SHORT REPORT

No evidence of increased parental investment by Common Swifts *Apus apus* in response to parasite load in nests

MARK D. WALKER* and IAN D. ROTHERHAM
Geography, Tourism, and Environment Research Unit, Sheffield Hallam University, City Campus, Howard Street, Sheffield S1 1WB, UK

Capsule Common Swifts did not increase levels of parental care in response to increased levels of Louse Flies *Crataerina pallida* in their nests

Parasitism is an inter-specific relationship in which one species, the parasite, utilizes the resources of the other, the host, to its detriment (Combes 2001). Parent birds may attempt to offset the costs caused through parasitism by increasing levels of parental effort to parasitized nestlings (Moss & Camin 1970). Such parental compensation may mask the potential detrimental effects of parasitism upon nestling hosts and account for the apparent avirulence observed in some host–parasite systems (Tripet & Richner 1997). However, the empirical evidence for parental compensation is limited and originates almost entirely from nestbox studies of tits (Paridae; Tripet & Richner 1997, Hurtrez-Boussès et al. 2000, Bouslama et al. 2002, Bañbura et al. 2004).

Nestling Common Swifts *Apus apus* Linnaeus 1758 (Aves: Apodidae) are hosts to an obligate ectoparasitic Louse Fly *Crataerina pallida* Latreille 1812 (Diptera: Hippoboscidae). *C. pallida* has a life cycle closely synchronized with that of its host, with adults emerging from winter diapause at the commencement of Common Swift breeding each spring. *C. pallida* parasites remove considerable amounts of blood regularly from their nestling hosts and can occur at high population abundances (Kemper 1951, Walker & Rotherham 2010a). The impact of such parasitism would, therefore, be expected to be great. Despite this, no detrimental effect from such infestation upon hosts has been observed (Lee & Clayton 1995, Tompkins et al. 1996, Walker & Rotherham 2010b).

Parental compensation may account for this apparent lack of parasitic virulence. Swift life-history traits make the use of such a strategy particularly likely. Swift breeding is severely time-constrained. Vagaries in weather and food abundance make nestling success particularly precarious (Lack & Lack 1951, Thomson et al. 1996). Any mechanism that could negate the additional pressures caused by parasitism would, therefore, be particularly advantageous in enhancing host reproductive success and overall fitness. The benefits of increasing reproductive success may offset the longer-term costs of increased parental effort and may enhance overall fitness.

We have investigated the levels of parental care provided by Common Swifts to broods experiencing experimentally enhanced or reduced levels of Louse Fly parasitism. Parasite abundances were manipulated during the 2009 breeding season at swift nests situated in a colony within a highway bridge spanning the Bigge reservoir at Olpe, Germany (51°04′00″N, 07°81′00″E). In 2009 30 breeding pairs successfully incubated eggs at this site producing 74 nestlings, of which 45 fledged.

Nests were randomly allocated to one of two experimental treatment groups. Nests within each group were paired with partner nests from the other which had had similar brood sizes and had experienced similar parasite abundances in 2008. Parasites were transferred from the nests within one group to nests within the other to create nests experiencing either reduced or enhanced levels of parasitism. The aim was to produce nests experiencing parasitism of approximately 0% or of 100% greater than that seen in the previous year. Initially
C. pallida pupae were transferred between paired nests in April 2009 before the arrival of adult swifts. Following the cessation of adult brooding in early June, emerged C. pallida adults were transferred between paired nests approximately every five days until the fledging of the nestlings to ensure that parasite abundances remained reduced or elevated.

Parental effort was recorded through video recording of parental feeding visits to nests. Recordings were made at 11 nests, six with elevated and five with reduced levels of C. pallida parasitism. The average brood size at all these nests was 2.72 ± 0.46 (sd), the average brood size at parasitized nests being 3.00 ± 0.00, and at reduced parasite nests 3.20 ± 0.51. Recordings were made using infra-red cameras (Conrad electronics, Germany) attached to standard video recorders (Orion 6-Head HiFi Stereo) and 14-inch Colour-Quad-Monitors (ELV Elektronik AG, Leer). The number of adult C. pallida parasites at study nests was ascertained on a daily basis as described in Walker & Rotherham (2010a). Accurate surveying of parasite populations was possible as parasites are closely associated with nests; have a relatively large size (approximately 1 cm in diameter) making ascertaining their presence easy; and have a conspicuous mobile nature, all of which aids quantification. Population counts were made through visual inspection over several minutes at each nest. Counts were made in a methodical manner with nestlings first being removed; then the interior, sides, and finally underside of nests being examined. In cases of doubt counts were repeated. The maximum and mean levels of parasitic pressure were calculated following Lee & Clayton (1995) and Tompkins et al. (1996).

Recordings were made on alternate days, on a total of 18 days spanning a total of 32 days of the swift breeding season. Recording was conducted over two sessions running from 08:00 to 12:00 and from 13:00 to 15:00 daily. A total of 2226 hours of recording at all nests over all days were made. Each nest was observed for a mean of 202.41 ± 0.22 hours (range 185–215).

The mean hourly rate of parental visits per nest per day was calculated, as was the overall mean hourly rate of parental visits over the entire period. The mean visitation length per nest per day and the mean visitation length for the overall recording period were likewise calculated. Differences between parasite enhanced and reduced nests were sought using non-parametric Mann–Whitney testing. A two-way repeated-measures ANOVA with parasitism as the factor and parental provisioning rates on different dates as variables was used to gauge the influence of day on parental provisioning.

There may be differences in the rate of parental provisioning during different periods of the day or because of different weather conditions. For example, less parental provisioning occurs during periods of poor weather, or parental provisioning may be greater in early mornings when nestlings are most hungry and demanding of food. However, these differences were not examined here as parental provisioning was recorded at nests over the same periods of time and for the same lengths of time. This meant each nest experienced identical time frames and weather conditions. Thus, any differences in parental provisioning are likely to be because of other factors such as differences in parasitism rather than through differences in the times of day or weather experienced by each nest.

The transfer of C. pallida pupae and larvae between nests resulted in the successful establishment of nests with enhanced and reduced levels of parasitic abundance. The maximum number of C. pallida seen per nest on any one occasion during the breeding season provides a reliable index of parasitic pressure (Lee & Clayton 1995). The maximum parasitic load seen at nests with enhanced levels of parasitism (mean = 10.17 ± 5.10) was significantly higher than that seen at parasite reduced nests (mean = 3.00 ± 2.53) (U = 3.05, z = 2.01, P ≤ 0.05). Additionally the mean number of C. pallida seen per nest over the entire season was calculated and this was also significantly higher at parasitized nests (mean = 3.41 ± 1.27) than non-parasitized nests (mean = 0.21 ± 0.23) (U = 0, z = 2.65, P ≤ 0.05). In comparison, the mean parasite load at unmanipulated nests was 3.72 ± 2.65 at 47 nests in 2007, and 4.21 ± 3.09 at 37 nests in 2008 (Walker & Rotherham 2010a). In 2009 eggs were laid at 38 nests and the mean parasite load over all nests at the colony, including nests not included in the video study, was 9.94 ± 6.26 at 20 parasite-enhanced nests and 2.14 ± 2.24 at 18 nests with reduced parasitism.

Parent birds at nests facing an artificially elevated level of parasitism had slightly lower hourly visitation rates than those parents where parasite abundances had been reduced (Fig. 1). However, this difference was small and was not significant (U = 13, z = 0.27, P = 0.39).

Parents caring for offspring at nests facing an enhanced level of parasitism spent longer at the nests when provisioning with food than parents at nests facing the reduced abundances of parasitism (Fig. 2). This difference was statistically significant (U = 3, z = 2.1, P ≤ 0.05), unlike that seen for mean hourly visitation rate. No significant interaction between date and parental provisioning level was seen (F = 3.99, P = 0.60).
A small sample of parental behaviour at eight nests was made over a single day: 34.37% of parental time at nests was engaged in feeding young; 9.56% in nestling care; and 56.07% in other activities. A greater percentage of time, 40.87%, was spent feeding young at parasite-reduced nests than at parasite-enhanced nests, where it was 26.82%. Nestling care comprised 9.56% at parasite-reduced nests and 15.64% at parasite-enhanced nests. Although limited, these results show that future study of parental behaviour may be possible.

In summary, no convincing evidence of differences in the level of parental provisioning between nests experiencing different levels of parasitism was found. Thus, there is no evidence either supporting or against the parental compensation hypothesis. The difference in parental provisioning between nests was very small and not statistically significant and no conclusions can be drawn from it. Parents at nests where parasitism had been enhanced did spend significantly more time at the nests when provisioning offspring. One possible explanation for this could be that such birds increase the quality and quantity of food they provide to their more heavily parasitized broods, and thus their feeding takes longer.

The costs to Common Swifts of parasitism are not clear. A reduction in parasitic virulence is expected within host–parasite relationships over evolutionary time and has been postulated as a reason for the lack of virulence observed within this relationship (Tompkins et al. 1996). However, research on a closely-related host–parasite system between Alpine Swifts Apus melba, and their associated louse fly species has found evidence of detrimental effects (Bize et al. 2004); thus, reduced parasite virulence cannot simply be assumed.

A number of studies have found evidence supporting the parental compensation hypothesis since it was first proposed by Moss & Camin (1970). Although no negative effect of Bird Fleas Ceratophyllus gallinae were found on nestling Blue Tits Cyanistes caerules, parents were found to increase their rates of provisioning when Bird Fleas were present (Tripet & Richner 1997). A similar increase in parental provisioning by parent Blue Tits was found by Bouslama et al. (2002). Adult Blue Tits were found to provide more care in response to parasitism (Hurtrez-Boussès et al. 2000). Blue Tits parasitized by blow-fly (Bæbura et al. 2004) increased both the quantity and quality of food provisioned.

This study acts as an interesting introduction to this topic of research and suggests numerous other avenues of potential study. An interesting question for further research will be examining differences in the quality or amount of food provided to nests experiencing different levels of parasitism. Although the weight and composition of swift food pellets can be easily determined, as adult swifts readily drop pellets when disturbed at the nests, their collection is difficult. The return to the nest by adults is unpredictable and occurs only a limited number of times per day. In addition the disturbance entailed to swifts can lead to their desertion from nests. Thus obtaining substantial sample sizes of pellets could be difficult.

This investigation is limited in that only a small number of nests could be examined. Additional nests could not be studied owing to the financial costs of equipment, the sensitive nature of some birds, and the lack of similar accessible nesting sites in the locality to act as replicates. The sample size used is, however, consistent with that.
seen and used in similar studies. Hopefully, data collected in subsequent years can lead to firmer conclusions. The results, despite the limitations, are useful in that parental compensation was not readily apparent, thus indicating that parental compensation may not be occurring.

The parasitic nature of C. pallida and the substantial resources it removes from hosts should lead to clear costs to hosts. If, as is suggested here, these costs are not borne by parental compensation, they may be borne by various host life-history traits. These could include nestling developmental stability, host lifespan or reproductive success, or nestling rates of growth. Examination of these and other traits may lead to the discovery of such costs. Another potential avenue of research is an examination of the influence of short-term weather changes on parental provisioning. Differences in parental provisioning between parasitized and non-parasitized nests may be more pronounced in poor weather periods and thus lead to high parasitic costs during adverse conditions.

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