings related to parental care and nest ectoparasites

Avian species	Nest ectoparasite	Parasites experimentally manipulated?	Males and females observed separately?	Time points observed	Effect of ectoparasites on parental care	Source
Barn swallow, <i>Hirundo rustica</i>	Tropical fowl mites (<i>Ornithonyssus bursa</i>)	Disinfected and parasites added	No	16: daily	Provisioning rates decreased	Møller (1994)
Blue tit, <i>Cyanistes caeruleus</i>	Hen flea (<i>Ceratophyllus gallinae</i>)	Disinfected and parasites added	No	1: day 13	Provisioning rates increased	Tripet and Richner (1997)
	Blow fly larvae (<i>Protocalliphora</i> spp.)	Disinfected	Yes	1: day 13	Females increased sanitation behaviour; males did not change	Hurtrez-Boussès et al. (1998)
	Ticks (<i>Ixodes ricinus</i>); hen fleas (<i>Ceratophyllus gallinae</i>); blow fly larvae (<i>Protocalliphora</i> sp.)	Disinfected	No	2: day 9, day 13	Provisioning rate increased	Bouslama et al. (2002)
	Hen flea (<i>Ceratophyllus gallinae</i>)	Disinfected and parasites added	Yes	1: day 10	Females increased provisioning and decreased sanitation behaviours; males did not change	Tripet et al. (2002)
Common swift, <i>Apus apus</i>	Blow fly larvae (<i>Protocalliphora</i> sp.)	Disinfected	Yes	1: day 13	Total provisioning decreased; males and females did not differ significantly	Bañbura et al. (2004)
	Louse flies (<i>Crataerina pallida</i>)	Disinfected and parasites added	No	18: every other day	No effect	Walker and Rotherham (2011)
Eurasian kestrel, <i>Falco tinnunculus</i>	Carnid fly (<i>Carnus hemapterus</i>)	No: nestboxes (more parasites) vs natural nests	No	1: day 9	No effect	Fargallo, Blanco, Potti, and Viñuela (2001)
Great tit, <i>Parus major</i>	Hen fleas (<i>Ceratophyllus gallinae</i>)	Disinfected and parasites added	No	1: day 13	Males increased provisioning; females did not change	Christe et al. (1996a)
	Hen fleas (<i>Ceratophyllus gallinae</i>)	Disinfected and parasites added	Only females	1: day 12	Sanitation behaviour increased; no change in provisioning	Christe et al. (1996b)
	Hen fleas (<i>Ceratophyllus gallinae</i>)	Disinfected	No	1: day 9	No effect	Fitze, Clobert et al. (2004); Fitze, Tschirren et al. (2004)
	Hen fleas (<i>Ceratophyllus gallinae</i>)	Disinfected and parasites added	No	1: day 9	Reduced brooding; no change in provisioning	Gallizzi et al. (2008)
House finch, <i>Carpodacus mexicanus</i>	Mites (<i>Pellonyssus reedi</i>)	No: early (more parasites) vs late in season	Yes	1: day 11	Decreased provisioning for both males and females	Stoehr, Nolan, Hill, and McGraw (2000)
House wren, <i>Troglodytes aedon</i>	Blow fly larvae (<i>Protocalliphora</i> sp.)	Disinfected	No	1: day 12	No effect	Morrison and Johnson (2002)
Marsh tit, <i>Parus palustris</i>	Hen fleas (<i>Ceratophyllus gallinae</i>)	Parasites added	No	1: day 10–12	No effect	Nilsson (2003)
Penduline tit, <i>Remiz pendulinus</i>	Mites (<i>Dermanyssus hirundinis</i>)	Disinfected	No	11: days 7–17	Decreased provisioning	Darolova et al. (1997)
Pied flycatchers, <i>Ficedula hypoleuca</i>	Mites (<i>Dermanyssus gallinoides</i>); blow fly larvae (<i>Protocalliphora azurea</i>); hen fleas (<i>Ceratophyllus gallinae</i>)	Disinfected	Yes	2: day 3, day 9	Females increased nest sanitation behaviour; no change in provisioning	Cantarero et al. (2013)
Tree swallow, <i>Tachycineta bicolor</i>	Fleas (<i>Siphonaptera</i>); blow flies (<i>Protocalliphora braueri</i>)	No	No	1: day 10	No effect	Thomas and Shutler (2001)
Spotless starling, <i>Sturnus unicolor</i>	Carnid flies (<i>Carnus hemapterus</i>)	Eggs cleaned to remove spots left from parasites	Yes	1: day 4	Males decreased provisioning; females did not change	Avilés et al. (2009)

Study Design

This study was conducted at 11 barn swallow breeding sites in Boulder, Jefferson and Weld counties in Colorado between July and August of 2013. All of the field sites used for this study were horse barns and represented medium-sized breeding colonies ranging from 15 to 40 breeding pairs. Parental care observations were part of a reciprocal cross-fostering experiment focused on the heritability and effects of ectoparasites on feather colour development in the North American barn swallow. All nests used in this study had brood sizes of four to five nestlings upon hatching. For the reciprocal cross-fostering experiment, nestlings were paired by hatch date and two of the nestlings were exchanged between paired nests, matching mass between the exchanged nestlings as closely as possible and thus maintaining the size rank order of the nestlings in each nest. When finished, each nest had the same number of nestlings that were approximately the same size and in the same size rank order as the original brood.

We captured adult barn swallows at each field site using mist nets and targeted night captures. Each individual was marked with both a U.S. Geological Survey metal numbered leg band and a unique combination of colour bands. We then conducted visual observations to match individual males and females, and thus breeding pairs, to their respective nests using their unique colour combinations.

We monitored nests every 3–4 days to determine clutch initiation and every day near the end of the incubation period to determine hatch date. The ectoparasite loads of experimental nests were manipulated by first disinfecting all nests and then adding parasites back into a random subset of half of the nests. We disinfected nests by first temporarily removing nestlings and heating the nest to 125 °C using a heat gun (Hund et al., 2015) on day 2 of the nestling period (day 0 = hatch date). Heating nests took <5 min. Nestlings were returned to the nest when the nest temperature returned to <29 °C, usually within 8 min after heating. Temperatures during heating and cooling were monitored using a digital infrared thermometer. Nests were then either left disinfected, or had 100 live field-collected mites added to them. This number of mites represents a mild to moderate parasite infection in natural barn swallow nests (Hund et al., 2015). This parasite addition technique is similar to that used in other studies, yet our study differs in that we were able to disinfect nests in both treatment groups in the field (Christe et al., 1996a; Christe, Richner, & Oppliger, 1996b) without the use of chemicals (Møller, 1994), thus controlling for and minimizing the effects of nest disinfection on nestlings. Nest parasite levels were monitored for both treatment groups on days 2, 6, 9 and 12 of the nestling period ($N = 23$ parasitized nests, $N = 22$ disinfected nests). Specifically, we counted mites on these days by placing a cupped hand into the nest for 30 s and then counting the number of mites on the hand (Møller, 1994), and by counting the number of mites on each nestling as well as on the container used to hold each nestling. We combined both mite counts (from the nest and from each nestling) together as one mite score for each nest and used these scores to examine the effect of treatment on mite intensity.

Behavioural Observations

We conducted parental care observations for 45 nests early in the nestling period (day 7) and for 36 of these nests late in the nestling period (day 13). Altricial barn swallow nestlings fledge from the nest in 18–20 days, thus observations on day 7 captured the early to middle stage of development (hereafter referred to as 'early') and observations on day 13 captured a late stage of development (hereafter referred to as 'late'). Barn swallow nestlings

show rapid growth during the nestling period and the 6 days between the two observation periods encompass significant changes in nestling body size, behaviour and development. In the beginning of the nestling period (days 0–5), nestlings are unable to sufficiently thermoregulate on their own (Marsh, 1980), and thus females devote a large portion of parental care to brooding (Sanz & Tinbergen, 1999). As we were interested in male and female differences in provisioning behaviour, we choose day 7 of the nestling period for our first set of behavioural observations since both females and males begin to devote a large proportion of parental effort to feeding nestlings at this time. Day 13 represents the last time point that nestlings could be safely handled (without premature fledging) to quantify nest parasites accurately.

Behavioural observations took place in the mornings between 0600 and 1000 hours because this is the most active feeding time for barn swallows (Maguire & Safran, 2010). After a 15–30 min habituation period when parents returned to normal behaviour (no alarm calling), we collected data on parental care behaviour for 1 h. We observed only one experimental nest at a time during the observational time period. Parents were observed from as far away as possible while still being able to identify individual colour combinations (approximately 9–10 m from the nest) using binoculars to reduce disturbance. Because of the layout of some field sites, we collected observations from behind a blind or after longer habituation periods (similar to Maguire & Safran, 2010). We counted the number of visits by both males and females to their nests during each observation period. We used a total tally of all visits (male and female combined) as an indication of the total provisioning effort (Maguire & Safran, 2010). An examination of combined visits allowed us to determine whether parasites influence overall parental care in addition to sex-specific responses. As is typically the case for provisioning behaviour studies, we could not precisely identify or quantify food items that parents brought to nestlings during each visit; however, we used visits to the nest as a proxy for provisioning effort (e.g. Avilés et al., 2009; Nilsson, 2003; Spencer, 2005; Thomas & Shutler, 2001). When possible, we also kept track of sanitation behaviour, which involved the removal of nestling faecal sacs by parents. Sanitation behaviour was rare compared to feeding behaviour and typically always preceded feeding behaviour when it did occur. On average, parents performed sanitation behaviour 1.2 times per observation period on day 7 and 1.1 times on day 13. Given the low frequency of this behaviour, we chose not to analyse it as part of this study. Each visit to the nest by parents has some energetic cost, regardless of the activity, and since the most common activity at the nest by parents was feeding, we believe using the number and frequency of visits during a standard observation length provides a robust estimate of provisioning behaviour.

We also recorded data on nest attendance by quantifying the total length of time during the observation period that parents spent at the nest. The time at the nest was not correlated with visit number and we used it as a proxy for other forms of parental care behaviour such as brooding, nest sanitation, preening and guarding. Regardless of the behaviour, we considered time spent at the nest to be an investment in parental care. As with visits, we looked at nest attendance for each sex separately, as well as total time at the nest (male and female combined) to quantify the total parental care that nestlings received. Some nests ($N = 9$) were only observed on day 7 due to field constraints or nest failure prior to day 13; thus the sample size for these two observation periods varies slightly.

Ethical Note

Behavioural observations and handling of adults and nestlings were done in accordance with guidelines set by the University of

Colorado Institutional Animal Care and Use Committee (IACUC). All procedures in this study were approved by IACUC (protocol number 1303.02). Birds in both experimental groups did not appear to suffer from nest manipulations or from measurements and blood collection.

Statistical Analysis

We used the statistical package R version 3.1.2 (R Foundation for Statistical Computing, Vienna, Austria) to analyse data collected on day 7 ($N = 45$ nests) and day 13 ($N = 36$ nests, a subset of the 45 nests analysed on day 7). Using a Welch two-sample t test, we compared mite intensity and brood size across treatments for both time points. Both visit frequency and time at the nest were compared using a mixed-effects linear model for both day 7 and day 13. We applied general mixed-effects linear models using the 'nlme' package (version 3.1-115). For each model, we included clutch size and observation date as fixed effects, and we controlled for site as a random effect to account for potential nonindependence of nests at the same breeding site. The variables clutch size, observation date and site (identity of the breeding site where nests were located) were kept in all final models whether they were statistically significant or not, as we wanted our models to reflect the structure of our data (across sites, dates and brood sizes). We report the least square means (LSM) for parasitized and disinfected treatment groups for all significant results. When warranted, we applied log transformations to normalize data distributions; this was done for all nest attendance data. We also report raw means and standard errors for all nest attendance data. For each time point, we created models for the combined provisioning rate and nest attendance time, as this was the total care experienced by nestlings. Because we were interested in how parasites were influencing parental care behaviour within each sex specifically, we also created models for females and males separately during each time point for visits and nest attendance. As observed in the past (e.g. Maguire & Safran, 2010), it is clear that male and female barn swallows show significant underlying differences in their provisioning behaviour. Thus, we modelled female and male parental care behaviour separately. Although our data were part of a reciprocal cross-fostering experiment (broods were of mixed parentage), all nests were subjected to the same treatment and the effect of this manipulation did not influence behaviours of interest in this study (parental care). Hubbard (2014) used the same cross-fostering methods used in our study at the same breeding sites in 2012 and found no significant differences in nestling mass or mortality between experimental and nonexperimental nests. Hubbard (2014) also found that nestling growth rates, final mass and mortality were not significantly different between exchanged nestlings and nestlings that remained in their home nest.

RESULTS

Nests in the parasitized treatment had significantly higher combined mite scores than nests in the disinfected treatment on day 7 (parasitized: mean \pm SD = 19.88 ± 27.38 , minimum = 5, maximum = 87; disinfected: 0.92 ± 2.21 , minimum = 0, maximum = 10; Welch two-sample t test: $t_{23,28} = 3.38$, $P = 0.0025$) and on day 13 (parasitized: mean \pm SD = 105.96 ± 123.35 , minimum = 6, maximum = 380; disinfected: 4.00 ± 7.96 , minimum = 0, maximum = 32; $t_{23,12} = 4.04$, $P = 0.0005$), indicating that our experimental parasite manipulations were effective. Brood size did not differ significantly between treatment groups at either time point, on day 7 (mean \pm SD: parasitized: 4.41 ± 0.50 ; disinfected: 4.31 ± 0.55 ; $t_{47,9} = 0.732$, $P = 0.47$) or day 13 (mean \pm SD:

parasitized: 4.17 ± 0.76 ; disinfected: 4.08 ± 0.63 ; $t_{44,72} = 0.45$, $P = 0.65$). For each parent, visit number was not correlated with time spent at the nest on day 7 (mixed-effects linear model: males: $F_{1,37} = 0.361$, $P = 0.72$; females: $F_{1,37} = 0.046$, $P = 0.83$) or on day 13 (males: $F_{1,32} = 0.84$, $P = 0.31$; females: $F_{1,32} = 1.54$, $P = 0.221$), indicating that these behaviours were independent from each other.

Day 7

Provisioning

Disinfected nests had significantly more combined visits than parasitized nests (LSM: parasitized: 21.95 ± 1.83 ; disinfected: 26.93 ± 1.89 ; mixed-effects linear model: $F_{1,37} = 4.52$, $P = 0.04$; Fig. 1a). This pattern was driven by females, which visited disinfected nests significantly more than parasitized ones (LSM: parasitized: 11.38 ± 0.93 ; disinfected: 15.38 ± 0.89 ; mixed-effects linear model: $F_{1,37} = 9.46$, $P = 0.0039$; Fig. 1c). There was no significant difference in male visits between parasitized and disinfected nests (mixed-effects linear model: $F_{1,37} = 0.087$, $P = 0.77$; Fig. 1b).

Nest attendance

There was no significant difference in the combined nest attendance time between treatment groups (mean \pm SE: parasitized: 22.19 ± 3.36 min; disinfected: 13.39 ± 1.91 min; mixed-effects linear model: $F_{1,37} = 2.77$, $P = 0.12$; Fig. 2a). Female nest attendance time did not differ significantly between treatment groups (mean \pm SE: parasitized: 15.17 ± 1.96 min; disinfected: 9.83 ± 1.64 min; mixed-effects linear model: $F_{1,37} = 3.32$, $P = 0.078$; Fig. 2c), but males spent significantly more time at parasitized nests than at disinfected nests (LSM: parasitized: 0.63 ± 0.09 ; disinfected: 0.37 ± 0.09 ; mean \pm SE: parasitized: 7.03 ± 1.78 min; disinfected: 3.55 ± 0.85 min; mixed-effects linear model: $F_{1,37} = 4.64$, $P = 0.038$; Fig. 2b).

Day 13

Provisioning

During the late nestling period, parasitized nests had significantly more combined visits compared to disinfected nests (LSM: parasitized: 23.62 ± 2.18 ; disinfected: 17.55 ± 2.40 ; mixed-effects linear model: $F_{1,32} = 4.39$, $P = 0.044$; Fig. 3a). This pattern was driven by males, which visited parasitized nests significantly more compared to disinfected nests (LSM: parasitized: 12.33 ± 1.20 ; disinfected: 8.25 ± 1.25 ; mixed-effects linear model: $F_{1,32} = 5.54$, $P = 0.025$; Fig. 3b). There was no significant difference in female visits between parasitized and disinfected nests (mixed-effects linear model: $F_{1,32} = 1.07$, $P = 0.31$; Fig. 3c).

Nest attendance

The combined nest attendance time was significantly greater for parasitized nests than for disinfected nests (LSM: parasitized: 0.57 ± 0.074 ; disinfected: 0.33 ± 0.076 ; mean \pm SE: parasitized: 5.95 ± 1.21 min; disinfected: 2.29 ± 0.55 min; mixed-effects linear model: $F_{1,32} = 4.93$, $P = 0.033$; Fig. 4a). This pattern was consistent for both females (LSM: parasitized: 0.57 ± 0.074 ; disinfected: 0.33 ± 0.076 ; mean \pm SE: parasitized: 4.64 ± 1.09 min; disinfected: 1.90 ± 0.55 min; mixed-effects linear model: $F_{1,32} = 4.92$, $P = 0.034$; Fig. 4c) and males (LSM: parasitized: 0.33 ± 0.031 ; disinfected: 0.131 ± 0.031 ; mean \pm SE: parasitized: 1.32 ± 0.19 min; disinfected: 0.39 ± 0.06 min; mixed-effects linear model: $F_{1,32} = 19.88$, $P = 0.0001$; Fig. 4b).

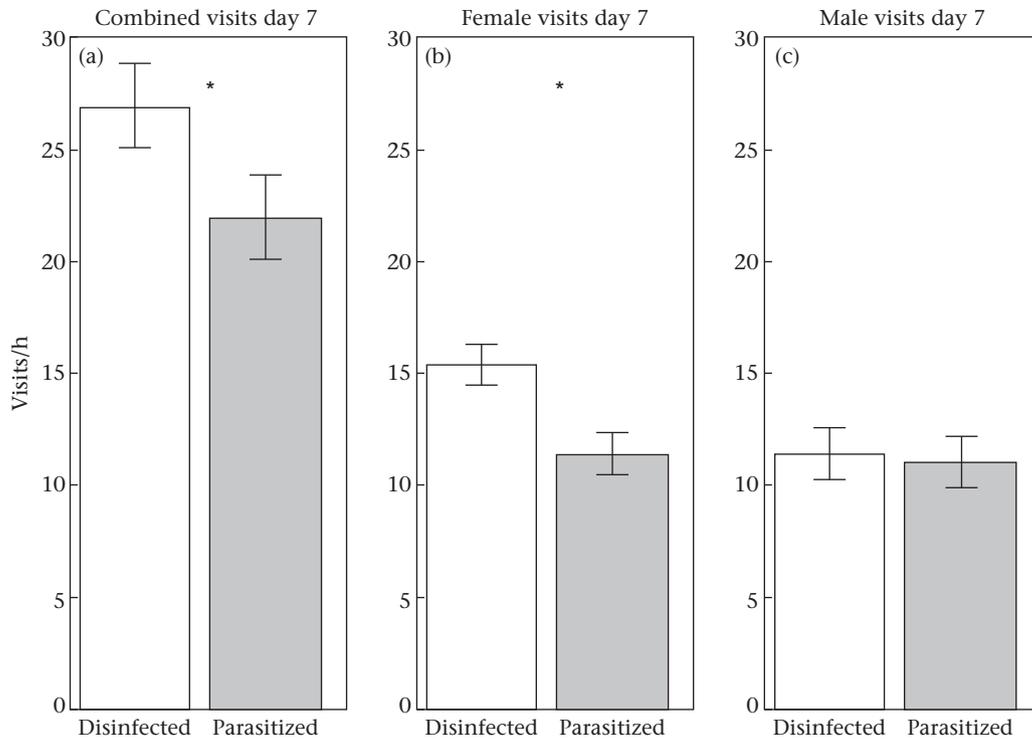


Figure 1. Least square mean \pm SE rate of nest visits by parental barn swallows on day 7 for disinfected (white bars, $N = 22$) and parasitized (grey bars, $N = 23$) treatments: (a) combined (male and female) nest visits; (b) female nest visits; (c) males nest visits. Mixed-effects linear models with brood size and date as fixed effects and breeding site as a random effect: * $P < 0.05$.

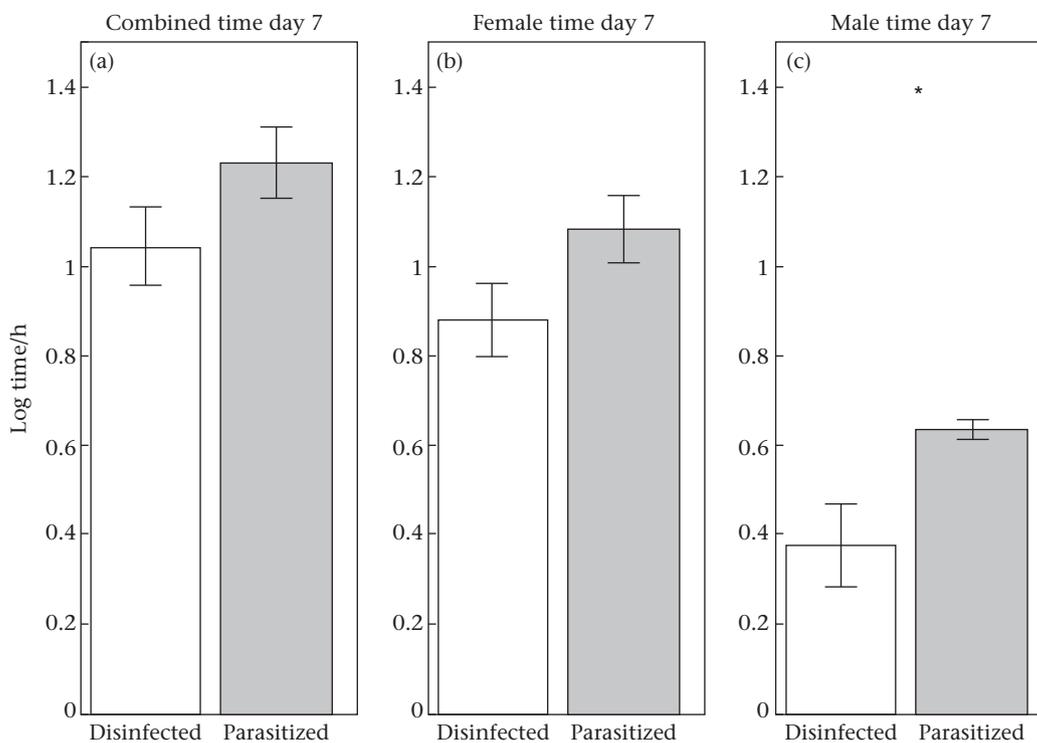


Figure 2. Least square mean \pm SE nest attendance (log time/h) by parental barn swallows on day 7 for disinfected (white bars, $N = 22$) and parasitized (grey bars, $N = 23$) treatments: (a) combined (male and female) nest attendance; (b) female nest attendance; (c) male nest attendance. Mixed-effects linear models with brood size and date as fixed effects and breeding site as a random effect: * $P < 0.05$.

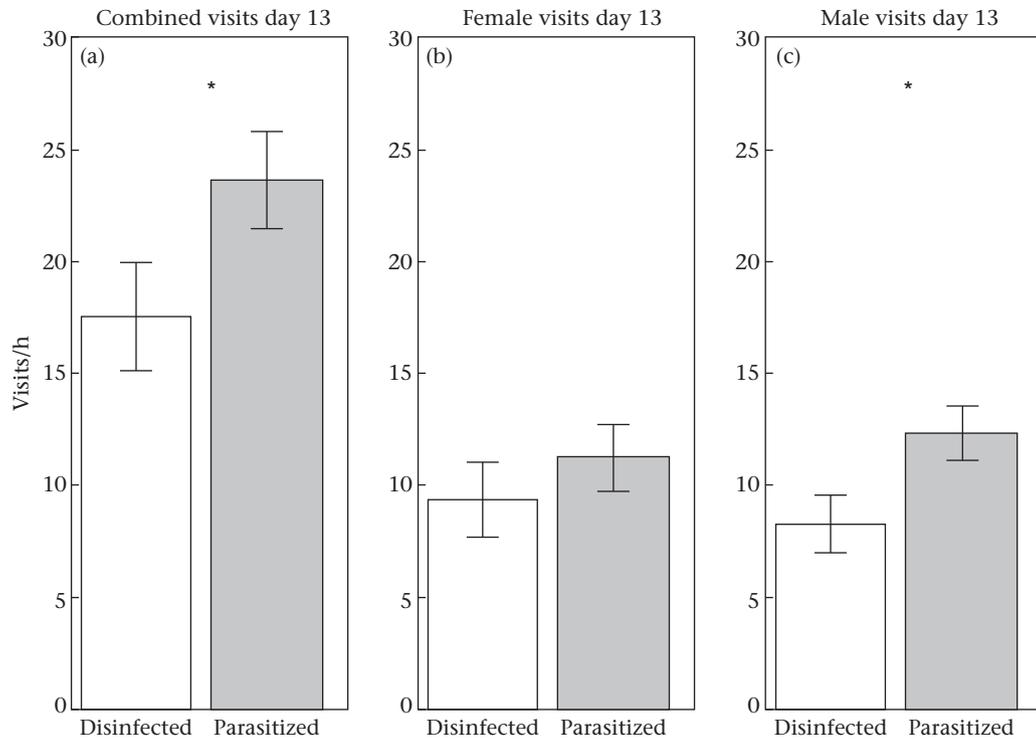


Figure 3. Least square mean \pm SE rate of nest visits by parental barn swallows on day 13 for disinfected (white bars, $N = 18$) and parasitized (grey bars, $N = 18$) treatments: (a) combined (male and female) nest visits; (b) female nest visits; (c) males nest visits. Mixed-effects linear models with brood size and date as fixed effects and site as a random effect: $*P < 0.05$.

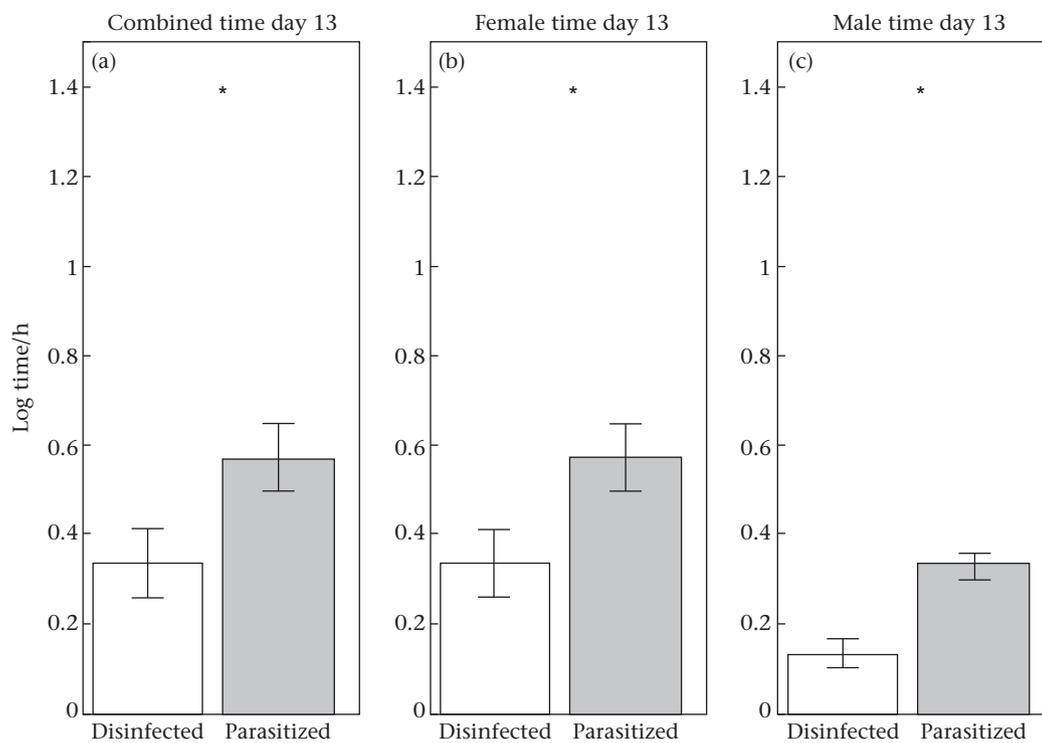


Figure 4. Least square mean \pm SE nest attendance (log time/h) by parental barn swallows on day 13 for disinfected (white bars, $N = 18$) and parasitized (grey bars, $N = 18$) treatments: (a) combined (male and female) nest attendance; (b) female nest attendance; (c) male nest attendance. Mixed-effects linear models with brood size and date as fixed effects and site as a random effect: $*P < 0.05$.

DISCUSSION

Early in the nestling period, nests infected with ectoparasites were visited at a significantly lower rate than disinfected nests. This pattern was largely driven by females, which visited parasitized nests at a lower rate than disinfected nests, whereas males did not differ in their provisioning behaviour as a function of the experimental treatment. Interestingly, this pattern was reversed later in the nestling period when nestlings were much larger and near fledging; parasitized nests were visited at a higher rate than disinfected nests. Males visited parasitized nests 1.6 times more than disinfected nests during this time period, while females did not differ in the number of visits between treatments.

There are several possible explanations for why male and female provisioning rates might vary in response to ectoparasites. One potential explanation, as shown in a previous study (Avilés et al., 2009), is that males and females may detect and respond to different cues of parasitic infestations. These cues could include visible detection of the parasites themselves or marks left on eggs or nestlings from parasites (Avilés et al., 2009). Such visible cues may be dependent on the intensity of the infection, but should be present from the start of breeding if a nest is infected. Alternatively, parents may detect cues of parasite infections from the nestlings themselves as changes in body condition, growth rates or begging behaviour. Prior research has shown that nestlings significantly increase rates of begging when exposed to parasites in order to replace lost resources (Cantarero, López-Arrabé, Redondo, & Moreno, 2013; Christe et al., 1996a). Such behavioural changes may not be present until later in development when nestlings have been exposed to parasites for a longer period. If males and females detect and respond to different parasite cues that are present at different time points in development, this could lead to our observation of temporal sex differences in parental care behaviour.

Another potential explanation for the strong sex differences in provisioning between development stages is a difference in investment strategies for each sex based on the cost of, and opportunities for, current and future reproduction (Trivers, 1972). In biparental care species, it is thought that investing in parental care yields fewer rewards for males, which face reduced fitness through extrapair mating, than for females, as they could be caring for offspring that are genetically unrelated (Matysioková & Remeš, 2013; Queller, 1997; Sheldon, 2002). Time spent provisioning nestlings can also result in lost mating opportunities for males (Queller, 1997). It is possible that early in nestling development males provision at a minimal rate and do not respond to the presence of parasites. For females, there could be greater advantage in investing in future broods with higher-quality nestlings (Ackerman & Eadie, 2003; Horvathova, Nakagawa, & Uller, 2012; Sargent & Gross, 1985), hence this might be one explanation for why female barn swallows with parasites in their nests provisioned nestlings at a lower rate during the early nestling period and did not alter rates during the latter part of nestling development in our study. Towards the end of the nestling period, males may increase their feeding rate to avoid divorce if breeding success is low (Christe et al., 1996a). In this case, males may compensate for the costs of parasites when the probability of fledging is greater (Ackerman & Eadie, 2003). If nestlings survive until day 13 while exposed to parasite infestations, this may indicate to the male parent that they are more fit than nestlings that do not survive. If this is true, males may gain a greater reproductive benefit by investing more heavily in nestlings with parasites at a later stage of development compared to early in development. To a lesser extent, the same principle may be true for females who go from visiting parasitized nestlings less early in development to visiting them the same as disinfected nestlings later in development.

While provisioning rates changed dramatically between the sexes across developmental time, nest attendance behaviour (time spent at the nest per hourly observation period) was similar for males and females both early and late in the nestling period. We predicted a priori that parental barn swallows might show avoidance behaviour in response to the presence of nest ectoparasites, as blood mites have been shown to have negative consequences for both adults and nestlings (Gallizzi, Alloitteau, Harrang, & Richner, 2008; Møller, 1990; Morrison & Johnson, 2002). If this were the case, we would expect parents to spend less time at the nest in order to avoid transmission. Instead, the combined nest attendance time early in development did not differ significantly between treatments, and males actually spent more time at parasitized nests than at disinfected nests early in the nestling period. Later in development, this pattern was even stronger; combined nest attendance time was significantly greater for parasitized nests, and both males and females spent nearly double the nest attendance time at parasitized nests than at disinfected nests. These patterns suggest that avoidance of parasites may not be an important factor driving parental care in barn swallows. Parents appear to be attending parasitized nests perhaps at the expense of greater exposure to haematophagous mites (Hurtrez-Boussès & Renaud, 2000).

Prolonged nest attendance may also indicate that parents are prioritizing behaviours other than provisioning to care for parasitized nestlings. Longer nest attendance times align with findings of other studies showing that parents allocate more time to nest sanitation and to brooding when their nestlings are infected with parasites (Cantarero et al., 2013; Triplet & Richner, 1999; Simon et al., 2005). Occasionally, female adults will even decrease sleep to engage in sanitary behaviours in response to ectoparasites (Christe et al., 1996b). We could be seeing evidence of such a trade-off between provisioning and other parental care behaviours in our study when males early in development and females later in development both had higher nest attendance but showed no changes in provisioning between treatments.

Given the differences we found in parental behaviour care behaviour between day 7 and day 13, we would encourage future studies to measure how parasites impact behaviour at even more time points during development. In particular, with newly hatched and very young nestlings (days 0–6), as this time period may be important but was not covered in our study. Future work could also focus on behavioural responses to nest parasites across the entire breeding season, including comparisons not only among different nestling periods but also among different broods (first versus second or third).

Conclusions

We examined the parental care responses of male and female barn swallows at two times during the nestling period (early and late) as a function of an ectoparasite addition and removal experiment. Parental care responses to parasites were both sex-specific and dynamic across the nestling period. Multiple observations across development for males and females were required to capture the nature of these complex behavioural responses to nest parasites. Future research on nestling begging behaviour and specific nest attendance behaviours for both males and females will further illuminate the trade-offs and costs associated with nest parasites and how they change over the course of nestling development. As of yet, there is no definitive pattern of how parasites affect parental care behaviour across species. The lack of a detectable pattern across species has been attributed to varying life history traits across species such as food sources, habitat and frequency of reproduction, and to variation in the costs associated

with different parasite intensities and species (Christe et al., 1996a; Kölliker & Richner, 2001; Møller, Allander, & Dufva, 1990; Morrison & Johnson, 2002; Walker & Rotherham, 2011). Another important factor to consider is that by observing differences in provisioning rate across the nestling period and for each parental sex, we were able to take into account the dynamic relationship between ectoparasites and behaviour. Studies that exclusively examine total provisioning rate and ectoparasite intensity at one point during the nestling period may miss more complex patterns. Our results demonstrate that parental care changes over time for both males and females and, thus, that behavioural responses to nest ectoparasites are far from static.

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