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Male spotless starlings adjust feeding effort based on egg spots revealing ectoparasite load

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Parents may vary their parental behaviour and investment in reproduction in response to parasite-induced changes in the fitness prospects of their offspring. Thus, parents may use the physical condition of their offspring, or any other trait related to parasite load, to adjust parental effort. The immaculate eggs of the spotless starling, *Sturnus unicolor*, often become densely spotted owing to the activity of the ectoparasite carnid fly *Carnus hemapterus*. Spot density anticipates the intensity of fly infestation suffered by nestlings and, therefore, may serve as a cue for parents to adjust reproductive investment. By cleaning spots produced by *C. hemapterus* on eggs of spotless starlings, we manipulated the parasite's traces revealing its presence in broods of starlings, without modifying the level of infestation, to test whether parents use these signals to adjust reproductive effort. We found support for the hypothetical negative effect of *Carnus* flies since nestlings raised in nests with a higher fly load had lower body mass. The experimental egg cleaning during incubation did not change the intensity of carnid fly infestation during nestling development. However, it had a significant positive influence on paternal but not maternal effort. Our experimental results support the idea that spotless starling males adjust their effort in response to their perception of the fitness prospects of their nestlings as indirectly estimated by traces of parasites on the eggshells. As far as we know, this is the first evidence of the use of parasite traces to infer risk of parasitic infestation by animal hosts.

Parasites can impose fitness costs by reducing their host's fecundity, survival and reproductive success when they affect developing offspring. Selection therefore favours the evolution of physiological and behavioural defensive mechanisms in the hosts to reduce the harmful effects of parasitism (e.g. Loye & Zuk 1991; Toft et al. 1991). In birds, it has been experimentally demonstrated that ectoparasites negatively affect both offspring body mass and fledging success (Richner et al. 1993). Nestling body mass is a reliable predictor of nestling survival (e.g. Perrins 1965; Smith et al. 1988; Tinbergen & Boerlijst 1990; Moreno et al. 2005a) and, therefore, ectoparasites may considerably lower the value of the current brood to the parent. Parents may, therefore, vary their parental behaviour and the investment in reproduction in response to parasite-induced changes in the fitness prospects of their offspring. For instance, parents could reduce their investment in the current parasitized brood in order to invest more in future broods (see Linden & Møller 1989; Richner & Tripet 1999). Alternatively, parents could increase their investment to compensate for the negative effects of parasites on the current brood (e.g. Christe et al. 1996; Tripet & Richner 1997). The optimal reproductive strategy of parents in terms of reproductive effort is likely to depend on the fitness costs of parasite infestation for parents and their offspring, as well as on the possibility of future reproduction (e.g. Stearns 1992; Møller 1997).

Studying behavioural responses of parents to ectoparasite-induced changes in the reproductive value of the offspring is difficult because parental responses may, for instance, be driven by the effects of ectoparasites on offspring begging behaviour. Parasites may affect the begging behaviour of nestlings that parents evaluate to adjust provisioning rates either directly for their own benefit or indirectly through an increase in nestling needs (e.g. Wright & Leonard 2002). Parents, thereby, by simply following the rule of adjusting parental effort to the honest begging behaviour of their offspring, might adaptively compensate for the negative effects of parasitism (Christe et al. 1996; Tripet & Richner 1997). On the other hand, a reduction in parental effort may reflect the negative effects of ectoparasite infestation on parents rather than an adaptive parental response to a parasite-induced change in the reproductive value of the offspring (e.g. Råberg et al. 2000; Gallizzi

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et al. 2008). Consequently, such negative or positive relationships between experimental parasitism loads and parental effort might not be the direct adaptive responses to parasitism suffered by offspring, but the consequence of parasites affecting nestling needs and/or the energy budget of parents.

One way to disentangle parasite effects on parents' perception of offspring value from a parasite-induced effect on offspring begging or parental behaviour would be to explore the possibility that parents could detect the parasite before hatching and examine parental feeding behaviour after removing parasites from the nest (see Gallizzi et al. 2008). However, even in this case, a reduction in parental effort could be caused by parasites affecting the parents (Gallizzi et al. 2008). Another unexplored way of testing the hypothesis of parasitism 'per se' influencing the reproductive investment of parents is related to the idea that parents could infer intensity of infestation from parasite traces in the nest that could be experimentally manipulated without modifying the actual level of infestation.

The immaculate blue-greenish eggs of some members of the genus *Sturnus* often became finely spotted with red-brownish spots that increase in density as incubation progresses (Feare & Constantine 1980; López-Rull et al. 2007; Fig. 1a). Recent observations suggest that these spots are the droppings of the imagos of an ectoparasite of nestlings: the carnid fly *Carnus hemapterus* (López-Rull et al. 2007). In general, the imagines of the carnid fly acquire food resources by feeding on carcasses, faeces or umbelliferous flowers. However, imagines of the genus *Carnus* are blood-sucking ectoparasites of nestling birds (Grimaldi 1997). Carnid flies are highly prevalent and abundant in *Sturnus* colonies, and are present in nests in their adult form a few days before incubation starts (Liker et al. 2001). The abundance of flies in a nest at the nestling phase can be anticipated some days after the beginning of egg incubation by the density of spots on the eggshell (López-Rull et al. 2007). Indeed, the experimental reduction of carnid fly load with an insecticide resulted in a reduction in the number of spots 4 days after the treatment, which suggests that spot density on the eggshell is an indicator of carnid fly density in spotless starling broods (López-Rull et al. 2007).

We tested the hypothesis that male spotless starlings, *Sturnus unicolor*, use egg spottiness, revealing parasite load, to adjust parental investment because spottiness would predict the fitness prospects of their offspring. The hypothesis is based on a visual mechanism of assessing fitness prospects based on egg spottiness that requires covariation between the parasite load of the brood and the current value of reproduction. A number of correlative studies have found a negative correlation between carnid fly load in the nests and different estimators of nestling health that suggest that carnid fly parasitism generates costs (e.g. Soler et al. 1999; Martín-Vivaldi et al. 2006; Václav et al. 2008), although a number of studies have failed to find such a link (e.g. Dawson & Bortolotti 1997; Liker et al. 2001). More convincingly, Wiebe (2009) experimentally fumigated half of the nests of a northern flicker, *Colaptes auratus*, population parasitized by carnid flies. Nestlings from control nests had lower body mass than those from fumigated nests after 15 days and fledged at a lower weight, suggesting that carnid fly parasitism has a negative effect on nestling development (Wiebe 2009). None the less, as a prerequisite for testing the hypothesis that male starlings use carnid fly costs related to egg spottiness, we first evaluated whether fly load relates to the fitness prospects of nestlings in spotless starling nests in terms of their body mass. Second, we manipulated egg spottiness during incubation to explore the behavioural responses of the targeted males. Our prediction was that the experimental cleaning of eggs would affect parental feeding investment of males.

METHODS

Study Site and System

We carried out the study in a spotless starling colony in Guadix, southeastern Spain (37°18′N, 3°11′W), during the breeding seasons in 2006–2007 with the authorization of the Dirección General de Gestión del Medio Natural, Consejeria de Media Ambiente, Junta de Andalucia. Starlings in the colony breed in nestboxes established since the early spring of 2005. Adults were captured inside nestboxes during the nest-building phase, then sexed (Hiraldo & Herrera 1974) and marked with a metallic numbered ring and a unique combination of coloured plastic rings.

Females lay one egg per day, mainly during the morning, and start incubation before clutch completion which leads to asynchronous hatching (Cramp 1998). In our population, females mostly lay one clutch of four or five eggs and, with a few exceptions, incubation is a female task (Soler et al. 2008; unpublished data). Nestlings are fed mainly with insects (Motis et al. 1997) by both male and female (Cramp 1998; Veiga et al. 2002) and paternal feeding effort is mainly concentrated in the first third of the nestling period (Soler et al. 2008).

The carnid fly is a 2 mm blood-sucking ectoparasite of nestling birds of a wide diversity of species excluding ground-nesting species (e.g. Dawson & Bortolotti 1997; Grimaldi 1997; Roulin et al. 2003; Martín-Vivaldi et al. 2006; Chakarov et al. 2008; Václav et al. 2008). The parasite overwinters as pupae inside the nests. After emergence the adult dispersive form is winged, but it loses its wings soon after finding a suitable host (Roulin 1998, 1999). Fly populations increase from host hatching through nestling

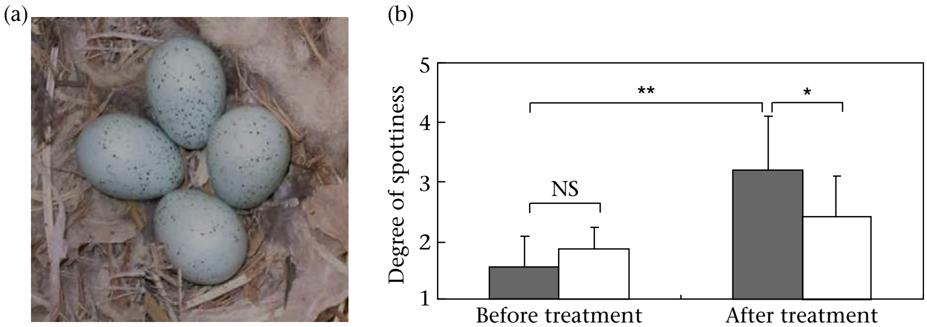

Figure 1. (a) Representative spottiness coverage of eggs in control nests 2 days before hatching. (b) Average spottiness coverage ± SD of the eggshell in nests where spots were experimentally removed (□; $N = 11$) and in control nests (■; $N = 13$) before (the day of clutch completion) and after (2 days before egg hatching) treatment application. **$P < 0.01$; *$P < 0.05$.