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An investigation into the host-parasite interrelationship between Common Swifts and Hippoboscid Louse-Flies

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**An investigation into the
host-parasite interrelationship between
Common Swifts and Hippoboscid Louse-Flies**

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ABSTRACT

Parasitism is defined as an obligatory hetero-specific relationship where resource transfer between a host and parasite occurs. This results in the sub-optimal expression of host life-history traits and a consequent reduction in host fitness.

The Louse Fly, *Crataerina pallida* (Diptera: Hippoboscidae), is a monoxenous haematophagous nest ectoparasite of the Common Swift, *Apus apus* (Aves: Apodidae). Despite expectations, no detrimental effect to hosts from *C. pallida* has been determined. Here this relationship is re-apprised. *C. pallida* life-history is investigated, with particular reference to those traits of pertinence to its parasitic efficacy. Whether *C. pallida* has a detrimental effect upon *A. apus* is subsequently investigated.

C. pallida was found to exhibit life-history characteristics strongly indicative that it is parasitic in nature. Morphological and ecological adaptations towards a parasitic life-style were identified. Higher levels of prevalence, aggregation, and population abundance were observed than previously reported. Populations were discovered to decline over time and to be heavily female biased. Evidence for previously unreported phenomena such as horizontal parasite transmission, intra-brood host selection, population fluctuations, male mating competition, and host facultative heterothermy was discovered. However, no detrimental impact upon a number of host traits, including previously unstudied aspects of nestling post-natal development and parental investment, were ascertained as a result of *C. pallida* parasitism.

Therefore *C. pallida* does not fulfil the criteria of the standard definition of a parasitic species. The long term intimacy of the association between *C. pallida* and *A. apus* may have resulted in the development of reduced parasitic virulence as expected by host-parasite theory. The discoveries made, especially those pertaining to *C. pallida* population stability and abundance, may have implications for further studies investigating *C. pallida* virulence. This study emphasizes the need for substantial knowledge of parasitic life-history before the functioning of host-parasitic relationships can be understood. When examining host-parasitic systems the underlying species specific context in which parasitism occurs needs to be considered.

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DEDICATION

I dedicate this research to my family who supported me through my studies and ensured my eventual success. I also dedicate it to the swifts who allowed me a privileged glimpse into their lives.

THE AUTHOR: SPRING 2007

“Success is a science; if you have the conditions, you get the result.”

Oscar Wilde

“Ce qui vaut la peine d'être fait vaut la peine d'être bien fait.”

Nicolas Poussin

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**CHAPTER ONE:
GENERAL INTRODUCTION
HOST-PARASITIC RELATIONSHIPS**

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GENERAL INTRODUCTION:

HOST-PARASITE RELATIONSHIPS

1.1: CHAPTER AIMS

The aim of this introduction is to:

- Introduce the biological concepts behind inter-specific relationships and in particular for one such interaction; parasitism.
- Provide an example of one inter-specific relationship; that occurring between the Common Swift and the Hippoboscid Louse Fly.
- Raise an overriding research problem and associated research question around which an investigation into the nature of this relationship can be framed. Suggest methods how this problem will be tackled.
- Lay down a clear and methodical dissertation structure showing how this relationship will be examined.

A treatise of inter-specific relationships and of one such association, parasitism, will allow the context of research to be understood and the subsequent results to be appreciated. Providing a clear overriding research problem and hypothesis facilitates the clear structuring of investigations and allows easier understanding of the specific research conducted and its implications.

1.2: INTRODUCTION

This dissertation considers the nature of the relationship between the Common Swift, *Apus apus* Linnaeus 1758 (Aves: Apodidae) and the Hippoboscid Louse fly, *Crataerina pallida* Latreille 1812 (Diptera: Hippoboscidae). Biologically all species form associations with others. These inter-specific associations are traditionally classified according to the costs and benefits incurred or accrued to each partner species (Begon *et al.* 1996). Examples of such associations include mutualism, commensalism and parasitism. To be defined as parasitism some detrimental effect or 'cost' must be incurred by one species as a result of interacting with the other, which obtains some benefit (Price 1977). The species obtaining such trophic resources must exhibit some specialized adaptations for this life-style and be dependant to some extent upon the other (Price 1977).

The hetero-specific relationship between *A. apus* and *C. pallida* is generally assumed to be parasitic in nature (e.g. Hutson 1981, Lee and Clayton 1995, Tompkins *et al.* 1996). *C. pallida* removes considerable amounts of resources from hosts and should therefore have a detrimental effect upon hosts. But there is a puzzling contradiction. Previous studies have failed to establish clearly any negative influence of *C. pallida* upon *A. apus* hosts (Hutson 1981, Lee and Clayton 1995, Tompkins *et al.* 1996). This is despite such costs being clearly apparent upon a number of host life-history traits in related inter-specific associations (e.g. Bize *et al.* 2003). These include upon host lifespan, host developmental stability, and host lifetime reproductive success.

This dissertation investigates this association anew. Knowledge of the biological and ecological traits of *C. pallida*, particularly those of pertinence to its parasitic efficacy, are investigated. The expected detrimental costs to *A. apus* of being involved within such a relationship with *C. pallida* are sought. Possible reasons accounting for the apparent lack of parasitic virulence, or which may be mediating the virulence exhibited by *C. pallida*, are suggested.

This chapter introduces concepts and classifications of inter-specific interactions. Parasitism, as an example of one such hetero-specific association is presented. The two species used in investigations are introduced. The current state of knowledge about this interaction is considered. An overriding research problem and an associated investigation question, around which the following study will be structured, are proposed.

1.3: INTER-SPECIFIC RELATIONSHIPS

Inter-specific relationships are ubiquitous within the natural world. The nature of hetero-specific interactions, in which trophic transfers occur between two parties, have traditionally been classified according to the costs and benefits accrued or incurred to each partner species (Begon *et al.* 1996). Examples of such relationship categories include; neutralism, where costs are incurred by neither species; mutualism, where individuals of both species benefit through inter-action; commensalism, where individuals of one species benefit while the other is unaffected; and parasitism, where one species benefits to the other's detriment (Cheng 1991, Begon *et al.* 1996) (Table 1). This table illustrates a number of characteristics of inter-specific relationships:

- Relationships can be classified according to the costs experienced by the host. The extent of negative effects caused by one species upon the other become increasingly reduced as one progresses down the list of relationship categories.
- Where one species incurs costs as a result of being involved in a relationship with another, there should be some evolutionary pressure for it to either disassociate from the relationship or to mediate the costs.
- Inter-specific relationships where there is a cost to both partner species do not occur as there is an incentive to both species to disassociate.
- Evolutionary thought proposes that inter-specific relationships that initially result in costs to one interacting species will develop to become increasingly commensal with increasing length and closeness of association between the two species.

Table 1: A summary of some recognized categories of hetero-specific associations

Category of relationship	Description of relationship	Costs (-), benefits (+), neutrality (None)	
		Species 1	Species 2
Predation	Transfer of trophic resources from species 2 to species 1. Results in immediate mortality of species 2.	+	-
Amensalism	Species 1 hinders and has a cost on species 2, to no benefit for itself	None	-
Parasitoidism	Form of parasitism leading to eventual host mortality.	+	-
Parasitism	Species 1 removes resources from species 2. Does not result in immediate host mortality.	+	-
Inquilism	Species 1 removes resources from species 2 causing no detriment.	+	None
Commensalism	Trophic transfer from species 2 to species 1.	+	None
Mutualism	Both species benefit.	+	+

1.4: PARASITISM

Parasitism is one inter-specific interaction. The term parasite is of Greek origin from the word "parasitos" being composed of 'para' (along or to the side of) and 'sitos' (food). Thus a definition based on etymological origins is that a species eating along side or upon another. However, more precise definitions have been made. Clayton and Moore (1997) summarize a number of definitions within the introduction to their primer on avian host-parasites. The most commonly provided definition is that provided by Price (1977, 1980). Another frequently used definition is that used by Kim (1985) where a parasite is defined as „an organism which lives in, or on a host, from which it derives food and other biological necessities. Watts et al. (1995) definition includes that there is a detriment to the host. Clayton and Loye define parasitism as 'causing host mortality (death), morbidity (weakness or other debility), or reduced fecundity (reproductive success)

As mentioned, a frequently used definition of parasitism is that provided by Price (1977) which denotes parasitism as being where individuals of one species, the parasite, utilize the resources of the other, the host, to their own benefit and to the detriment of the other. Parasitism is arguably the most successful of life strategies, with parasites probably accounting for a half of all animal taxa (Price 1980). Many of the species still to be described will be parasitic in nature (Hammond 1992). Parasitism is commonly cited as being obligatory, with their being unilateral dependency of the parasite upon the host. Parasites demonstrate clear biological specializations towards such a mode of life. Hosts act as donors while parasites act as recipients of trophic resources. A key feature of definitions of parasitic relationships are that these trophic transfers result in detrimental 'costs' being incurred to the host species (e.g. Price 1977, Lehmann 1993, Møller 1997).

The 'costs' resulting to host species as a result of being engaged in a parasitic relationship cause the sub-optimal expression of host life-history traits (Stearns 1992). Biologically each species possess a number of characteristic life-history features or characteristics. Typical avian life-history traits include post-natal rates of development, lifespan, clutch size, and brood size (Lack 1968).

Natural selection acts to promote the expression of these traits at some optimum that

maximizes individual reproductive success and thus by consequence evolutionary fitness (Stearns 1992). However as a consequence of the resource transfers occurring as a result of parasitism, the trade-offs between the expression of such traits is affected, thus resulting in a consequent reduction in host fitness (Poulin and Combes 1999). The reduction in host fitness expressed through the sub-optimal expression of these life-history traits is thus commonly termed as being the ‘costs’ of parasitism. The extent to which parasites influence host life-history traits is termed parasitic virulence (Bull 1994, Poulin and Combes 1999).

Parasitic virulence can be considered as the ‘strength’ of the parasite species in affecting host life-history traits. The level of parasitic virulence observed is not only a result of parasitic potency, but is a delicate balance between parasitic efficacy and host resilience (Bull 1994). Parasitic virulence is a parasite life-history trait which is likewise under selection pressure. Host resilience to parasitism is influenced by inter-connected aspects of host genetics, immunological competence, and physical condition. The selection of hosts with heightened levels of resilience should be avoided by parasites.

The level of parasite efficacy and virulence is influenced by a number of ecological parasite and host features including amongst others; the method and type of resource extraction by the parasite, the population dynamics of the parasite and host, the mode and extent of parasite transmission between hosts, and the length of the evolutionary relationship between host and parasite (Bull 1994). Host-parasite theory postulates that an increasingly close association between host and parasite species, with a corresponding linkage of parasite fitness with that of the hosts, will favour and result in the selection of reduced parasitic virulence (Combes 2001, Poulin 2007). Therefore, over evolutionary time, the host-parasite association is expected to become more commensal in nature, with the detrimental effects of the inter-action becoming reduced.

The influence of parasitism upon host species can be great. Parasite-mediated natural selection has been found to be a major engine of evolution; parasites have been shown to have wide ranging effects upon their hosts, including regulating host population sizes (Anderson and May 1978), affecting host population demographic structure and stability (Freeland 1976), driving population cycling (Hudson *et al.* 1998a, Hudson *et al.* 1998b), affecting community structures (Minchella and Scott 1991), and promoting

the evolution of secondary sexual traits (Hamilton and Zuk 1982, Møller 1990).

1.5: AVIAN HOST-PARASITIC RELATIONSHIPS

Avian hosts have proved favourite targets of studies investigating host-parasitic relationships. Avian species are hosts to a large number and wide variety of parasitic species (Møller *et al.* 1990, Loye and Zuk 1991, Clayton and Moore 1997). The ubiquity, small size and ease of access, which many avian species offer to biological researchers accounts for the popularity of this biological group as targets of such research. Their endothermy means that implications deciphered through study of these host-parasitic interactions is of direct relevance to study of mammalian and human host-parasitic relationships.

Investigation of avian host-parasitic relationships has proved fruitful in identifying and confirming assumptions and principles underlying general host-parasitic research. Avian host-parasite systems have allowed, for example, the demonstration of clear parasite costs (Møller *et al.* 1990, Møller 1997), or showed the epigenetic effect parasitism can have upon host populations (Hudson *et al.* 1998a, Hudson *et al.* 1998b). Table 2 provides a selection of noted seminal studies into different aspects of avian parasitism. It helps demonstrate that:

- Avian host-parasitic systems provide useful model systems for the general study of host-parasitic interactions.
- Avian study systems allow the quantification of the effects of parasitism upon traits indicative of host reproductive success, including brood size, post-natal development and mortality rates. This is often not the case with less tractable study species.
- Clear negative effects of parasitism upon a number of host life-history traits have been identified.

These example studies all examined haematophagous nest ectoparasites of either nestling or adult hosts. In each case clear detrimental effects due to parasitism could be identified. *C. pallida* is similarly a blood sucking insect, and is clearly associated with host nests. Therefore a similar negative effects could reasonably be expected.

Table 2: A selection of important studies on avian host-parasitic relationships. Each of these studies examined blood sucking nest ectoparasites and found clear detrimental effects of such parasitism upon the host. *C. pallida* is likewise a haematophagous nest ectoparasite, so one might expect such costs also to occur to swift hosts.

Study	Host	Parasite	Traits Studied	'Costs' found
Arendt (1985)	Pearly-eyed Thrashers (<i>Margarops fuscatus</i>)	Blow Fly (<i>Philornis deceptiveus</i>)	Nestling development	Yes
Brown and Brown (1986)	Cliff Swallows (<i>Petrochelidon pyrrhonota</i>)	Swallow Bugs (<i>Oeciacus vicarius</i>)	Nestling development and mortality	Yes
Møller (1990)	Barn Swallows (<i>Hirundo rustica</i>)	Mites (<i>Ornithonyssus bursa</i>)	Adult breeding success	Yes
Richner <i>et al.</i> (1993)	Great Tit (<i>Parus major</i>)	Hen Flea (<i>Ceratoophyllus gallinae</i>)	Reproductive success	Yes

**1.6: AN EXAMPLE OF AN AVIAN INTER-SPECIFIC RELATIONSHIP:
THE COMMON SWIFT, *A. APUS* AND HIPPOBOSCID LOUSE FLY, *C. PALLIDA*.**

The Hippoboscid Louse Fly, *C. pallida*, is involved in an inter-specific relationship with an avian host, the Common Swift *A. apus*. The relationship is generally assumed to be parasitic in nature as *C. pallida* is totally dependent upon swift nests and resources for its survival, and because large amounts of resources are known to be removed from swift hosts (Reviewed by: Kemper 1951, Hutson 1984). These two species and the study site used in the following investigations are briefly introduced below.

The Common or European Swift: This summary is based on the comprehensive reviews of Common Swift biology and ecology by Weitnauer (1947), Lack (1956), Bromhall (1980) and Del Hoyo *et al.* (2000). The European or Common Swift (*A. apus*) is a small 50 to 60 gram migratory insectivorous avian member of the Apodiform Order of birds. Common Swifts are predominately aerial, and have become extremely highly specialized and adapted to such a life-style. Many of their physical characteristics reflect this aerial specialization. Common Swifts have an aerodynamic profile being torpedo shaped in outline. Such a profile acts to reduce wind resistance and improve aerodynamic performance. The head is small and unobtrusive. There is almost no neck, which enhances flow of air around the body. The slender body tapers smoothly to a distinct short forking tail, which enhances wind flow around the body and thus reduces drag. The most noticeable physical features of the swift in flight are its long backwards swept wings, which possess high aspect ratios and low drag coefficients, thus offering optimum flight economy. As can be seen in Photograph 1 which shows a close up view of an adult swift head, the eyes are situated on the side of the head within small feather niches to offer protection from the constant flow of air experienced during its high altitude, high velocity flight.

Common Swifts have a uniform dark grey or black pelage, which has a slight greenish sheen. This sinister all black colouration, along with its distinctive harsh call, led to it being given the alternative English name of the 'Devil's bird.' The only marking is a small white chin patch found directly beneath the beak. This develops from a young age and is present in nestlings once plumage develops from 20 days of age onwards (Photograph 2).

Common Swifts have a migratory life-cycle. The autumn and winter months are spent in sub-Saharan Africa. Swifts migrate to northern Europe each spring, arriving approximately on the 1st of May each year in order to breed. The exact arrival of the swifts is dependent on prevailing weather conditions. The alternative appellation of 'European Swift' is somewhat of a misnomer as approximately only 100 days of each year are spent in Europe before its return to Africa on completion of breeding. Swifts are socially monogamous and form long lasting pair bonds. Offspring are raised at colonial nesting sites, which contain between five and one hundred breeding pairs. These are typically situated within the roof cavities of buildings, under bridges, in gables, or between guttering. Originally swifts would have nested on cliff faces, rocky ledges or within old trees. The historical increase in European human population probably led to a concurrent augmentation in swift populations due to the enhanced availability of nesting opportunities. Swift pairs will typically reuse the same nest at the same colony from year to year. Mating takes place mostly at the nesting site, but there are anecdotal reports of in flight copulation.

The shallow cup shaped nests are made from grasses, straw, and assorted debris collected by swifts on the wing. Clutches are initiated five days subsequent to the onset of clement weather. Between one and four eggs are laid, with clutches of two or three eggs being most typical. Egg laying can be delayed or interrupted should weather conditions deteriorate. The incubation period is twenty to twenty-one days. The nestlings are altricial with both parents providing parental care. Post-natal development is rapid, with offspring gaining up to seven grams in mass daily. Photograph 2 shows a nestling of approximately 20 days of age. The average time span of nestling development is forty-two days, but fledging can be obtained from thirty days of age onwards. Full independence is obtained on leaving the nest. It is thought that immediately after fledging the offspring begin migration immediately for the winter feeding grounds in Africa, a trip they make without parental guidance. Adults remain for a further two or three weeks before initiating migration.

The Common Swift Louse Fly: Systematically the Louse Fly, *C. pallida*, is classified within the Hippoboscidae Family Samouelle 1819 of Dipterous insects. Members of this monophyletic family are obligate mammalian or avian parasites, with the generic

common name of either 'Keds' when present on mammalian, or as 'Louse Fly' when present upon avian hosts. Here the name 'Louse Fly' will be used specifically for *C. pallida*, unless otherwise mentioned. Photograph 3 taken from Lack (1956) illustrates *C. pallida* morphology. As can be seen from this photograph a distinctive feature of *C. pallida* are the long outstretched legs, large body size, and the hairiness of the body. A characteristic feature of Hippoboscidae biology is the in-uterine development of larvae, with pupation occurring immediately on deposition. An picture of a pupae is shown in photograph 4. Emergence of adult parasites occurs following a winter diapause. Another apomorphic trait of this family is wing and flight atropism; their parasitic life-style making independent flight unnecessary. *C. pallida* is one of eight known, mostly tropical living, species within the *Crataerina* genus von Olfers, 1816 (Table 3). All species within this genus specialize upon Apodidae avian hosts.

Despite parasitizing a ubiquitous host species, *C. pallida* life-history has been seldom studied and is little known. This paucity of knowledge is likely associated with the predominately aerial life-style of the hosts and the inaccessibility of host nesting sites, which hinders access to *C. pallida* specimens and populations. The *C. pallida* life-cycle is thought to be closely synchronized with that of its host (Hutson 1984). Following the winter diapause emergence of adult parasites occurs on the return of swift hosts and the initiation of their reproduction each spring. Photograph 4 shows an emerged adult *C. pallida* and the pupae in which winter diapause occurs. This photograph illustrates the relationship between the size of the initially emerged adults and the pupae.

C. pallida is monoxenous, feeding exclusively from the blood of the adult and nestling Common Swift hosts. Each *C. pallida* adult is reported to feed approximately once every five days, removing a mean of 60 milligrams of blood on each occasion (Kemper 1951). This is a significant amount, and may result in the removal of the equivalent of five percent of adult blood volume (Campbell 1988).

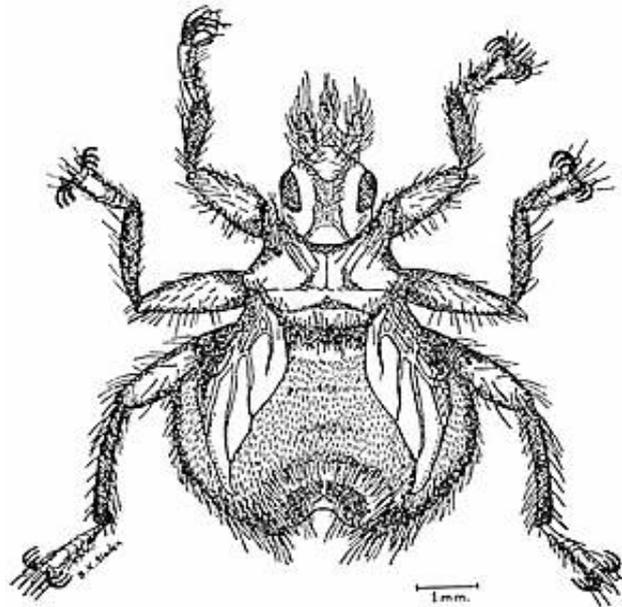
Photograph 1: A brooding adult *A. apus* Common Swift at the nest. Note the eyes, which are set within a clear depression at the side of the head, thus protecting them from abrasive air movement during flight.



Photograph 2: *A. apus* nestling of approximately 20 days of age. At this stage of development the distinctive white cheek patch has formed and is particularly prominent.



Photograph 3: Diagram of *C. pallida* adult. Taken from Lack (1956). Of particular note are the numerous short stiff hairs distributed across the entire body which aid attachment to the host. Although flightless the wings have possibly not degenerated completely as they likewise facilitate attachment.



Photograph 4: Adult *C. pallida* and pupae shown at approximately actual size. The pupae are bright and shiny with a dark black colouration. The surface is perfectly smooth. The adults have a brownish colour, but the abdomen is greyish. On squeezing the engorged abdomens release a greyish liquid; although in individuals which have recently fed this is reddish in colour.



Table 3: A summary of members of the *Crataerina* genus and their hosts, based on the taxonomy of Chick (2006). This table places *C. pallida* parasitism in context. It shows the specialization of these parasites upon avian aerial insectivore hosts. However, species of *Crataerina* can be either specialist upon single hosts, or more generalist with several.

Genus <i>Crataerina</i> (von Olfers, 1816)	Reported Host/Hosts	'Generalist' or 'Specialist'
<i>Crataerina acutipennis</i> Austen, 1926	The Little Swift, <i>Apus affinis</i> . White-rumped Swift, <i>Apus affinis</i> . Horus Swift, <i>Apus horus</i> . The Pallid Swift, <i>Apus pallidus</i> . The Plain Swift, <i>Apus unicolor</i> .	Generalist
<i>Crataerina debilis</i> Maa, 1975	House Martin, <i>Delichon urbica</i> . Asian House Martin, <i>Delichon dasypus</i> . Barn Swallow, <i>Hirundo rustica</i> . Sand Martin, <i>Riparia riparia</i> . Eurasian Crag Martin, <i>Ptyonoprogne rupestris</i> .	Generalist
<i>Crataerina hirundinis</i> Linnaeus, 1758	The Alpine Swift, <i>Apus melba</i> . The Pacific Swift, <i>Apus pacificus</i> . The Common Swift, <i>Apus apus</i> . The Mottled Swift, <i>Tachymarptis aequatorialis</i> .	Generalist
<i>Crataerina melbae</i> Rondani, 1879	The Alpine Swift, <i>Apus melba</i> .	Specialist

<i>Crataerina obtusipennis</i> Austen, 1926	-	-
<i>Crataerina pacifica</i> Iwasa, 2001	The Pacific Swift, <i>Apus pacificus</i>	Specialist
<i>Crataerina pallida</i> Latreille, 1812	The Common Swift, <i>Apus apus</i> .	Specialist
<i>Crataerina seguyi</i> Falcoz, 1929	Blue and white swallow, <i>Notiochelidon cyanoleuca</i> . Brown-bellied Swallow, <i>Notiochelidon murina</i> .	Generalist

Study Site: The following description of the study site used was published in the German ornithological journal *Vogelwarte* in German under the following citation:

- WALKER, M.D., WITTE, K. and ROZMAN, J. (2009). Brutkolonie des Mauerseglers (*Apus apus*) in einer Autobrücke. *Vogelwarte*, **47**, 1-3.

Here a previously unreported nesting colony of the Common Swift is described, which because of its special features offers an ideal and unique chance to study the breeding biology of this species. Although it may initially appear that the nests are difficult to access as they are situated over water, they can in fact be easily reached by entering and walking through hollow walkways which are situated on the underside of the bridge.

A concrete bridge is situated close to Olpe (North-Rhine Westfalia) upon the state highway B54/55 (Photographs 5 and 6). The building of this bridge was completed in December 1965. It is 372 metres long, 22.30 metres wide, and situated 19 metres above the surface of the water of the Bigge Reservoir. As can be seen in Photograph 5 this position, in close proximity to water, makes it an ideal location for a swift nesting colony. Swifts prefer such locations in close proximity to water. On the under surface of the bridge (Photograph 6) there are hollow concrete walkways which serve to stabilize the bridge and provide maintenance access. These walkways are divided into separate chambers which run the length of the entire bridge. Each chamber is approximately 40 metres long and 5 metres wide. On the floor of each chamber there are ventilation holes which are approximately 10 to 12 cm in diameter (Photograph 7). This photograph shows the general number and situation of entry holes in each chamber. Photograph 8 shows an adult swift entering a chamber through a ventilation hole. As can be seen swifts would scramble through holes, becoming increasingly adept at entering the bridge with practise as the breeding season progressed. These holes vary in depth from 13 to 56 cm. Most of the holes are between 20 and 25 cm deep. In total there are 264 holes, each chamber has on average 16 holes.

The Common Swifts use these holes to gain access into the chambers. They fly through the holes with wings held against their bodies or they scramble onto the outer sides of the holes and then crawl onto the floor of the chambers (Photographs 8 and 9). Most nests are found either against the walls of the chambers or in the middle of the chambers, close to an entry hole.

By marking adult birds on their heads with Tip-ex correcting fluid it was found that an individual swift pair would use a single hole for entry and exit into and out of the bridge. There was only one exception where two pairs used a single hole. In this instance the two nests were greatly separated from each other by a distance of approximately 3 to 5 metres. The Common Swift colony was discovered in 2003 by Josef Knoblauch and Dr. Matthias Klein. In 2003 29 swift pairs bred at the colony, in 2004 there were 30 pairs, and in 2007 there were a total of 38 breeding pairs. There are good chances that the colony will expand in future years as there is plenty of sufficient space for new nests.

The breeding biology of swifts at the colony was studied between May and August in 2007. The bridge was visited daily to determine the number of nests and eggs. The date of hatching of nestlings was recorded and their mass was measured regularly using portable scales (Ohaus Scout, accurate to 0.01 grams). Electronic measuring callipers (Lux tools, accuracy 0.01 mm) were used to determine different nestling physical parameters, for example wing length and beak length.

April of 2007 was very warm and sunny. The first adult swifts were seen in the vicinity of the bridge on the 20th of April. The first adults were seen within the bridge two days later. This date of return lies a good two weeks earlier than that reported as being normal by Lack (1956) and by Weitnauer (1947). The first eggs were laid on the 17th of May. The majority of eggs (17 from 42) were laid in the time period between the 18th and 23rd of May 2007.

From a total of 38 breeding pairs, 35 produced young. In total 75 nestlings hatched. The average number of nestlings per nest was 2.14 ± 0.65 . In five nests there was a single nestling, in 20 nests there were two nestlings, and in 10 nests three nestlings. These results were analysed with a Kolmogorov-Smirnov goodness of fit test ($Z = 2.11$; $n = 35$; $P = 0.01$). These results show that an equal number of clutches of different size did not occur. The parameters influencing the clutch size and the number of nestlings per nest is a topic of potential further study.

Photograph 5: The bridge over the Bigge Reservoir, showing its length and general situation.



Photograph 6: A view of the side and underside of the bridge. The walkways, which are divided into chambers, can be seen below the carriageway.



Photograph 7: The holes on the underside of the bridge, which allow access by the swifts into the walkways.



Photograph 8: An adult swift entering the bridge and returning to the nest. Nests were typically situated in close proximity to the entry holes.



The survival rate of nestlings in 2007 was, at only 9.3%, low. Only 7 from 75 nestlings survived and fledged successfully. The reason for this low level of success was most probably the extremely long and frequent periods of poor weather which occurred during the summer. On average nestlings which fledged reached their highest mass of 43.8 ± 9.05 g on their 31st day in the nest. On average nestlings fledged after 38 days within the nest (range 32-43). At this point nestlings weighed on average 41.17 ± 8.3 g. Similar fledgling weights were found by Lack and Lack (1951) and Martins and Wright (1993). That Common Swifts have begun to use the bridge as a nesting site shows the adaptability of this species and their opportunistic nature. Common Swifts are aerial specialists and seldom land. They are particularly well adapted to an aerial life-style (Lentink *et al.* 2007). They therefore require nesting locations which are relatively easy to access from the air, but which at the same time prevent access to potential nest predators. The availability of such locations is extremely limited, and as for many other colonially breeding birds, this is probably the main factor limiting population levels.

Originally Common Swifts would nest in the crevices found on the sides of cliff faces. Today they also use the numerous opportunities offered to them by man-made structures. Suitable nesting locations can be found under house roofs (e.g. Kaiser 1993), beneath guttering, or as in our case, in bridges. Unfortunately the number of such locations is limited. Common Swifts will readily use artificial nest boxes if they are provided for them (Weitnauer 1947, Kaiser 2003). Hopefully this article alerts others to possible Common Swift colonies situated in similar locations to this, thus opening up further research opportunities.

Because of the easy accessibility that this highway colony offers to researchers it provides an ideal opportunity to study the Common Swift. It may allow the answering of numerous ecological, behavioural and life-history questions. An additional advantage of this colony is its similarity to natural breeding colonies of the Common Swift found within cliff faces. The data collected in 2007 show the potential for further research at this colony.

1.7: THE RESEARCH PROBLEM

What is the nature of the inter-specific relationship between *C. pallida* and *A. apus*?

There are various definitions of parasitism, as summarized in the introductory sections of this chapter. However, one single commonly cited definition will be selected here to provide a starting point from which the host-parasitic relationship between Louse Flies and Common Swifts can be considered. Research can then be structured around this definition and with the purpose of examining whether this parasitic relationship fulfils the criteria of this definition.

Price (1977) defined a parasite as:

'an organism in or on another living organism obtaining from it part or all of its organic nutriment, commonly exhibiting some degree of adaptive structural modification, and causing some degree of real damage to its host.'

According to this definition there are three main assumptions underlying parasitic relationships and which a species must fulfil in order to be considered as a parasite. A parasite must:

- Remove trophic resources from the partner species.
- Exhibit a high level of biological specialization and adaptation towards a parasitic mode of life .
- Have a detrimental effect upon its partner species, causing a reduction in its biological fitness.

These assumptions provide a good starting point to examine the Louse Fly interaction with swifts. By selecting this definition with these assumptions, whether *C. pallida* fulfils these criteria can be studied. There are good grounds to suppose that the inter-specific relationship between *C. pallida* and *A.apus* does fulfil the criteria of this definition:

- *C. pallida* is known to remove a substantial amount of resources from its hosts: *C. pallida* adults are haematophagous. They feed approximately once every 5 days, taking a mean of 60 mg of blood on each occasion (Kemper 1951). The cumulative amount of resource removal experienced by hosts is likely therefore to be considerable.

- *C. pallida* has become dependant upon this host species. *C. pallida* requires swift nesting sites and access to hosts as sources of food (Kemper 1951, Hutson 1981). *C. pallida* is monoxenous, having an exclusively *A. apus* blood diet. The Common Swift is the only potential host for *C. pallida*. This would appear to indicate that it has become specialized upon this host.
- There anecdotal reports of Common Swifts in poor condition harbouring high abundances of *C. pallida*, suggesting that the loss of trophic resources as a consequence of their removal by *C. pallida* has a detrimental effect upon them (e.g. Kemper 1951, Hutson 1981). There is evidence that parasitism by a Louse Fly species closely related to *C. pallida* causes significant costs to a similar Apodidae host (e.g. Bize *et al.* 2004a, Bize *et al.* 2004b, Bize *et al.* 2005).

The level of specialization of *C. pallida* to a parasitic life-style is unclear

Although it is known that *C. pallida* is dependant upon *A. apus*, as this host is the sole source of its diet (Kemper 1951, Hutson 1981), the extent of specialization it exhibits remains unknown. There is a paucity of information about *C. pallida* biology and ecology (Lee and Clayton 1995). Whether *C. pallida* possesses morphological specializations and exhibits the population structures characteristic of a parasitic species is unclear. Factors affecting the level of detrimental effect it may be having upon *A. apus* hosts remain likewise unstudied.

There is no clear evidence that *C. pallida* has a negative effect upon its host

Despite possessing features indicative that it is parasitic in nature, the evidence that *C. pallida* actually has a detrimental effect upon hosts is contradictory. Table 4 summarizes research looking at the relationship between *C. pallida* and *A. apus*, and that conducted on related host-parasitic systems, and assesses whether clear parasite costs have been demonstrated or not.

A number of authors have provided anecdotal evidence that *A. apus* host fitness is related to parasitic abundance. Büttiker (1944), for example, stated that host nestling success was related to *C. pallida* nest population size. Weitnauer (1947), in a comprehensive treatise of Common Swift biology, described the relationship occurring

between the *C. pallida* and *A. apus* as being parasitic in nature and stated that hosts in poor condition tended to harbour greater numbers of adult Louse Flies. Likewise Lack (1956) mentioned a link between host condition and *C. pallida* abundance. Hutson (1981) stated that such detrimental effects were expected to occur and sought for an association between the number of *C. pallida* adults harboured by *A. apus* and their bodily condition.

However, subsequent more detailed study has failed to identify or determine such a detrimental influence. Despite his anecdotal reports, Hutson (1981) failed to establish any link between adult host fitness and condition and *C. pallida* abundance. Lee and Clayton (1995) failed to show a correlation between *C. pallida* population size and host reproductive fitness. Tompkins *et al.* (1996), who investigated a variety of host traits related to host reproductive fitness, failed to show any negative effect of parasitism upon hosts in a study where *C. pallida* parasitic loads and abundances were experimentally manipulated.

Common Swifts have a particularly precarious life-style. As aerial insectivores they have specialized upon a source of food which is highly unpredictable in nature. Adverse weather conditions are known to strongly influence breeding success (Koskimies 1950, Martins and Wright 1993, Thomson *et al.* 1996). This is likely to be due to the effect of prevailing weather upon food abundance, as has been shown for other avian aerial insectivores (Bryant 1973, Bryant 1975, Bryant 1978, Alato and Lundberg 1989). In addition reproduction is extremely time constrained. Nestlings are fully independent after around thirty days of development, and thus by this time must have obtained the strict physical constraints such an aerial life-style imposes. These challenges to swift breeding success might be thought to make this species especially vulnerable to additional environmental stresses such as parasitism. Why are such effects not clearly apparent?

Table 4: Examples of studies examining host-parasitic relationships, by Hippoboscid parasites, within the avian Apodidae Family. This table illustrates that there is no consensus as to whether parasitic costs are present upon Apodidine hosts, or upon the Common Swift, *A. apus*, in particular. It also demonstrates that research on this host-parasite system is limited in nature and extent.

HOST	PARASITE	AUTHORS	TRAITS EXAMINED	'COSTS' FOUND
<i>A. apus</i>	<i>C. pallida</i>	Hutson (1981)	Adult bodily condition	No
	<i>C. pallida</i>	Lee and Clayton (1995)	Nestling number per nest/ mortality	No
	<i>C. pallida</i>	Tompkins <i>et al.</i> (1996)	Nestling number per nest/ mortality	No
<i>A. melba</i>	<i>C. melbae</i>	Tella <i>et al.</i> (1995)	Adult condition	No
	<i>C. melbae</i>	Bize <i>et al.</i> (2004a)	Nestling growth	Yes
	<i>C. melbae</i>	Bize <i>et al.</i> (2004b)	Life span	Yes

Why are detrimental effects upon *A. apus* due to resource removal by *C. pallida* not readily apparent?

Why have these previous studies failed to find any evidence that *C. pallida* has a negative influence upon its hosts fitness, despite expectations? There are a number of possible reasons:

- *C. pallida has evolved to become non-virulent*: Host-parasite theory postulates that where host and parasite fitness become linked, reduced parasitic virulence should develop as this increases parasitic fitness (e.g. Anderson and May 1978, Bull 1994, Poulin 2007).
- *True level of parasitic pressure caused by *C. pallida* is unknown*: There is a paucity of knowledge about *C. pallida* life-history. Thus factors possibly of importance in determining the level of its parasitic pressure are unknown. Previous studies have attempted to correlate host fitness with the abundance of *C. pallida*. However, the relationship between abundance and parasitic pressure is unknown, possibly leading to a failure to decipher expected parasitic costs.
- *Limited number of studies*: The limited range of studies conducted to date means that they may not provide a truly representative impression of the influence *C. pallida* has. Parasitic costs may be more readily apparent at other sites with different underlying conditions than the one previously examined empirically. It may also be the case that interactions with other parasites to which swifts are prey may result either in reduced *C. pallida* virulence or may act to enhance host success. *C. pallida* may eliminate other parasites from nests thus countering their own detrimental effect. How *C. pallida* interacts with other nest fauna requires investigation.

These possible reasons accounting for the lack of virulence exhibited by *C. pallida* suggest two main aspects upon which further research can be conducted. Firstly, more information about the biological and ecological traits of *C. pallida* is required. This would allow a re-examination of the level of parasitic specialization exhibited by *C. pallida* and a reassessment of the accuracy of previous studies assessing this relationship. Secondly, further investigation as to whether *C. pallida* has a detrimental effect, and upon which traits these effects may be expressed, needs to be conducted.

1.8: DISSERTATION RESEARCH QUESTION AND STRUCTURE

Is the Louse Fly, *C. pallida*, a parasite?

In summary, despite being generally considered as a host-parasitic interaction, previous research has failed to demonstrate the clear parasitic nature of *C. pallida*. Biological adaptation towards a parasitic life-style and the presence of such 'costs', a key feature of many definitions of parasitism, have not been shown. This problem allows the formation of a general over-riding research question which forms the foundation of the following research and around which this dissertation will be structured:

DISSERTATION RESEARCH QUESTION:

‘Does the Louse Fly, *C. pallida*, fulfil the conditions of the definition of parasitism provided by Price (1977)?

In other words; 'Is *C. pallida* parasitic? Individual investigations will be framed around this specific research question and objective and the definition of (Price 1977). An overview of the investigation is provided in Table 5. Two aspects of the *C. pallida* and *A. apus* relationship will be examined. In the first part of this dissertation *C. pallida* life-history will be examined; the level of specialization exhibited, the closeness of the relationship with *A. apus*, and population parameters of consequence to its parasitic pressure will be investigated. In the second part of the dissertation evidence that *C. pallida* has a negative effect upon its hosts will be sought. These avenues of inquiry will allow an assessment as to the true nature of the relationship between *A. apus* and *C. pallida* and the answering of the research question. From the research question, the following dissertation hypothesis can be formulated:

MAIN DISSERTATION HYPOTHESIS:

‘The inter-specific relationship between the Louse Fly, *C. pallida*, and the Common Swift, *A. apus*, is parasitic in nature.’

Ways in which this research will enhance existing research

This research will enhance previous study of this host-parasitic system and fill in existing gaps in knowledge in a number of ways:

- This research will provide new information from a new previously unstudied site. Given the limited number of opportunities available to investigate this species this is a valuable addition. Results collected here will therefore be of importance in enhancing and confirming previous knowledge.
- Research will examine a number of *C. pallida* traits previously unstudied. For example how the sexual composition of populations changes over time, the mode and extent of parasite transmission between hosts, and the level of population stability, remain unknown. Other factors, such as levels of parasite aggregation or prevalence are only reported from a handful of locations so confirmation is desired.
- The study will examine a number of host traits not previously investigated, for example whether parasitism influences parental provisioning or nestling growth. Given the specialized nature of swift life-history it may well be that parasitic costs are being expressed upon such previously unstudied traits.

1.9: DISSERTATION STRUCTURE

Here, a definition of parasitism was selected to frame research around and examples given. A potential study system, Common Swifts living in association with Louse Flies, was identified. Puzzlingly, despite being apparently parasitic, previously no clear costs to swifts from this species have been seen. This dissertation aims to determine the true nature of this relationship.

Research aims initially to study *C. pallida* life-history, then to investigate whether there is any detrimental effect upon hosts. Thus the dissertation is divided into two parts. Section A considers *C. pallida* biology, in particular its morphology, population structure and parasitic specializations. Section B investigates whether *C. pallida* influences *A. apus* success.

A review of literature pertaining to *C. pallida* is provided in chapter two. This is necessary to ascertain the state of established knowledge before deciding which aspects require further study or could be productive research avenues. The most basic knowledge relating to any species relate to its population structure. In addition the pristine nature of *C. pallida* populations at the study site offer a uniquely opportunity to quantify population parameters. Therefore basic population parameters are determined in Chapter three.

Chapters four, five and six variously consider more closely particular aspects of *C. pallida* life-history, which are thought particularly pertinent to its virulency. Chapter four examines parasite movement. Chapter five studies parasite host preference. Population fluctuations, mating competition, and host temperature regulation are studied and are presented in chapter six. Section B concentrates on the consequences to swifts from *C. pallida*. Chapter seven contains an initial observational study examining whether there is an association of parasitic abundance with various host traits. Empirical study aimed at establishing a causative effect of parasitism is then conducted for chapter eight. Nestling development has been identified as a trait particular likely to exhibit costs, and this trait was thus studied in depth. Chapter nine provides the results of preliminary research studying parent provisioning. Finally research is summarized. Thus the logical and step-wise nature in which research was conducted is reflected in the structure of this dissertation.

Table 5: DOCTORATE OVERVIEW

Research Question: Does the Louse Fly, *C. pallida*, fulfil the conditions of the definition of parasitism provided by Price (1977)?

Overall Hypothesis: The inter-specific relationship between the Louse Fly, *C. pallida*, and the Common Swift, *A. apus*, is parasitic in nature.

AREA/QUESTION OF STUDY	CHAP.	AIM	PROPOSED METHOD
OVERALL HYPOTHESIS:			
The relationship between <i>C. pallida</i> , and <i>A. apus</i> , is parasitic.	ALL	To demonstrate that <i>C. pallida</i> fulfils the criteria of a parasite in possessing parasitic adaptations and ecological traits, and has a detrimental effect upon the <i>A. apus</i> host.	Results of all chapters
DOES <i>C. PALLIDA</i> EXHIBIT LIFE-HISTORY TRAITS INDICATIVE THAT IT IS PARASITIC?			
Does <i>C. pallida</i> possess adaptations indicative of a parasitic life-style? What evidence is there that <i>C. Pallida</i> has a detrimental effect on hosts?	2	To collate and re-examine previous research literature on this host-parasite system. To identify areas of parasite life-history requiring further research.	Literature review.
Does <i>C. pallida</i> possess population parameters indicative that it is parasitic?	3	To confirm previous investigations of parasite population structure and study previously unreported parameters such as population abundance and sexual ratio changes over time.	Observation of natural parasite populations.
Can <i>C. pallida</i> disperse between nests?	4	Identify whether horizontal dispersal of adult <i>C. pallida</i> between host nests occurs. Develop method of marking adult <i>C. pallida</i> .	Marking and subsequent examination of host nests.

Are there intra-brood differences in <i>C. pallida</i> populations?	5	To identify whether there is any evidence for preferential host selection by <i>C. pallida</i> .	Quantification of <i>C. pallida</i> on difference ranking nestlings.
What features of <i>C. pallida</i> may influence its parasitic pressure?	6	To study the constancy of nest populations daily, gather evidence for mating competition, to investigate effect of temperature on emergence.	Examination of nest populations Experimental study of parasite hatching
DOES <i>C. PALLIDA</i> HAVE AN IMPACT ON <i>A. APUS</i> FITNESS?			
Is there a relationship between <i>C. pallida</i> abundance and <i>A. apus</i> reproductive success?	7	To demonstrate that higher <i>C. pallida</i> infestation results in lower fitness, indicating that <i>C. pallida</i> causes clear costs to hosts.	Correlation of <i>C. pallida</i> abundance with various <i>A. apus</i> traits indicative of reproductive success.
Do <i>A. apus</i> experiencing higher levels of <i>C. pallida</i> infestation have lower fitness?	8	To empirically demonstrate that higher <i>C. pallida</i> abundances causes reductionx in success.	Experimental manipulation of <i>C. pallida</i> abundance.
Do adult <i>A. apus</i> bear the costs of parasitism which their nestlings face?	9	To show that parent <i>A. apus</i> may mediate parasite costs by increasing provisioning to heavily infested broods.	Recording of parental provisioning to broods with altered <i>C. pallida</i> abundances.

1.10: CHAPTER SUMMARY

This chapter introduced the concept that species interact with others. One form of such interaction is parasitism, and this is where one species utilises the resources of another to its own benefit but to the detriment of the other. The Louse Fly, *C. pallida* and the Common Swift, *A. apus*, which provide an example of a possibly parasitic relationship and potential targets of study were introduced. The study site used for investigations within a highway bridge was described.

A structure for the dissertation was presented and a research question, asking whether *C. pallida* fulfils the criteria of a parasitic species, was proposed. A hypothesis, that the relationship between *C. pallida* and *A. apus* is parasitic, was stated. The dissertation will consider aspects of *C. pallida* biology, before later examining whether this species has any effect upon its *A. apus* host.

1.11: CHAPTER REFERENCES

- ALATALO, R.V. and LUNDBERG, A. (1989). Clutch size in the pied flycatcher-*Ficedula hypoleuca*- an experiment. *Ornis Fennica*, **66**, 15-23.
- ANDERSON, R.M. and MAY, R.M. (1978). Regulation and stability of host-parasite population interactions. 1. Regulatory processes. *The Journal of Animal Ecology*, **47**, 219-247.
- ARENDT, W.J. (1985). *Philornis* ectoparasitism of pearly-eyed thrashers. I. Impact on growth and development of nestlings. *The Auk*, **102**, 270-280.
- BEGON, M., HARPER, J.L. and TOWNSEND, C.R. (1996). *Ecology: individuals, populations, and communities*. Blackwell Science Publishing, Cambridge, Massachusetts.
- BIZE, P., ROULIN, A., BERSIER, L.P., PFLUGER, D. and RICHNER, H. (2003). Parasitism and developmental plasticity in Alpine swift nestlings. *Journal of Animal Ecology*, **72**, 633-639.
- BIZE, P., ROULIN, A. and RICHNER, H. (2004a). Parasitism, developmental plasticity and bilateral asymmetry of wing feathers in alpine swift (*Apus melba*) nestlings. *Oikos*, **106**, 317-323.
- BIZE, P., ROULIN, A., BERSIER, L.F. and RICHNER, H. (2004b). Additive effects of ectoparasites over the reproductive attempts in the long-lived alpine swifts. *Journal of Animal Ecology*, **73**, 1080-1088.

- BIZE, P., ROULIN, A., TELLA, J.L. and RICHNER, H. (2005). Female-biased mortality in experimentally parasitized Alpine Swift *Apus melba* nestlings. *Functional Ecology*, **19**, 405-413.
- BROMHALL, D. (1980). *Devil birds. The life of the swift*. Hutchinson, London.
- BROWN, C.R. and BROWN, M.B. (1986). Ectoparasitism as a cost of coloniality in Cliff Swallows (*Hirundo: Pyrrhonota*). *Ecology*, **67**, 1206-1218.
- BRYANT, D.M. (1973). The Factors influencing the selection of food by the House martin (*Delichon urbica* (L.)). *Journal of Animal Ecology*, **42**, 539-564.
- BRYANT, D.M. (1975). Breeding biology of House Martins *Delichon urbica* in relation to aerial insect abundance. *Ibis*, **117**, 180-216.
- BRYANT, D.M. (1978). Environmental influences on growth and survival of nestling House Martins *Delichon urbica*. *Ibis*, **120**, 271-283.
- BULL, J.J. (1994). Perspective; Virulence. *Evolution*, **48**, 1423-1437.
- BÜTTIKER, W. (1944). Die Parasiten und Nestgäste des Mauerseglers (*Micropus apus* L.). *Der Ornithologische Beobachter*, **41**, 25-35.
- CAMPBELL, T.W. (1988). *Avian hematology and cytology*. Iowa State University Press, Ames, Iowa.
- CHENG, T.C. (1991). Is parasitism symbiosis? A definition of terms and the evolution of concepts. In: TOFT, C.A., AESCHLIMANN, A and BOLIS, L.(eds.). *Parasite-host associations*. Oxford University Press, Oxford.
- CLAYTON, D.H. and MOORE, J. (1997). *Host-Parasite Evolution: General principles and avian models*. Oxford University Press, New York.
- COMBES, C. (2001). *Parasitism: the ecology and evolution of intimate interactions*. University of Chicago Press, Chicago.
- CHICK, C.W. (2006). *Checklist of world Hippoboscidae (Diptera: Hippoboscidea)*. Field Museum of Natural History, Chicago.
- DEL HOYO, J., ELLIOTT, A. and SARGATAL, J. (eds.) (2000). *Handbook of the birds of the world*. Lynx Editions, Barcelona.
- FREELAND, W.C. (1976). Pathogens and the Evolution of Primate Sociality. *Biotropica*, **8**, 12-24.
- HAMILTON, W.D. and ZUK, M. (1982). Heritable true fitness and bright birds: a role for parasites? *Science*, **218**, 384-387.
- HAMMOND, P. M. (1992). Species inventory. In: GROOMBRIDGE, B. (ed.). *Global biodiversity, status of the earth's living resources*. Chapman and Hall publishers,

London.

HUDSON, P.J., NEWBORN, D. and DOBSON, A.P. (1998a). Regulation and stability of a free-living host-parasite system: *Trichostrongylus tenuis* in Red Grouse. I. Monitoring and parasite reduction experiments. *Journal of Animal Ecology*, **61**, 477-486.

HUDSON, P.J., DOBSON, A.P. and NEWBORN, D. (1998b). Prevention of population cycles by parasite removal. *Science*, **282**, 2256-2258.

HUTSON, A. M. (1981). The population of the Louse Fly, *C. pallida* (Diptera, Hippoboscidae) on the European Swift, *A. apus* (Aves, Apodidae). *Journal of Zoology, London*, **194**, 305-316.

HUTSON, A.M. (1984). *Keds, flat-flies and bat-flies (Hippoboscidae and Nycteribiidae)*. Handbooks for the identification of the British insects. Volume **10** Part 7. Royal Entomological Society, London.

KAISER, E. (1993). Schutzmöglichkeiten für Mauersegler. *Vogel und Umwelt*, **7**, 307-312.

KAISER E. (2003). Faszinierende Forschung an einem 'Hausvogel'. *Der Falke*, **50**, 10-15.

KEMPER, H. (1951). Beobachtungen an *C. pallida* Latr. und *Melophagus ovinus* L. (Diptera, Pupipara). *Zeitschrift für Hygiene (Zoologie)*, **39**, 225-259.

KIM, K.C. (ed.). 1985. *Coevolution of Parasitic Arthropods and Mammals*. New York: John Wiley and Sons,

KOSKIMIES, J. (1950). The life of the swift (*Micropus apus* L) in relation to the weather. *Ann. Acad. Sci. Fenn. Biol. IV Biology*, **15**, 1-151.

LACK, D. and LACK, E. (1951). The breeding biology of the swift, *A. apus*. *Ibis*, **93**, 501-546.

LACK, D. (1956). *Swifts in a tower*. Methuen, London.

LACK, D. (1968). *Ecological adaptations for breeding in birds*. Methuen, London.

LEE, P.L.M. and CLAYTON, D.H. (1995). Population biology of swift (*A. apus*) ectoparasites in relation to host reproductive success. *Ecological Entomology*, **20**, 43-50.

LENTINK, D., MÜLLER, U.K., STAMHUIS, E. J., DE KAT, R., VAN GESTEL, W., VELDHUIS, L.L.M., HENNINGSSON, P., HEDENSTRÖM, A., VIDELER, J.J., VAN LEEUWEN, J.L. (2007). How swifts control their glide performance with morphing wings. *Nature*, **446**, 1082-1085.

LOYE, J.E. and ZUK, M. (1991). *Bird-parasite interactions: Ecology, evolution and*

- behaviour*. Oxford University Press, Oxford.
- MARTINS, T.L.F. and WRIGHT, J. (1993). Cost of reproduction and the allocation of food between parent and young in the common swift (*A. apus*). *Behavioural Ecology*, **4**, 213-223.
- MØLLER, A.P. (1997). Parasitism and the evolution of host life-history. In: CLAYTON, D.H. and MOORE, J. (eds.) *Host-parasite evolution: general principles and avian models*. Oxford University Press, Oxford.
- MØLLER, A.P., ALLANDER, R. and DUFVA, R. (1990). *Fitness effects of parasites on passerine birds: a review*. In: BLONDEL, J., GOSLER, A., LEBRETON, J.D. and MCCLEARY, R.H. (eds.). *Population biology of passerine birds: an integrated approach*. Springer-Verlag, Berlin.
- MØLLER, A. P. (1990). Fluctuating asymmetry in male sexual ornaments may reliably reveal male quality. *Animal Behaviour*, **40**, 1185-1187.
- MINCHELLA, D. J. and SCOTT, M.E. (1991). Parasitism: A cryptic determinant of animal community structure. *Trends in Ecology and Evolution*, **6**, 250-254.
- POULIN, R. (2007). *Evolutionary Ecology of Parasites; from individuals to communities*. Chapman and Hall Publishers, London.
- POULIN, R. and COMBES, C. (1999). The concept of virulence: interpretations and implications. *Parasitology Today*, **15**, 474-475.
- PRICE, P.W. (1977). General concepts on the evolutionary biology of parasites. *Evolution*, **31**, 405-420.
- PRICE, P.W. (1980). *Evolutionary biology of parasites*. Princeton Press, Princeton.
- RICHNER, H., OPPLIGER, A. and CHRISTE, P. (1993). Effect of an ectoparasite on reproduction in great tits. *Journal of Animal Ecology*, **62**, 703-710.
- STEARNS, S.C. (1992). The evolution of life histories. *Chapman and Hall, New York*.
- TELLA, J.L, GORTÁZAR, C., GAJÓN, A. and OSÁCAR, J.J. (1995). Apparent lack of effects of a high louse fly infestation (Diptera, Hippoboscidae) on adult colonial Alpine Swifts. *Ardea*, **83**, 435-439.
- THOMSON, D.L., DOUGLAS-HOME, H., FURNESS, R.W. and MONAGHAN, P. (1996). Breeding success and survival in the common swift *Apus apus*: a long-term study on the effect of weather. *Journal of Zoology, London*, **239**, 29-38.
- TOMPKINS, D.M., JONES, T. and CLAYTON, D.H. (1996). Effect of vertically transmitted ectoparasites on the reproductive success of Swifts (*A. apus*). *Functional Ecology*, **10**, 733-740.

WEITNAUER, E. (1947). Am Neste des Mauerseglers, *A. apus apus* (L.). *Der Ornithologische Beobachter*, **44**, 133-182.

PART A:
LIFE-HISTORY OF *C. PALLIDA*

**CHAPTER TWO:
THE COMMON SWIFT LOUSE FLY**

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THE COMMON SWIFT LOUSE FLY (*C. PALLIDA*): AN IDEAL SPECIES FOR STUDYING HOST-PARASITE INTERACTIONS

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2.1: CHAPTER AIMS

The aim of this chapter is to provide a comprehensive review of *C. pallida* biology and parasitism through an examination of the existing scientific literature. The specific objectives are:

- Determine whether *C. pallida* possesses life-history features indicative that it is parasitic and has become specialized to a parasitic mode of life.
- Find evidence that *C. pallida* removes trophic resources from its *A. apus* hosts.
- Assess the evidence that *C. pallida* has a detrimental effect upon its avian hosts.
- Identify areas of *C. pallida* life-history which have been little studied and where further study may prove to be productive. Also to identify host traits particularly likely to bear costs due to parasitism and whose study would lead to the successful establishment of parasitic costs upon swifts.

The rationale behind these objectives is that it is necessary to know what research has already been conducted, and of what quality it is, before deciding where further study is required. Collating existing knowledge of *C. pallida* and *A. apus* biology may facilitate understanding of this system in the following investigations. Knowledge of parasite biology is a pre-requisite to the understanding of any host-parasite system.

2.2: CHAPTER ABSTRACT

Little is known of the life-history of many parasitic species. This hinders a full understanding of host-parasitic interactions. The Common Swift Louse Fly, *Crataerina pallida* Latreille 1812 (Diptera:Hippoboscidae), an obligate haematophagous parasite of the Common Swift, *Apus apus* Linnaeus 1758, is one such species. No detrimental effect of its parasitism upon the host has been identified. This may be because too little is known about *C. pallida* ecology, and therefore detrimental effects are also unknown. This is a review of what is known about the life-history of this parasite, with the aim of promoting understanding of its ecology. New, previously unreported observations about *C. pallida* made from personal observations at a nesting swift colony are described. Unanswered questions are highlighted, which may aid understanding of this host-parasite system. *C. pallida* may prove a suitable model species for the study of other host-parasite relationships.

2.3: INTRODUCTION TO *C. PALLIDA*

In order to understand host-parasite systems, the life-history of the parasite species being studied needs to be well known. However, for many parasitic species information about basic biological traits is missing. This lack of knowledge could be hindering a full understanding of host-parasite relationships. Although a number of studies have shown that parasites do have an effect on their hosts (reviewed: Møller *et al.* 1990, Lehmann 1993, Møller 1997) other studies have shown no such effect (e.g. Johnson and Albrecht 1993, Clayton and Tompkins 1995, Lee and Clayton 1995, Eeva *et al.* 1994). This apparent lack of pathogenicity may be because of a lack of knowledge of parasite life-history.

The Common Swift Louse Fly *Crataerina pallida* Latreille 1812 (Diptera: Hippoboscidae) may be an excellent example of a parasitic species where no apparent pathogenetic effect has been found, but this may be because of such a lack of detailed knowledge of its life-history. This is an obligate avian nest ectoparasite of the Common Swift *Apus apus* Linnaeus 1758. However, despite being relatively large, tractable, and having a host species that is common and widely distributed throughout Europe, surprisingly little is known of their biology (Marshall 1981). Much of what is known is scattered among the scientific literature, is of substantial age, or is in a language other than English which is the current hegemonic language of science. Studies have failed to

find an effect of its parasitism upon the host (Lee and Clayton 1995, Tompkins *et al.* 1996).

This is the first review of what is known about this parasite species. This review aims to collate life-history information about *C. pallida* and highlight questions requiring further study in order to promote a better understanding of this host-parasite system. New observations made from personal experiences with *C. pallida* from a nesting colony of the Common Swift situated beneath a roadway bridge close to the town of Olpe, Germany (51° 04' 00" N, 07° 81' 00" E) (Site described by Walker *et al.* 2009) are described. Several features not previously observed are described. *C. pallida* may prove to be an excellent model species of a nest ectoparasite, and many of the themes and problems raised may also apply to other host-parasite systems. There are many possible advantages of *C. pallida* as a model nest parasite species, including its large size and easy tractability, which make conducting experimental work and quantifying levels of parasitism relatively easy compared with other types of nest parasite. It is hoped that this review will prompt investigations of the life-history traits of other species in host-parasite systems.

2.4: TAXONOMY

Louse Flies belong to the Hippoboscidae family of cyclorrhaphous insects within the Suborder Brachycera, Subfamily Ornithomyinae. Hippoboscids are viviparid haematophagous obligate ectoparasites of mammals and birds (Hutson 1984). Formerly the Hippoboscidae were classified along with the Bat Fly families Nycteribiidae and Streblidae within the single grouping of the Pupipara. The Hippoboscidae family contains 213 species, and is divided into three subfamilies with 21 genera (Hutson 1984). This family contains a number of well-known and common parasitic species of birds and mammals; for example the Avian Louse Fly *Ornithomya avicularia* from the Ornithomyinae subfamily which is a common parasite of a variety of bird species. The Hippoboscinae subfamily contains the Horse Ked *Hippobosca equine*. The Lipopteninae subfamily contains the Deer Ked *Lipoptena cervi* and the Sheep Ked *Melophagus ovinus*.

Those species of Hippoboscids that parasitize birds are commonly known as 'Louse Flies', while those that parasitize mammals, although similar to their avian counterparts,

are known as 'Keds' (Hutson 1984). Most Hippoboscid species occur in the Old World tropics, but 16 species occur in Europe, seven of these on avian hosts (Hutson 1984). There are eight species within the genus *Crataerina*, three of which occur in Europe. *C. pallida* parasitizes the Common Swift *A. apus*, *C. melbae* parasitizes the Alpine Swift *A. melba*, and *C. hirundinis* parasitizes the House Martin *Delichon urbicum*.

2.5: PHYSICAL CHARACTERISTICS OF *C. PALLIDA*

This species possesses a number of features that aid attachment to its host and reduce the chance of removal through host grooming. It has the standard Arthropod physical structure with there being three tagma - a distinct head, thorax, and abdomen. The entire body is dorso-ventally flattened, which allows it to burrow with ease right to the base of bird feathers and reach its source of food. The exoskeleton is tough, protecting them from being crushed by the host.

The thorax and abdomen are covered with short sharp black hairs, which are also found on the legs and head capsule, and these presumably get caught on the barbs of feathers and provide points of attachment to the host. They are particularly prominent on the posterior abdomen. The joints between the legs are shaped like short sharp hooks, and the legs themselves end in three sharp claws that are ideal for attachment. Adult *C. pallida* have no difficulty in walking upside down across glass or plastic surfaces. The head is sunk into the thorax, and the mouth parts are partially retractable, which protects them from abrasion with the host integument (Lehane 1991).

As for many Hippoboscid flies, *C. pallida* has atrophied vestigial wings that are borne on the thorax and are not capable of sustaining powered flight. A number of Hippoboscid species do retain functional wings, for example the Horse Ked *H. equine*. Some species lose their wings on finding a host, such as those of the *Allobosca* genus, where the wing tips are lost, or the Deer Fly *L. cervi* where the wings are lost entirely once a suitable host is found (Lehane 1991). *C. pallida* is closely associated with their hosts' nests, and therefore an ability to fly is probably not necessary. However, the wings probably have not degenerated completely and this is because of their value in providing another type of 'hook' to allow attachment to the host.

The head capsule of the Hippoboscidae has become specially adapted for their

haematophagous diet, but is nevertheless similar in structure to that seen in the Muscidae (Bequaert 1953). The mouth parts form a distinct prognathous which is found on the ventral mid-line of the head capsule and ends in a closed sclerotized tube or torma. As in all cyclorrhaphids, there is a cibarial pump. There are a pair of sensory antennae.

C. pallida are large insects, with females being larger than males. Photograph 3 shows an emerged adult female, while photograph 4 shows a male. Fifteen female and fourteen male engorged adult Louse Flies were measured during July 2008. The fifteen engorged females had a body length of 7.43 mm (SD \pm 0.45), average abdomen width of 5.45 mm (SD \pm 0.53), and abdomen length of 4.01 mm (SD \pm 0.36). Males were smaller with an average body length of 7.16 mm (SD \pm 0.49), abdomen width of 3.78 mm (SD \pm 0.41), and abdomen length of 4.58 mm (SD \pm 0.42). This difference in size is not simply due to the fact that females can store a larger volume of blood. Females have been found to be larger than males both in the engorged and unengorged states (Kemper 1951). Females probably have to be larger than males as they are the sex which produces eggs and provisions the larvae internally.

The legs are held away from the body when at rest, and this gives *C. pallida* a characteristic 'spider' or 'star-like' stance. In colouration, the adult imagines are a light to dark brown colour. Teneral specimens have a translucent sheen, which is, however, soon lost. In imagines that have fed, the abdomen is noticeably larger and more swollen and is a light to dark grey colour. *C. pallida* with dark red coloured abdomens are occasionally seen, and these have presumably recently fed.

Differentiating between the sexes of engorged *C. pallida* is easily done with the naked eye, as can be seen in photograph 5 (Kemper 1951). The sexual differences between males and females are illustrated in figure 1. In males, a black, semicircular ring is present on the rear of the abdomen. Females instead have two spot-like triangular black marks (Figure 1). Females have much larger, wider, more engorged abdomens than the males. Males are hairier than females. Discriminating between males and females that have not fed is more difficult. Males have more heavily segmented abdomens than the females, but a magnifying microscope is needed to see this. The genitalia of male *C. pallida* can be exposed by gently pressing on the abdomens of the males thus

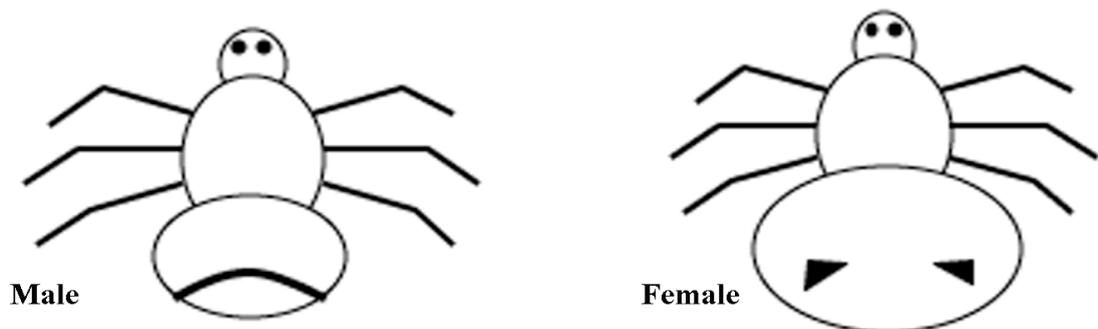
facilitating sexing.

2.6: LIFECYCLE

There is a strong association between the life-cycle of *C. pallida* and that of the host's breeding season. 4th in-star imagines emerge synchronously with the return of the Common Swift in spring. Pupae are cyclorrhaphous. Although emergence has been found to coincide with the hatching of swift nestlings (Büttiker 1944, Lack, 1956), others have found that it occurred earlier (Bromhall 1980, Hutson 1981). In 2007, the first *C. pallida* emerged during the period of swift egg laying (e.g. Photographs 1 and 2). Photograph 1 shows emerged *C. pallida* at the nests while swift eggs are being incubated. Photograph 2 shows a close up view of a cluster of adult *C. pallida* adults around host eggs. This photograph shows the sometimes large numbers of parasites sometimes present at nests during this period. In 2008, *C. pallida* had emerged before the 3rd of June, when nestlings began to hatch.

Weather conditions may influence the exact timing of emergence of *C. pallida*. The emergence from the pupae appears to be temperature mediated. Anecdotal reports suggest that pupae left on a radiator began to hatch after several days (Kemper 1951). In a more analytical study, emergence of the House Martin Louse Flies occurred more rapidly at elevated temperatures (Popov 1965).

Figure 1. Schematic diagram showing differences between *Crataerina pallida* sexes after Kemper (1951)



Photograph 1. Adult *C. pallida* at the nest during the incubation period of the *A. apus* eggs.



Photograph 2. A nest particularly heavily parasitized by adult *C. pallida*. There are approximately 20 adult *C. pallida* in this nest.



Photograph 3: Female *C. pallida* showing double triangular abdomen markings. The sexing of adult *C. pallida* was relatively easy at the nests with practise simply with the naked eye.



Photograph 4: Male *C. pallida* adult with more 'ring like' abdominal markings. The abdomens of males are also not as broad as those of the females. In addition the abdomens of males are more clearly segmented, but this can only be seen with the use of a hand lens.



Photograph 5: Heavily engorged adult *C. pallida*. The abdomens decrease in size when adults are unable to feed.



Mating of *C. pallida* usually takes place on or in close proximity to the nest, but may also occur on the adult or nestling swifts. As in Bat Flies (Strebilidae and Nycteribidae), blood ingestion may be necessary for successful copulation to occur (Yuval 2006). Mate guarding seems to occur, with male *C. pallida* sometimes remaining mounted on the females for several minutes at a time. Two or three *C. pallida* males may attempt to mount a single female. Mating competition may increase as the summer progresses perhaps due to the limited amount of time available before swift departure and due to the falling number of females. 'Clusters' of *C. pallida* often occur in which more than 20 *C. pallida* may congregate together in one large mass (Photograph 2).

Female *M. ovinus* are able to store enough sperm after a single mating to fertilize all their subsequent eggs (Evans 1950, Small 2005). Should this prove to be the case with *Crataerina* species, it might mean that males able to fertilize females first could be at a significant advantage than later emerging males. This may explain why males hatch from the winter diapause earlier than the females. It may also help explain the female dominated sex ratios seen during the summer, as there may be no advantage for males in staying alive after they have copulated. Their presence may increase the parasitic burden on the hosts that their own offspring will ultimately rely on.

Larvae develop singly within the female's uterus in a mechanism known as adenotrophic viviparity. Larvae are nourished through special milk glands found within the common oviduct (Baker 1967) and, if development is similar to that of other Hippoboscids, takes approximately three weeks (Small 2005). Larvae are deposited when they reach the 3rd in-star, and they then pupate almost immediately (Baker 1967). Larvae are deposited either underneath or some distance away from the nest. In comparison, other Hippoboscids deposit pupae at no specific location, for example those of the genus *Lipoptera*, or the pupae are purposely attached to the host as is the case in *M. ovinus* (Lehane 1991). On deposition, pupae are a light brown colour and require six hours to become hardened and dark in colouration. Photograph 6 shows some freshly laid pupae which have a brown colouration contrary to the darker black seen in aged pupae.

Hippoboscids have relatively low fecundity. It is unknown how many larvae a single female can produce, but female Sheep Keds can produce new larva every six to eight

days, and so can therefore probably produce between 12 and 15 larvae over the course of a lifetime (Small 2005). A similar figure in *Crataerina* is likely. Other Hippoboscids have lifespans of between six and ten weeks (Lehane 1991, Small 2005). The number of pupae seen at the nest has been found to be higher at the end of July than in June (Kemper 1951). This indicates that most pupal production occurs during the month of July, and therefore during the nestling period. Pupae remain in diapause until the following spring. Basic life-history information about *C. pallida* is missing, for example information on the lifespan of adults, the number of pupae females are capable of producing, and the factors affecting adult emergence each spring.

2.7: POPULATION DYNAMICS

Population size: At the study site, the population of *C. pallida* found at the nests during 2007 peaked during mid-May, which coincided with the incubation of the eggs. In 2008, *C. pallida* numbers peaked during the incubation and were falling by the time the nests could be first examined at the end of incubation. Throughout the nestling period of both years, the number of *C. pallida* seen, steadily dropped. A similar pattern has been reported for *C. hirundinis* (Bequaert 1953). Studies on the number of *C. pallida* on captured adult birds also show a decrease in numbers as the summer progresses (Hutson 1981).

A. apus pairs are nest-site faithful, often returning year after year to the same nest site (Weitnauer 1947, Lack 1956). This may affect *C. pallida* populations, allowing them to increase on a year by year basis at individual nests with progressive use. At the study site, new and young nests do appear to be less heavily parasitized than obviously older, well-established nests, although not enough time has passed to show this conclusively. It may be the case that a build-up of parasite numbers over several years may be a factor causing nest abandonment and the establishment of new nests in an attempt to forego parasitism.

Other factors, such as the weather or climate, may also influence *C. pallida* numbers. A correlation between the abundances of a Louse Fly species on Serins, *Serinus serinus*, and the weather has been seen (Summers 1975). Recently fledged nestlings of the North Island Robin, *Petroica australis*, were more likely to be parasitized by *C. pallida* if they came from wetter territories (Berggren 2005).

Photograph 6. Pupae deposited to the side and beneath the nest. Two of the pupae are a dark brown in colouration, indicating that they have only recently been deposited. Pupae are typically black in colouration. Beneath the nest to the right is a small aggregation of adult *C. pallida* that may be the result of mating competition.



The number of *C. pallida* seen at particular nests can vary considerably on a day by day basis. This may be due to *C. pallida* moving onto and off the adult hosts and thus being removed temporarily from the nests. This, along with the general changes in *C. pallida* numbers that occur throughout the swift breeding season may lead to a false picture of the true intensity of parasitism being made if the population is sampled on only a small number of occasions. Data on the consistency of *C. pallida* populations over the entire season and on a day by day basis are needed.

Another factor which may influence the population size of *C. pallida* seen at a nesting colony is the size of the colony involved. Generally speaking larger nesting aggregations of birds are more heavily parasitized. Whether this occurs with *C. pallida* is difficult to decipher, as relatively few colonies have been studied. The population of *C. pallida* seen at the well studied Oxford colony of the Common Swift is smaller in

size than that seen at the study site despite the fact that it houses considerably more nesting swifts.

Host predation may be a major cause of Hippoboscid mortality (Hutson 1984). However, this is not the case for *C. pallida*. Adult *A. apus* are reported to ignore adult Louse Flies and to take no measures to remove them from themselves (Lack 1956, Bromhall 1980). *A. apus* nestlings do not feed on adult *C. pallida*. Should an *A. apus* manage to preen a *C. pallida* with its beak, the parasite will simply wait until the bird opens its mouth and crawl out (G. Candelin, personal observation). Ironically, *C. pallida* may be the prey of a parasitic wasp. Two species of Hymenoptera of the Pteromalidae family, *Nasonia vitripennis* and *Dibrachys cavus* have been reared from the puparia of *C. pallida* and maybe also *C. hirundinis* (Bequaert 1953).

Aggregation and prevalence: Parasitic species typically exhibit aggregated population distributions. This is the case for *C. pallida* (Hutson 1971, Hutson 1981) and for *C. melbae* (Tella and Jovani 2000), although the level of aggregation seen by these species is lower than seen in other host-parasite systems. The prevalence of parasitism exhibited by Louse Flies is much higher than is normally seen in other parasites. On adult Alpine Swifts infestation rates by *C. melbae* of 70.8% (Tella and Jovani 2000) and of 74% (Tella *et al.* 1995) averaged over the summer were found. On *A. apus* adults parasitized by *C. pallida* the average infestation over the entire season was 34.4% (Hutson 1981), and at *A. apus* nests 67% (Tompkins *et al.* 1996). For comparison, the prevalence of the Louse Fly *Ornithomyia avicularia*, on Serins *S. serinus*, was found to be 3% (Senar *et al.* 1994), and the prevalence of other Hippoboscid flies on other species has been shown to be no greater than 20% (McClure 1984).

The infestation rate of adult swifts has been found to vary with date, being at around 10% in early spring, raising quickly to 50% during the incubation period, and reaching a maximum of 50% to 60% around the time of nestling hatching, before declining rapidly during the second period of nestling growth (Hutson 1981). These changes can probably be explained through changes to the *A. apus* life-cycle, with infestation being highest during incubation when *A. apus* are at the nest for the longest periods, and falling when they are feeding the young and are there less often. It has been proposed that the high prevalence of Louse Flies on swifts could be due to their short legs and lack of easily

moveable head, which prevents birds from effectively removing parasites (Tella *et al.* 1998).

The prevalence of *C. pallida* and their intensity of parasitism has been determined at only one nest site, at the Oxford University Museum site used in the original study by Lack (1956). At this study site, a mean parasitic intensity of only one adult *C. pallida* per nest has been found, with the maximum number in any one nest being nine adult *C. pallida* (Lee and Clayton 1995). At the study colony, where nests were left in place between breeding seasons, the maximum number of *C. pallida* seen in a single nest in 2007 was 27, and the average number of *C. pallida* seen per nest was 3.64 (SD \pm 2.65). These figures are substantially higher than those seen at Oxford. However, it is usual at the nesting site at the museum for nests to be removed on a yearly basis (G. Candelin, personal communication). This may lead to a distortion of Louse Fly populations and to an artificially lower number of parasites per nest than would normally occur. It has been shown that the removal of old, heavily parasitized nests affects the distribution and intensity of parasitism in nest box studies (Møller 1989). The removal of nests and the resulting unnaturally lower levels of parasite abundance seen may be the reason why studies at Oxford failed to find any negative costs of *C. pallida* parasitism.

Sex ratio: Louse Fly populations are female biased. More female than male *C. hirundinus* were found at House Martin nests and on adults (Hardenberg 1929, Popov 1965, Summers 1975); likewise for *C. melbae* at Alpine Swift nests (Tella and Jovani 2000). A greater proportion of female than male *C. pallida* has been seen on adult *A. apus* (Hutson 1981). This female bias is puzzling as an equal number of males and females are thought to hatch (Bequaert 1953). Other Hippoboscids, such as *M. ovinus*, have more equal sex ratios (Small 2005). Distinct differences in the sex ratio at different stages of the summer have been found (Kemper 1951). In spring, female *C. pallida* were seldom found on adult *A. apus*. The proportion of males found dropped rapidly as incubation began. This may be due to males emerging and then dying off before females (Kemper 1951). This idea tallies with observations of pupae in the laboratory, where males consistently emerged first.

Tella and Jovani (2000) found that the ratio of male and female *C. melbae* Louse Flies on hosts was inter-connected with mate attraction being one possible cause. As mating

competition appears to be strong in *C. pallida*, this may also be a factor influencing sex ratios and population dynamics. The effect of such mate attraction as a factor affecting parasite population biology, and thus pathogenicity, has rarely been looked at, and this species may therefore prove an ideal model species for such studies.

Transmission and dispersal: When adult *A. apus* return from overwintering sites in Africa, they are *C. pallida* free (Zumpt 1966). Therefore, an easy way for *A. apus* to avoid *C. pallida* parasitism would be to build a new nest in a *C. pallida* free place. Where Louse Flies parasitizing House Martin nests have been marked, it has been seen that although they could move between nests, this rarely occurred, with only 6 from 96 flies moving to adjacent nests (Summers 1975). Whether this was active dispersal or whether they were carried between nests could not be determined. *C. pallida* have no mechanism themselves to move between nests discretely separated from each other or to new colonies some distance away from existing ones. Transmission has been assumed to be vertical (Lee and Clayton 1995, Tompkins *et al.* 1996). *C. pallida* are unlikely to move to other nests under their own locomotion and may be carried to other nests by nestlings or adult *A. apus*. However, the study by Summers (1975) showed only that Louse Flies are unlikely to move to other nests under their own locomotion and did not preclude them being carried to other nests by nestlings or adult hosts.

During the breeding season when the nestlings are at the nest, transmission is undoubtedly vertical. However, once the nestlings fledge, they can no longer be re-infected with *C. pallida* from the natal nest, and when they return from the winter migration, they are *C. pallida* free. Thereafter, transmission of *C. pallida* may be horizontal and occur from adult to adult, or from adult to nest to adult. Most likely is that *C. pallida* are transmitted to new sites through first year or full adults that visit new or existing nest sites and carry *C. pallida* with them. A greater proportion of female than male *C. pallida* were found on adult House Martins (Summers 1975), which may be the result of females feeding more often than males, but could also be because gravid females actively transfer onto adults as doing so they may be dispersed to new sites where they can deposit their pupae. Females acting in such a way as to facilitate their own dispersal would increase their lifetime reproductive success if they managed to get transferred to a new formerly uncolonised nest site which they and their offspring could successfully inhabit without experiencing intra-specific competition.

2.8: PARASITISM

Pathogenicity: No pathogenic effect of *C. pallida* parasitism on their *A. apus* hosts has been found (Hutson 1981, Lee and Clayton 1995, Tompkins *et al.* 1996). This is surprising. *C. pallida* feed once every five days, males taking 23 mg, and females 38 mg of blood (Kemper 1951). It has been calculated that if the total blood volume is estimated as being 10% of total body weight; then in an adult *A. apus* weighing 42 grams, *C. pallida* parasitism represents about 5% of its blood being lost (Campbell 1988). Therefore, substantial quantities of blood may be lost.

Adult *A. apus* with heavy infestations had weights within the normal weight range of adult swifts leading one author to conclude that there was no evidence that heavy *C. pallida* infestation affected adult condition (Hutson 1981). There are anecdotal reports of grounded *A. apus* having *C. pallida* (Büttiker 1944, Lack 1956). However, this is hardly strong evidence for a negative effect of these parasites. No correlation between *C. pallida* intensity and nestling body mass, the fledging date, or the number of chicks fledged from each nest has been found (Lee and Clayton 1995). Where *C. pallida* abundances were artificially manipulated, there were no differences in nestling growth or fledging success (Tompkins *et al.* 1996). Although no pathogenic effect has been found on *A. apus*, a number of studies have found an adverse effect of the closely related Louse Fly, *C. melbae*, on the Alpine Swift (Bize *et al.* 2003, Bize *et al.* 2004, Bize 2005).

The type and level of transmission and transfer of parasites between hosts is important in influencing the level of parasite virulence seen (Bull 1994). Parasites that transfer between hosts in a mainly vertical manner, from parent to offspring, typically exhibit lower levels of pathogenicity than parasites that transfer between unrelated hosts horizontally (Eward 1994). Tompkins *et al.* (1996) postulated that the lack of virulence seen by *C. pallida* may be due to the vertical nature of its transmission. Parasites which have not fed have been shown to be more active than those that have (Møller 1997), and thus may be more likely to transfer between closely situated nests where these are available. The pathogenicity of *C. pallida* may be dependant and may alter depending on the nature of the nest colony at which it is found; because of this *C. pallida* may prove an interesting model species for looking at the evolution and development of parasite transmission and pathogenicity.

By looking for more subtle effects of parasitism such as; compensatory growth during the nestling phase, the sex ratio of fledging nestlings, or the lifespan and reproductive success of adult parent birds; effects of parasitism by *C. melbae* on the Alpine Swift have been found (Bize *et al.* 2003, Bize *et al.* 2004, Bize *et al.* 2005). Saino *et al.* (1998) found that the speed of growth of Barn Swallow *Hirundo rustica* nestling wings was influenced through parasitism by the *O. biloba* Louse Fly. Future studies investigating *C. pallida* parasitism should likewise look at such finer aspects of *A. apus* reproductive success and not simply on the most obvious parameters such as adult weight, nestling fledging weight and nestling survival, as has been the case before. More direct effects of parasitism, such as parasite caused anaemia, have yet to be reported but are likely to occur as a result of the blood loss experienced by hosts parasitized by *C. pallida*.

Mode of parasitism: Louse Flies within the *Crataerina* genus, unlike other types of Louse Flies such as *O. avicularia*, are monoexous, being host specific (Kemper 1951, Tella and Jovani 2000). However, in addition to parasitizing *A. apus*, *C. pallida* is also reported to parasitize the Pallid Swift, *A. pallidus* (M. Cucco, personal communication). The development of host specificity within Louse Fly-avian parasite systems may be worth investigating further. Is there any separation in the *Crataerina* populations parasitizing Common and Pallid Swifts? Could divergence occur in the future?

When initiating feeding, *C. pallida* dive between the feathers to reach the skin. Feeding *C. pallida* appear somewhat like ticks, with the heads being burrowed into the host, while the legs and abdomen protrude outwards. When they finish feeding, they move backwards away from the skin of the host, before delving into a new position to feed. On nestlings, they are often found feeding on the lower rump area. On adults, they are reported to feed preferentially on the belly and neck (Kemper 1951). *C. pallida* which have not fed have abdomens that are noticeably smaller and have a light brown colouration. In adults that have fed, the abdomen is substantially larger and has a greyish colouration.

Host selection: When faced with a brood of chicks parasites have to choose one to feed from. Although large nestlings may offer large resources, they will have strong immune responses; weak nestlings on the other hand will offer fewer resources but will be less

able to invest in immune defences (reviewed: Sheldon and Verhulst 1996). Louse Flies are an ideal parasite to study these trade-offs. Host preference of *C. melbae* has been found to be linked to nestling age, with preference for older siblings with more developed feathers (Roulin 2003). Later when there was little difference in feather development between nestlings, these preferences disappeared and no nestling was favoured. Conversely, a later study found that nestlings intermediate in size were preferred; perhaps a compromise choice between nestling resources and immune response (Bize *et al.* 2008).

Attempts should also be made to try to explain features of parasite life-history in relation to their hosts and the host life-history. The parasite life-history features may be tuned to those of its host, thus enhancing parasite fitness. To what extent are the skewed sex ratios, the declining population sizes, and the intense mating competition exhibited by *C. pallida* the result of *C. pallida* attempting to maximise their fitness in the face of the biology and breeding biology of their avian hosts? Future studies should consider aspects of parasite life-history as being adaptations to the host species on which they prey.

Vectors: It is known that Hippoboscid flies act as vectors of various species of *Trypanosoma* and *Haemoproteus* (Baker 1967, Bize *et al.* 2005). *Crataerina* may also act as vectors of such parasites and such a role has been discussed (Kierans 1975, Soulsby 1968). *C. pallida* may engage in a phoretic association with feather mites (Astigmata), and thus aid their transmission (Jovani *et al.* 2001). Small numbers of feather mites have been found on Louse Flies collected from avian hosts (Hill *et al.* 1967). However, studies testing whether this transmission could be the case have found no evidence that such ‘hitch hiking’ occurs (Philips and Fain 1991).

Parasitic effect in conjunction with other parasites: This point is related to the previous one concerning vectors. This review has considered only the effect that a single species, *C. pallida*, has upon its swift host. However, as mentioned swifts are hosts to a number of other parasitic species including chewing lice (*Dennyus hirundinis*). The presence of such parasites may be influencing the pathogenic effect of *C. pallida* and requires further study. Likewise the presence of *C. pallida* may mitigate the effect of other parasites and thus there may be an advantage to swifts in harbouring

Louse flies. Observations of swift nests indicate that there are low levels of other parasites, for example Blowfly, which typically occur in great numbers in avian nests. This may indicate that *C. pallida* somehow inoculate nests. Further research into how *C. pallida* and other parasites interact is needed.

The Common Swift Louse Fly, *C. pallida*, is a fascinating example of an avian nest parasite, with many puzzling life-history features. When trying to understand parasite life-cycles and ecology it is important to consider what is occurring to the host species and how this may be affecting the parasite, or in what way the parasite may be using the host's own ecology to its own advantage. Considering *C. pallida* from this perspective may lead to a better understanding of the strategies it uses. The Common Swift Louse Fly *C. pallida* may prove to be an excellent model species for studying host-parasite systems. It offers a number of advantages to the parasite researcher including large size and the ease at which it can be manipulated. In comparison with other nest and avian parasites, its populations can be easily quantified and determined. *C. pallida* may also prove an excellent example of how hosts and parasites co-adapt, with the life-cycle of *C. pallida* appearing to be well in tune with that of their hosts. Connecting parasite life-cycles to that of their hosts may lead to a better understanding of a wide range of host-parasite systems.

2.9: CHAPTER SUMMARY

This review of the literature has successfully shown that:

- *C. pallida* possesses a range of features and traits indicative that it is parasitic in nature. These include its strong morphological specialization, that it removes resources from *A. apus* hosts, and that it exhibits population dynamics characteristic for parasites.
- Despite this apparently parasitic life-style and trophic removal, no determinable detrimental effect to *A. apus* hosts has previously been established.
- However, only a limited number of studies have looked for such detrimental effects upon hosts and the range of host traits examined for such costs was narrow. Studies are mainly observational or anecdotal in nature and concentrate on basic host traits such as nestling mortality rates. Further more in depth analysis of specialist traits such as nestling development or parental investment may lead to the establishment of detrimental effect upon hosts through *C.*

pallida resource removal.

- Information about *C. pallida* biology remains scant. Many of its life-history traits, such as whether it exhibits host selection, factors influencing its emergence, the exact nature of *C. pallida* populations and the closeness of its relationship with *A. apus* have never been investigated.

As a result of these findings it can be concluded that further study of the relationship between *A. apus* and *C. pallida* would be productive. This would provide more information about this specific study system and broaden the range of avian host-parasitic studies systems examined generally.

This literature review has enhanced the current knowledge about *C. pallida* by collating the existing disparate information about *C. pallida* into a single review, which allows easier understanding of this system for future researchers. Potentially productive avenues for further research have been identified. The information provided here will not only facilitate future study of this host-parasite system, but will hopefully prompt other parasitologist's to study the life-history features of their own study species.

2.10: CHAPTER REFERENCES

BAKER, J.R. (1967). A review of the role played by the Hippoboscidae (Diptera) as vectors of endoparasites. *The Journal of Parasitology*, **53**, 412-418.

BEQUAERT, J.C. (1953). The Hippoboscidae or Louse flies (Diptera) of mammals and birds. Part I. Structure, physiology and natural history. *Entomologica Americana*, **32**, 1-209.

BERGGREN, A. (2005). Prevalence and impact of the native blood-sucking Louse Fly (*Ornithoica sp.*) on the North Island Robin (*Petroica australis longipes*). *Notornis*, **52**, 114-116.

BIZE, P., ROULIN, A., BERSIER, L.P., PFLUGER, D. and RICHNER, H. (2003). Parasitism and developmental plasticity in Alpine swift nestlings. *Journal of Animal Ecology*, **72**, 633-639.

BIZE, P., ROULIN, A., BERSIER, L.F. and RICHNER, H. (2004). Additive effects of ectoparasites over the reproductive attempts in the long-lived alpine swifts. *Journal of Animal Ecology*, **73**, 1080-1088.

BIZE, P., ROULIN, A., TELLA, J.L. and RICHNER, H. (2005). Female-biased

- mortality in experimentally parasitized Alpine Swift *Apus melba* nestlings. *Functional Ecology*, **19**, 405-413.
- BIZE, P., JEANNERET, C., KLOPFENSTEIN, A. and ROULIN, A. (2008). What makes a host profitable? Parasites balance host nutritive resources against immunity. *American Naturalist*, **171**, 107-118.
- BROMHALL, D. (1980). *Devil birds. The life of the swift*. Hutchinson Publishers, London.
- BULL, J.J. (1994). Perspective; Virulence. *Evolution*, **48**, 1423-1437.
- BÜTTIKER, W. (1944). Die Parasiten und Nestgäste des Mauerseglers (*Micropus apus* L.). *Der Ornithologische Beobachter*, **41**, 25-35.
- CAMPBELL, T.W. (1988). *Avian Hematology and Cytology*. Iowa State University Press.
- CLAYTON, D.H. and TOMPKINS, D.M. (1995). Comparative effects of mites and lice on the reproductive success of rock doves (*Columba livia*). *Parasitology*, **110**, 195-206.
- EEVA, T., LEIHIKONEN, E. and NURMIS, J. (1994). Effects of ectoparasites on breeding success of great tits (*Parus major*) and pied flycatchers (*Ficedula hypoleuca*) in an air pollution gradient. *Canadian Journal of Zoology*, **72**, 624-635.
- EVANS, G.O. (1950). Studies on the bionomics of the Sheep Ked, *Melophagus ovinus* L., in west Wales. *Bulletin of Entomological Research*, **40**, 459-478.
- EWALD, P.W. (1994). *Evolution of infectious diseases*. Oxford University Press, Oxford.
- HARDENBERG, J.D. (1929). Beitrage zur Kenntnis der Pupiparen. *Zoologisches Jahrbuch (Anatomie)*, **50**, 497-570.
- HILL, D.S., WILSON, S. and CORBET, G.B. (1967). Mites associated with British species of *Ornithomya* (Diptera-Hippoboscidae). *Journal of Medical Entomology*, **4**, 102-122.
- HUTSON, A.M., BURTON, J.A. and STEPHENS, S.G.D. (1971). Some preliminary results of swift ringing at Beddington Sewage Farm, Surrey. *London Bird Report*, **35**, 81-87.
- HUTSON, A.M. (1981). The population of the Louse Fly, *Crataerina pallida* (Diptera, Hippoboscidae) on the European Swift, *Apus apus* (Aves, Apodidae). *Journal of Zoology, London*, **194**, 305-316.
- HUTSON, A.M. (1984). *Keds, flat-flies and bat-flies (Hippoboscidae and Nycteribiidae)*. Handbooks for the identification of the British Insects. Volume 10 Part

7. Royal Entomological Society, London.

JOHNSON, L.S. and ALBRECHT, D.J. (1993). Effects of haematophagous ectoparasites on nestling house wrens, *Troglodytes aedon*: who pays the cost of parasitism? *Oikos*, **66**, 255-262.

JOVANI, R., TELLA, J.L., SOL, D. and VENTURA, D. (2001). Are Hippoboscids flies a major mode of transmission of feather mites? *The Journal of Parasitology*, **87**, 1187-1189.

KEMPER, H. (1951). Beobachtungen an *Crataerina pallida* Latr. und *Melophagus ovinus* L. (Diptera, Pupipara). *Zeitschrift für Hygiene (Zoologie)*, **39**, 225-259.

KIERANS, J.E. (1975). A review of the phoretic relationship between Mallophaga (Phthiraptera: Insecta) and Hippoboscidae (Diptera: Insecta). *Journal of Medical Entomology*, **12**, 71-76.

LACK, D. (1956). *Swifts in a tower*. Methuen publishing, London.

LEE, P.L.M. and CLAYTON, D.H. (1995). Population biology of swift (*Apus apus*) ectoparasites in relation to host reproductive success. *Ecological Entomology*, **20**, 43-50.

LEHANE, M.J. (1991). *Biology of blood-sucking Insects*. Cambridge University Press, Cambridge.

LEHMANN, T. (1993). Ectoparasites: direct impact on host fitness. *Parasitology Today*, **9**, 8-13.

MARSHALL, A.G. (1981). *The ecology of ectoparasitic insects*. Academic press, London.

MCCLURE, H.E. (1984). The occurrence of Hippoboscids flies on some species of birds in southern California. *Journal of Field Ornithology*, **55**, 230-240.

MØLLER, A.P. (1989). Parasites, predators, and nest boxes: facts and artefacts in nest box studies of birds. *Oikos*, **56**, 421-423.

MØLLER, A.P., ALLANDER, R. and DUFVA, R. (1990). Fitness effects of parasites on passerine birds: a review. In: BLONDEL, J., GOSLER, A., LEBRETON, J.D. and MCCLEERY, R.H., (eds.). *Population biology of passerine birds: an integrated approach*. Springer-Verlag, Berlin.

MØLLER, A.P. (1997). Parasitism and the evolution of host life-history. In: CLAYTON, D.H. and MOORE, J. (eds.). *Host-parasite evolution: general principles and avian models*. Oxford University Press, Oxford.

PHILIPS, J.R. and FAIN, A. (1991). Acarine symbionts of Louse Flies (Diptera: Hippoboscidae). *Acarologia*, **32**, 377-384.

- POPOV, A.V. (1965). The life-cycle of the Louse Flies *Lipoptena cervi* L. and *Stenepteryx hirundinis* L. (Diptera, Hippoboscidae). *Entomologicheskoe obozrenie*, **44**, 573-583. (In Russian).
- ROULIN, A., BRINKHOF, M.W.G., BIZE, P., RICHNER, H., JUNGI, T.W., BAVOUX, C., BOILEAU, N. and BURNLEAU, G. (2003). Which chick is tasty to parasites? The importance of host immunology vs. parasite life history. *The Journal of Animal Ecology*, **72**, 75-81.
- SAINO, N., CALZA, S. and MØLLER, A.P. (1998). Effects of a dipteran ectoparasite on immune response and growth trade-offs in barn swallow (*Hirundo rustica*) nestlings. *Oikos*, **81**, 217-228.
- SENAR, J.C., COPETE, J.L., DOMENECH, J. and VON WALTER, G. (1994). Prevalence of louse flies Diptera: Hippoboscidae parasitizing a cardueline finch and its effects on body condition. *Ardea*, **82**, 157-160.
- SHELDON, B.C. and VERHULST, S. (1996). Ecological immunology: costly parasite defences and trade-offs in evolutionary ecology. *Trends in Ecology and Evolution*, **11**, 317-321.
- SMALL, R.W. (2005). A review of *Melophagus ovinus* (L.), the Sheep Ked. *Veterinary Parasitology*, **130**, 141-155.
- SOULSBY, E.J.L. (1968). *Helminths, arthropods, and protozoa of domesticated Animals*. Williams and Wilkins Co., London.
- SUMMERS, R.W. (1975). On the ecology of *Crataerina hirundinis* (Diptera; Hippoboscidae) in Scotland. *Journal of Zoology, London*, **175**, 557-570.
- TELLA, J.L., GORTÁZAR, C., GAJON, A. and OSÁCAR, J.J. (1995). Apparent lack of effects of a high louse fly infestation (Diptera, Hippoboscidae) on adult colonial Alpine Swifts. *Ardea*, **83**, 435-439.
- TELLA, J.L., GAJÓN, A., GORTÁZAR, C. and OSÁCAR, J.J. (1998). High host specificity of *Crataerina melba* (Diptera, Hippoboscidae) in a mixed colony of birds. *The Journal of Parasitology*, **84**, 198-200.
- TELLA, J.L. and JOVANI, R. (2000). Sources of variability in aggregation and sex ratios of *Crataerina melba* (Diptera: Hippoboscidae) among adult colonial alpine swifts. *Journal of Parasitology*, **86**, 933-938.
- TOMPKINS, D.M., JONES, T. and CLAYTON, D.H. (1996). Effect of vertically transmitted ectoparasites on the reproductive success of Swifts (*Apus apus*). *Functional Ecology*, **10**, 733-740.

- WALKER, M.D., ROZMAN, J. and WITTE, K. (2009). Brutkolonie des Mauerseglers (*Apus apus*) in einer Autobrücke. *Vogelwarte*, **47**, 41-43.
- WEITNAUER, E. (1947). Am Neste des Mauerseglers *Apus apus apus* (L.). *Der Ornithologische Beobachter*, **44**, 133-182.
- YUVAL, B. (2006). Mating systems of blood feeding flies. *Annual Review of Entomology*, **51**, 413-440.
- ZUMPT, F. (1966). The arthropod parasites of vertebrates in Africa south of the Sahara. 3 Insecta excl. Phthiraptera. *Publications of the South African Institute for Medical Research*, **13**, 1-283.

**CHAPTER THREE:
CHARACTERISTICS OF *C. PALLIDA*
POPULATIONS**

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CHAPTER ABSTRACT	3.2
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CHARACTERISTICS OF *CRATAERINA PALLIDA* POPULATIONS

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3.1: CHAPTER AIMS

This chapter aims to determine the characteristics of *C. pallida* populations through the use of standard ecological parameters. Particularly emphasis will be placed upon those parameters of pertinence to its parasitic mode and efficacy. The objectives are to:

- Quantify key parameters such as parasitic prevalence, population aggregation and parasitic load.
- Identify trends or changes in *C. pallida* population size occurring throughout the swift breeding season.
- Determine *C. pallida* population sex ratios and identify whether they change through the summer.

These aims will be met by censusing *C. pallida* pupal and adult populations during the summer breeding seasons of the *A. apus* hosts. This research is needed to confirm previous observations on *C. pallida* population ecology reported in the literature review in chapter 2. The population structure at nests have been described only once before, thus further examination is required. As explained in the literature review, a false impression of *C. pallida* populations may have been obtained due to the artificial nature of the study site studied. The more natural conditions experienced at the site used here means a more realistic impression of parasite populations can be gained. Knowledge about parasite population characteristics is required before the level of parasitic pressure exerted upon hosts can be quantified. The potential effect of a parasite can only be assessed once the parasitic load hosts experience has been correctly determined.

3.2: CHAPTER ABSTRACT

An essential pre-requisite to understanding the nature of a host-parasite relationship is a good knowledge of the parasite's ecology, including its life-history. Despite removing a significant amount of blood from their Common Swift (*Apus apus*) hosts, no detrimental effect of parasitism by the Louse Fly (*Crataerina pallida*) has been found. This may be because little is known of the characteristics of the populations of this parasite. We studied the structure of Louse Fly populations that may influence its pathogenicity. High levels of prevalence were seen, with 100% of nests being parasitized during 2007 and 2008. Louse Fly pupae were found to be aggregated, with a frequency distribution best described by the negative binomial model in 2006-2008. The mean parasitic load per nest was 3.72 ± 2.65 in 2007 and 4.21 ± 3.09 in 2008, much higher than that found in comparative studies. Louse Fly numbers declined throughout the swift breeding season. Parasite populations were heavily female biased, except for at the initial and final stages of the nestling period.

3.3: INTRODUCTION

Avian species have proved a favourite target for biologists wishing to examine parasite-host interactions (Loye and Zuk 1991, Clayton and Moore 1997). Detrimental effects of parasitism on hosts have been found in a large number of empirical studies (see Møller *et al.* 1990, Møller 1997). However, no negative effect of parasitism by the Louse Fly (*[Crataerina pallida* Latreille] Diptera: Hippoboscidae) has been found upon their Common Swift (*(Apus apus* Linnaeus) Aves: Apodidae) hosts (Lee and Clayton 1995, Tompkins *et al.* 1996). This is surprising as the literature review conducted in chapter 2 showed that *C. pallida* removes considerable quantities of blood from hosts. *C. pallida* is an obligate monoxenous parasite that feeds once every five days, with males taking on average 23 mg and females 38 mg of blood on each occasion (Kemper 1951); this has been calculated as being the equivalent to 5% of an adult swifts total blood volume (Campbell 1988). Although there are anecdotal reports of adult Common Swifts that carried Louse Flies being in poor condition (Büttiker 1944, Weitnauer 1947, Lack 1956), no effects of parasitism on swifts have been found (Hutson 1981, Lee and Clayton 1995, Tompkins *et al.* 1996). However, a number of wide ranging and considerable detrimental effects have been found by a closely related parasite species, *C. melbae* (Latreille (Diptera: Hippoboscidae), a parasite of the Alpine Swift (*(A. melba* Linnaeus) Aves: Apodidae)(e.g. Bize *et al.* 2003, 2004a, 2004b, 2005).

As shown in chapter 2, Louse Flies have been little studied and little is known of their life-history (Marshall 1981). However, a good knowledge of parasite ecology is required before the functioning of host-parasitic systems can be understood (Clayton 1991). Thus, a lack of knowledge of this parasite may have hindered the identification of detrimental effects that it may be having upon its host. Whether the population characteristics described in previous studies truly reflect natural levels is unknown. Hutson (1981) examined adult Common Swifts and found that *C. pallida* numbers declined throughout the summer and populations were predominately female biased but whether such patterns are seen at nests is unknown. Studies on related parasites such as the House Martin Louse Fly (*C. hirundinis* Rondani), and Alpine Swift Louse Fly (*C. melbae* Linnaeus), indicate that this may be the case (Summers 1975, Tella and Jovani 2000).

Whether figures for parasitic load, prevalence and aggregation seen in the studies of this parasite's efficacy reflect true levels is also uncertain. Nest prevalence of 67% and an average parasite load of 1 Louse Fly per nest (range 0-9) was observed at the famous Oxford Museum swift colony (Lee and Clayton 1995). Tompkins *et al.* (1996) manipulated Louse Fly numbers to create nests with enhanced parasitism, with a mean parasite load of 7.39 flies per nest, and reduced parasitism, with a mean load of 0.37. However, as nests are cleaned on a yearly basis at this site a distortion of parasite populations and a reduction in the parasite load may be occurring. Such cleaning affects parasitic abundances (Møller 1989). Thus a re-examination of *C. pallida* biology is pertinent.

Populations were studied at the Common Swift nesting colony described in chapter 1, which offered a unique opportunity to study Louse Flies because of the ease of access to nests that it offered. The lack of previous research on this parasite is probably due to the difficulty of obtaining access to swift nesting sites. Common Swifts, being almost totally aerial, are notoriously difficult to study, and their nesting colonies are usually situated in locations difficult for predators, and biologists, to access. Since nests at this site are not manipulated or cleaned from year-to-year, parasite populations are able to cycle in an undisturbed manner, thereby more closely reflecting levels of parasitism seen in this host-parasite system.

3.4: METHODS

Common Swifts have established a nesting colony within a highway bridge spanning the Bigge Reservoir in the Sauerland area of Germany (51° 04' 00" N, 07° 81' 00" E). The nests are situated beneath the carriageway in dual enclosed walkways, which run the entire length of the bridge. The walkways are divided into sets of chambers, 8 for each walkway. Swifts enter these chambers through small, 10-11-cm wide ventilation holes found on the floor of the chambers. In 2007 and 2008, between 0 and 8 active nests were found in each chamber. Nests are typically widely separated. The mean distance between nests in the same chambers in 2009 was 603 cm \pm 488 cm with a range of 98-1910 cm. Nests in different chambers are separated by closed concrete partitions. Movement of parasites between nests is, therefore, likely to be limited and parasites at each nest are likely to be isolated from each other.

Louse Fly populations were studied in 2007 and 2008. The swift colony comprised 38 breeding pairs of swifts in 2007 of which 35 produced nestlings. In 2008, there were 41 breeding pairs at the bridge, of which 37 incubated eggs and produced nestlings. Common Swifts are known to be nest-site faithful (Weitnauer 1947, Lack 1956), so it is likely that pairs were present at the same nests prior to 2007. Nests were examined regularly for Louse Flies and, when possible, daily, during the swift breeding seasons. Breeding Common Swifts are extremely sensitive to disturbance and will readily desert. Because of this, nests could only be closely examined from when the adults ceased the brooding of the nestlings, which occurs when nestlings are approximately 10 days of age. Louse Fly pupae were counted at the nests each autumn following the breeding season in 2006-2008.

Two aspects of parasitic load were studied, i.e., the prevalence of parasitism and the intensity of parasitism experienced by the host. Louse Flies are closely associated with the nest, so the nest was used as a discrete unit of parasitism. Prevalence is commonly defined as being the proportion of hosts that are infested with a parasite and, in our case, we defined prevalence as being the proportion of nests infested with Louse Flies, including flies on individual nestlings within a nest. Two measures of parasite intensity were calculated. First, the average parasite load was defined as the mean number of parasites infesting each nest while nestlings were present over the course of the swift breeding season. In addition, the maximum number of flies seen on any single occasion

at each nest was recorded to produce a measure of maximum parasite load per nest. Lee and Clayton (1995) and Tompkins *et al.* (1996) suggested that this might be the most accurate level of parasite load experienced at each nest since flies are not always present at the nests, but are sometimes carried away from the nest on the adult swifts and thus missed from counts. These authors counted Louse Fly populations on only a small number of occasions, which meant that using the maximum number of flies seen on any single occasion was more appropriate than calculating daily averages.

An important parameter of parasitic populations, influencing the pathogenic effect they have upon host populations, is their distribution between hosts. Parasite populations are typically aggregated in nature, with most parasites being concentrated upon a small number of hosts. The strength of this aggregation can be determined by comparing the parasitic frequency upon hosts with different statistical measures of distribution. The extent of aggregation exhibited by Louse Fly populations was discovered by producing frequency distributions using the maximum number of flies seen at each nest and the number of pupae found at each nest each autumn in the same manner as done by Lee and Clayton (1995). The statistical distribution these distributions most closely fitted was found using the Easy-fit software program (MathWave Technologies, San Diego, CA, USA). Additionally the k-parameter of aggregation, a typically described index which quantifies entomological population aggregation, was calculated for pupae and maximum adult Louse Fly number using the method introduced and outlined by Southwood (1978).

The average number of Louse Flies seen per nest per day at all nests studied for the period when nestlings were present was calculated for the entire breeding seasons of 2007 and 2008 to provide the mean parasite load. Nests at which there were no nestlings present were not included as Louse Flies quickly desert nests that are no longer occupied. In 2008, the sex of flies at each nest was established on a regular basis following the end of adult brooding using the method of sexing described by Kemper (1951).

3.5: RESULTS

Parasitic load: Results for parasite prevalence and parasitic intensity are summarized in Table 1. Of the 37 nests where nestlings hatched in 2008, Louse Flies were observed in all on at least 1 day during the course of the investigation, giving a prevalence for all nests for the entire season of 100%. On an average, $88.0\% \pm 0.10$ (SD) of nests were parasitized each day. The range in daily nest prevalence per day varied from 70% to 100%. On average over a 21-day period, each nest was free of Louse Flies for 3.1 ± 3.9 days. The most frequently parasitized nests had flies present on each day; the least parasitized nest was free of flies 16 days over this 21-day period. The distance of pupae from nests was measured in the autumn of 2008. Of the total number observed, 563, 19.7% were found either in, or directly beneath, a nest, 46% were found within 30 cm of a nest, and the remaining pupae were found more than 30 cm from the nest. Pupae and Louse Flies were aggregated in terms of frequency distributions. The distribution of pupae in 2006 (Figure 1a) was best described by a negative binomial model (K-S Test, $z = 0.13$, $n = 47$, $P = 0.38$) rather than by a Poisson (K-S Test, $z = 0.36$, $n = 40$, $P = 0.73$). In 2007, pupae distribution (Figure 1b) was best described by a negative binomial model (K-S Test, $z = 0.23$, $n = 42$, $P = 0.01$). In 2008, the frequency distribution of pupae (Figure 1c) was best described by the negative binomial model (K-S Test, $z = 0.16$, $n = 40$, $P = 0.19$) rather than the Poisson (K-S test, $z = 0.36$, $n = 40$, $P = 0.73$).

However, the adult louse fly distributions were more strongly aggregated (Figure 2a) (K-S Test, $z = 0.23$, $n = 47$, $P = 0.01$), but could not be described by either a Poisson in 2007 (K-S test, $z = 0.17$, $n = 36$, $P = 0.17$) or the negative binomial distribution (Figure 2b) (K-S Test, $z = 0.17$, $n = 4$, $P = 0.21$).

Trends in population size: Although not all nests could be examined on each day, the average number of Louse Flies seen per nest per day was calculated for 2007 (Figure 3) and 2008 (Figure 4). In both year, average fly numbers were initially high, but declined as the swift breeding season progressed. In 2007, the average number of flies seen peaked at 7.8 ± 8.8 on 19th June; the trend was for populations to fall until the 18th of July when no Louse Flies remained. Flies were seen on fewer days in 2007 than in 2008. In 2008, the peak in mean number occurred on the 9th of June, when an average of 7.5 ± 3.6 was seen per nest. As for 2007, the trend was for the population size to decrease, finally reaching zero on the 26th of July. There was a significant negative

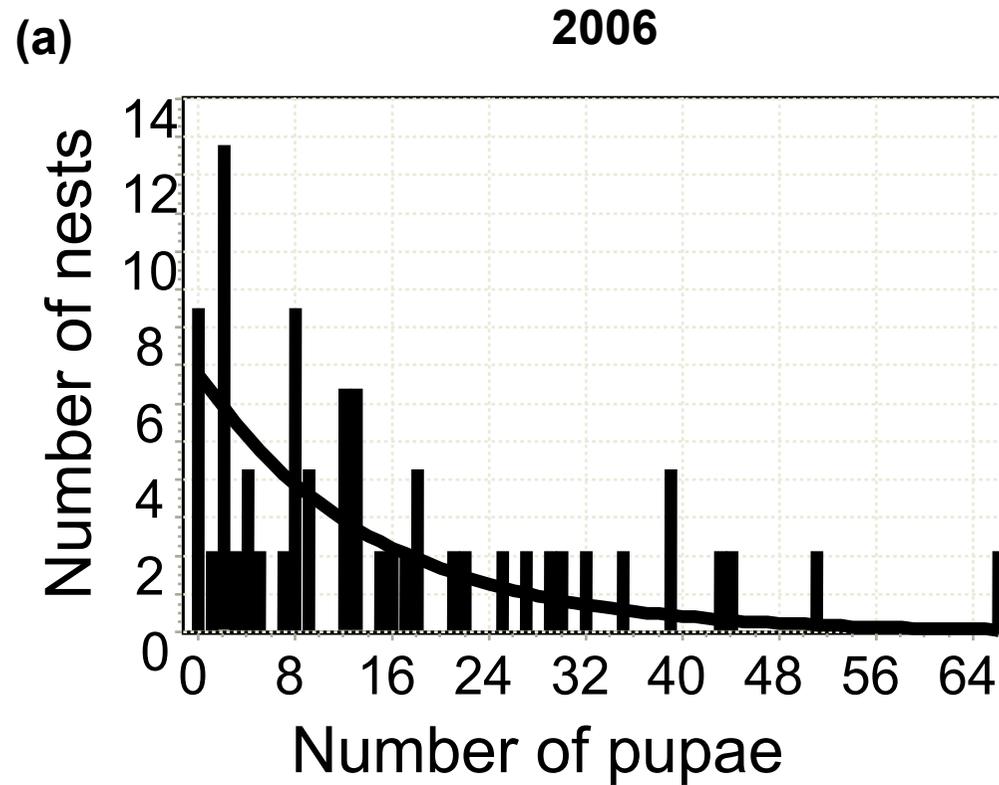
correlation between date and average fly number during 32 days of the nestling period of 2007 ($r_s = 0.80$, $n = 32$, $P < 0.01$). This was also the case in 2008 over 58 days considering at all 41 active ($r_s = 0.9$, $n = 58$, $P < 0.01$).

Nestling presence at the nests and brood size are related to *C. pallida* population size and prevalence. In 2008, in a sample of 10 nests studied over 31 days, there was a strong correlation between brood size and both prevalence ($r_s = 0.89$, $n = 31$, $P < 0.01$) and the total fly population ($r_s = 0.91$, $n = 31$, $P < 0.01$). Thus, generally the larger the brood size the more parasites a nest contains.

The number of male and female Louse Flies seen in total, at the nests and on the nestlings, can be seen in Table 2. In total, 1015 flies were sexed during the entire summer. The total sex ratio over the entire summer was 0.38 males to 0.62 females. The proportion of males to females observed was not constant and changed throughout the course of the swift breeding season (Figure 5). There was a significant difference in the total number of each sex seen on each day ($G = 1.22$, $P < 0.01$, d.f. = 32) when compared to an expected 50:50 ratio. On the 15th of June, when the sex of Louse Fly populations were first sampled, the proportion of males to females was almost equal, i.e., 0.40 males to 0.60 females. Thereafter, the population became strongly female biased. The highest proportion of females to males was seen on the 8th of July when there were 0.26 males to 0.74 females.

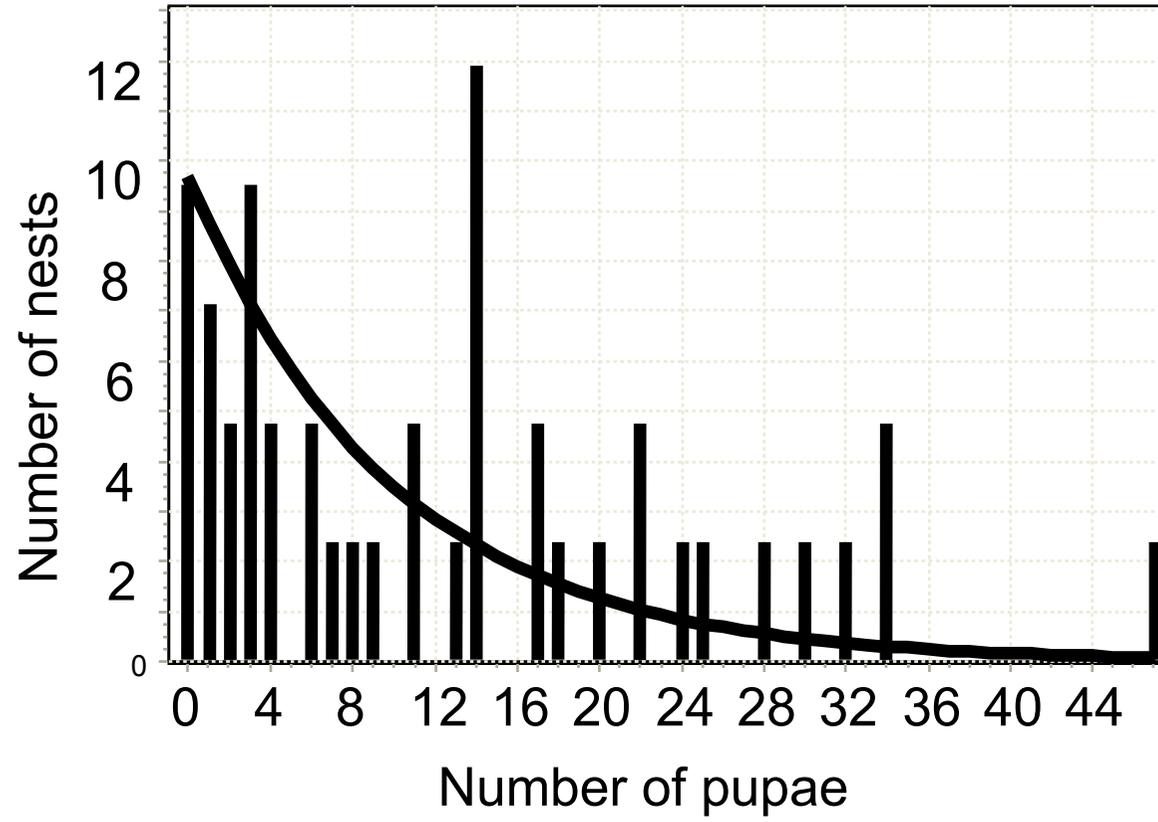
During latter stages of the nestling period, the proportion of males to females became more equal, reaching 50:50 on 16th July, which almost coincided with the time of nestling fledging, i.e., the first nestling fledged on 11th July. As might be expected given the decline in fly numbers, as the season progressed there were fewer males and females. The number of females fell more sharply than the number of males, which might be expected given their populations were larger initially. The total number of males seen during 32 days of the nestling period was strongly correlated with date ($r_s = 0.70$, $n = 32$, $P < 0.01$), as was the number of females ($r_s = 0.81$, $n = 32$, $P < 0.01$). The average number of males seen per nest was strongly correlated with date ($r_s = 0.66$, $n = 32$, $P < 0.01$), as was the average number of females seen per nest ($r_s = 0.92$, $n = 32$, $P < 0.01$).

Figure 1: The observed distribution of *Crataerina pallida* pupae at nests in autumn 2006 (a) ($k = 0.89$, mean = 14.075, $S^2 = 234.5$), autumn 2007; (b) ($k = 2.18$, mean = 15.91, $S^2 = 132.01$), and autumn 2008 and (c) ($k = 0.92$, mean = 12.80, $S^2 = 190.32$). Expected negative binomial distributions are shown as curves.



(b)

2007



(c)

2008

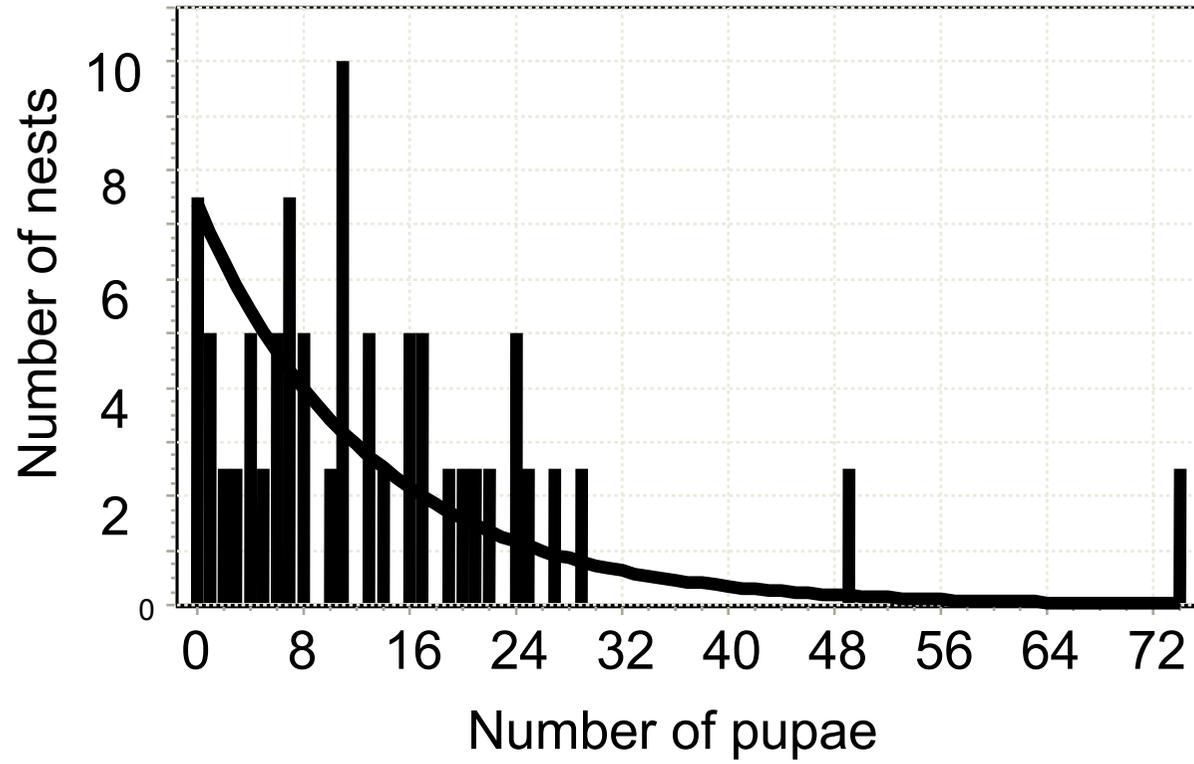
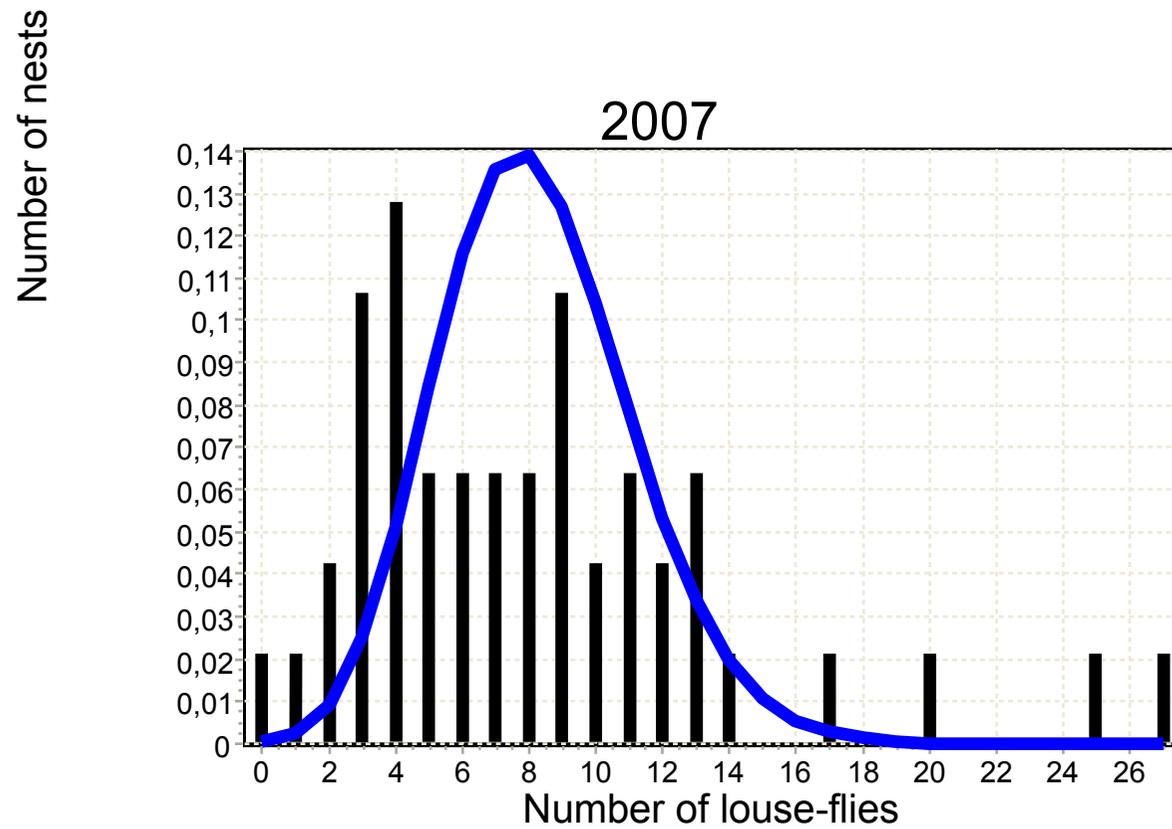


Figure 2: The observed distribution of *Crataerina pallida* adults at nests, (using maximum number of adults seen at each nest), for 2007 (a) ($k = 2.83$, mean = 8.212, $S^2 = 31.997$) and 2008 and (b) ($k = 4.12$, mean = 11.25, $S^2 = 41.91$). Expected negative binomial or Poisson distributions are shown as curves.

(a)



(b)

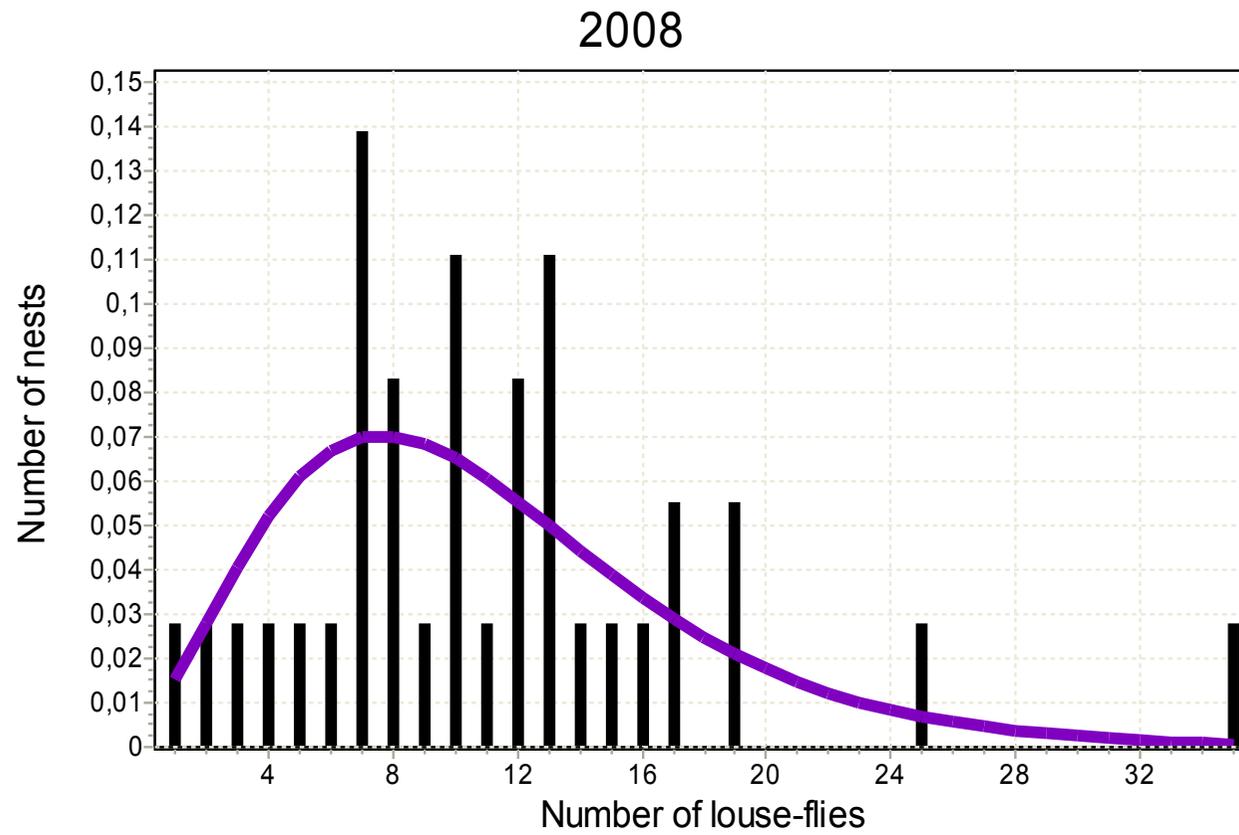


Figure 3: The average number of adult *C. pallida* per nest per day during the nestling period of 2007. The number of nests examined daily varied. Error bars indicate level of SD.

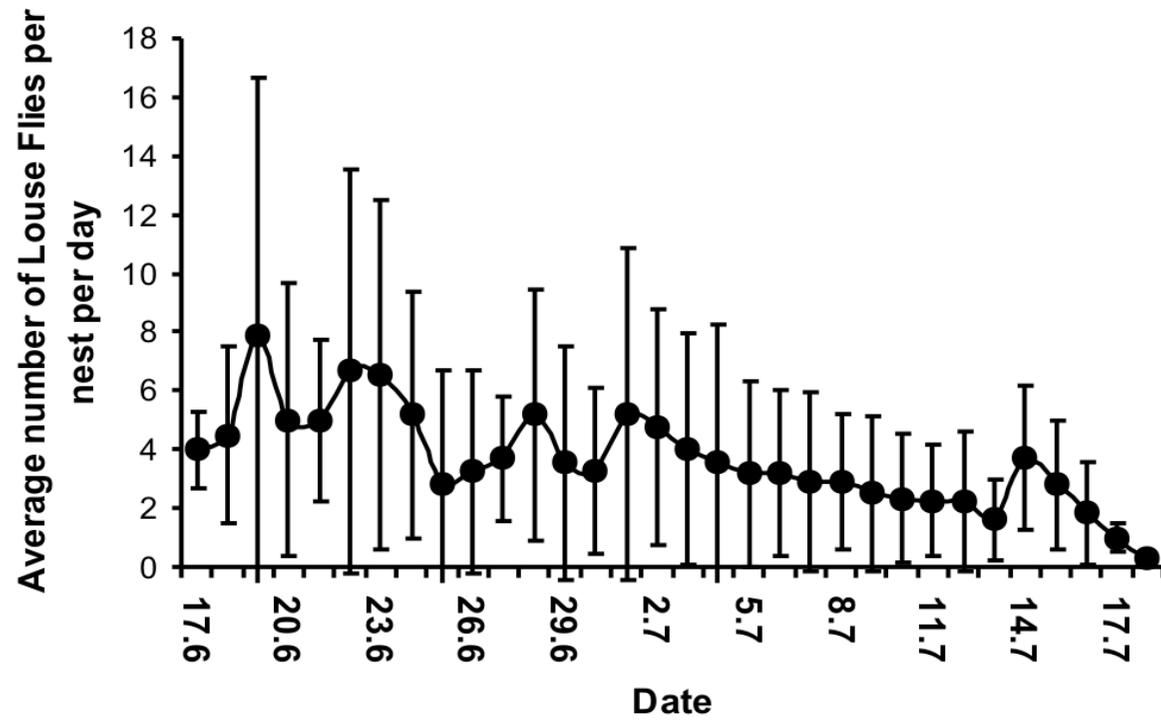


Figure 4: The average number of adult *C. pallida* per nest per day during the nestling period of 2008. The number of nests examined daily varied. Error bars indicate the level of SD.

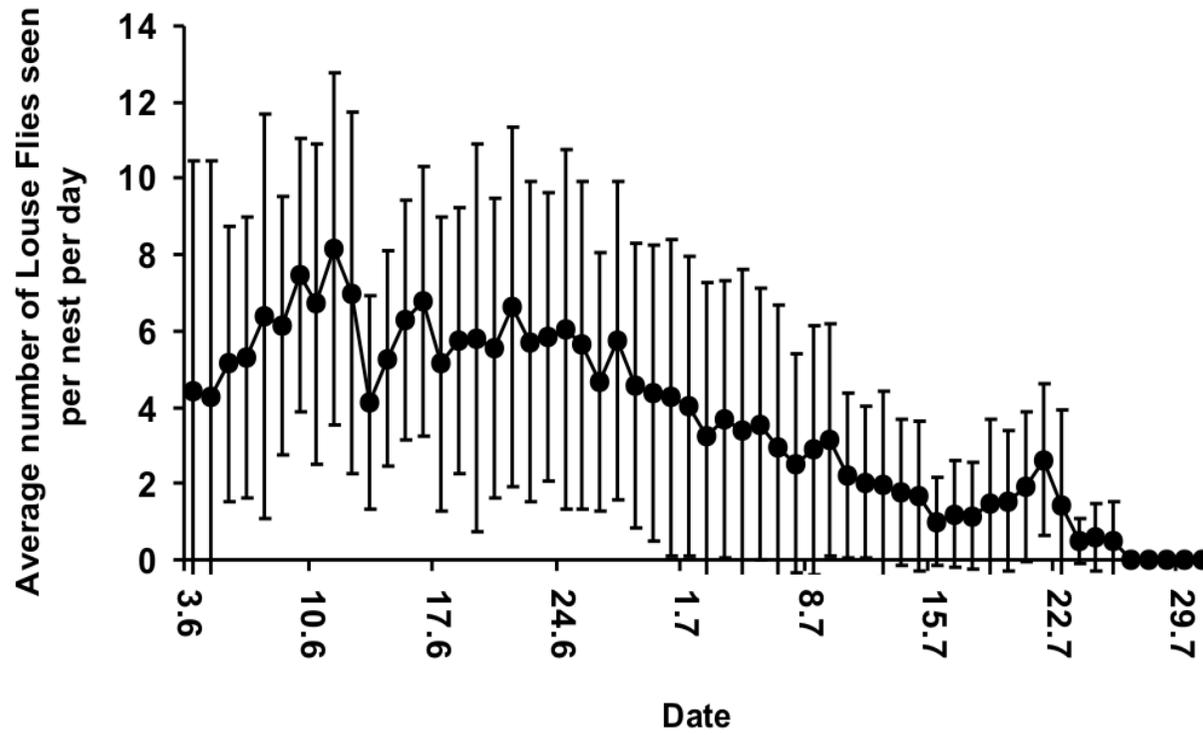


Figure 5: The proportion of male and female *Crataerina pallida* throughout the summer at a sample of 10 selected nests from 2008. Males represented as squares. Females represented by circles.

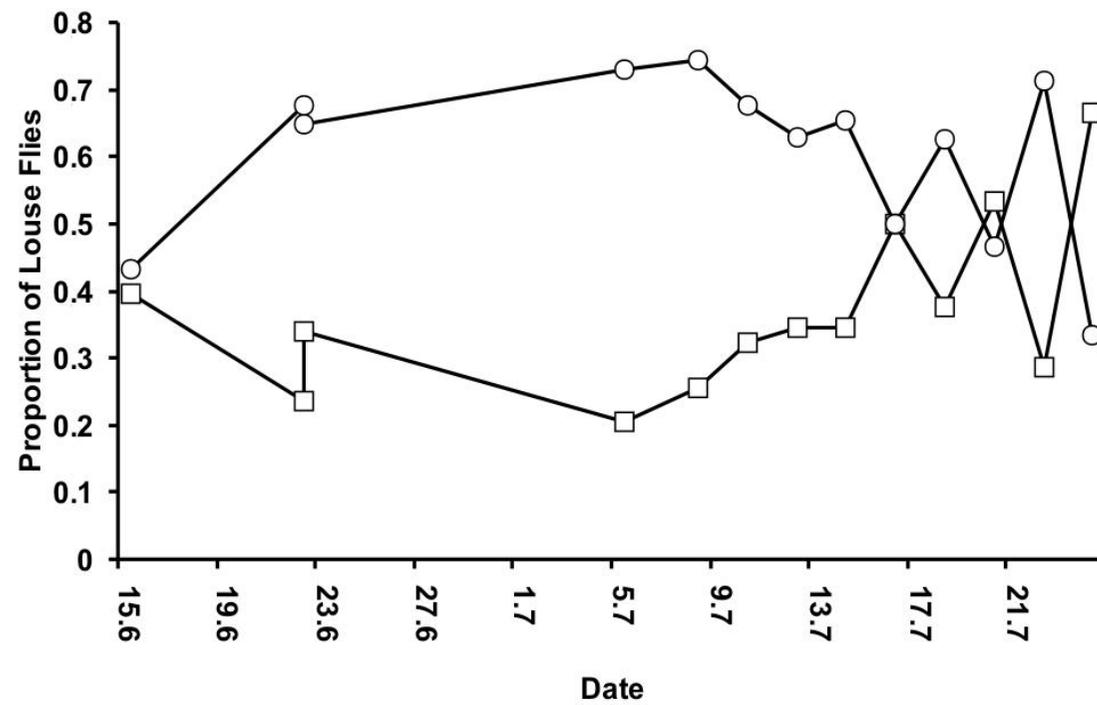


Table 1: The prevalence and mean parasitic intensity of *C. pallida* adults and pupae.

	Prevalence	Mean parasite load per nest \pm SD	Range
Pupae			
2006	93% ($n = 47$)	15.9 ± 15.5	0-66
2007	91% ($n = 45$)	12.8 ± 11.22	0-47
2008	92% ($n = 41$)	14 ± 13.97	0-74
Adults			
2007	100% ($n = 47$)	3.72 ± 2.65	1-25
2008	100% ($n = 37$)	4.21 ± 3.09	1-35

Table 2: The number of male and female Louse Flies seen in total, at the nests and on the nestlings during 2008.

	Male	Female	Total
Nestlings	75	154	229
Nests	311	475	786
Total	386	629	1015

3.6: DISCUSSION

The results show that *C. pallida* are highly prevalent and highly aggregated between nests, occur at high parasitic loads, that parasite populations decrease in size as swift breeding progresses, and populations are strongly female biased. Surprising variations in *C. pallida* population size and parasite sex ratio occurred.

These results some of the figures reported in chapter 2, but are contrary to others. The results for Louse Fly prevalence are much higher and thus contrary to those reported by Lee and Clayton (1995) or by Hutson (1981) who studied this species, or by McClure (1984) and Wood (1983) who studied other Hippoboscid species. Presently, there is no adequate explanation for this generally high prevalence. The average and maximum parasitic intensities observed are much higher than those reported by Lee and Clayton (1995), or even by Tompkins *et al.* (1996) where they were experimentally manipulated to be artificially high. However, *C. pallida* adults and pupae were found to be highly aggregated among nests confirming the findings of Lee and Clayton (1995). Louse Fly populations decreased in size as the swift breeding season progressed, in confirmation of Hutson's (1981) results from adult swifts and Summers (1975) from a related species. Populations are female biased for much of the nestling period in accordance with that observed by Hutson (1981), Tella and Jovani (2000), and Summers (1975).

These results have important implications for studies investigating the functioning of this host-parasitic system. Previously no detrimental effect of parasitism by *C. pallida* has been found upon hosts (Lee and Clayton 1995, Tompkins *et al.* 1996). This is surprising given the strong physical features indicating a parasitic lifestyle seen in chapter 2. The parasitic loads reported here may more realistically reflect natural levels than those used in these studies. At the Oxford site where these studies were conducted parasitic loads were substantially lower, possibly accounting for the apparent avirulence observed. The fluctuations and steady decrease observed in *C. pallida* populations means the frequency and timing of parasite population censoring are critical in determining the parasitic load observed. Censoring on too few occasions or during periods of population flux, may result in a false estimate of parasite abundance being obtained. Furthermore, the measure of parasitic intensity used by Tompkins *et al.* (1996), using maximum Louse Fly number seen at any single occasion at each nest, may have lead to a false and artificially high level of parasitism being reported. The

mean fly number over the entire breeding season may provide a more realistic indication parasite load. Negative effects of parasitism are most likely to be strongest early in the season when populations are highest. Due to the sensitive nature of swifts, *C. pallida* populations could not be quantified during clutch incubation. As Louse Fly populations were at their greatest immediately post nestling hatching, it is likely that parasite populations are at their highest during the preceding incubation period. Appearance of *C. pallida* during this period would be to their advantage as at this time swift adult hosts are present at the nest for great lengths of time and thus most available as hosts. Parasite abundance may decline later during nestling development as a result of increasing nestling immunity.

Aggregated population distributions are commonly seen in parasitic species (Anderson and May 1978). Thus the contagious distribution observed here in *C. pallida* populations is not unusual. The extremely poor weather conditions experienced during that summer of 2007 may account for the adult parasite distribution of that year which more closely fitted a normal distribution. The poor conditions meant swift breeding was curtailed at many nests, possibly preferentially at those which would have harboured the greatest abundances of parasites, thus causing the observed decrease in aggregation.

The short term variations in Louse Fly population size are surprising and probably the result of *C. pallida* moving from the nests onto adult hosts in order to feed, and then being transported temporarily away from the nests. Small changes in nest populations of 1 or 2 within 24 hours could have been caused by miscounting. However, the larger differences of 5 or more within 24- or 48-hour time periods must be the result of such movements. This again shows that the number of Louse Flies seen on any particular day may not be a reliable indication of parasitism. Instead, repeated measures of parasite intensity should be used to avoid false estimation. Large fluctuations appeared to occur during poor weather conditions when adult swifts spent more time at the nest and were thus more accessible to feeding Louse Flies thus facilitating such movement. Parasite abundance was found to be related to brood size. Greater parasite abundance may occur when there are the most available resources, such as when brood sizes and the number of potential hosts higher.

The female biased sex ratios confirm previous observations (e.g. Hutson 1981).

However, the changes in sex ratios over the season have not previously been described. Equal numbers of males and females are reported to emerge from pupae (Bequaert 1953). However, populations have been found to be male biased in the spring (Hutson 1981). A similar pattern would probably have been observed here could nests have been examined during swift incubation. This initial male bias is due to male emergence before females. The increasing predominance of females is probably due to higher male mortality early in the season (Kemper 1951), possibly due to male mating competition. Males increase in proportion late in the season, probably as a result of later female mortality. Alternatively phoretic dispersal may be occurring, with gravid females moving onto nestlings late in the season to be dispersed to new, previously uncolonized nest sites where their offspring would face lower intra-specific competition.

These results confirm some aspects of *C. pallida* biology seen in previous studies but are contrary to others. The higher parasitic loads and the variations in population size and sex ratio, may mean that previous studies falsely estimated parasitic abundance and this may account for the lack of detrimental parasitic effects reported. These factors should be considered in further investigations examining the effect this parasite has upon its host.

3.7: CHAPTER SUMMARY

The results of scientific enquiry upon *C. pallida* biological and ecological life-history traits were:

- Higher level of parasitic population prevalence and parasite load were seen than have been observed in previous studies of *C. pallida* and related parasites.
- High levels of host aggregation were seen, with most parasites being found upon at a small number of hosts nests, in confirmation of another study on *C. pallida*.
- An association of nestling presence with *C. pallida* abundance was discovered, with larger broods harbouring more parasites.
- Short term variations in *C. pallida* populations causing discrepancy in maximum and mean measures of parasite load observed.
- Populations found to be female biased. Changes in population sex ratio over summer discovered.
- A decline in abundance occurred throughout the swift breeding season in confirmation of previous reports.

These results have a number of implications. The high levels of parasite prevalence and population aggregation are features characteristic for parasitic species. Thus the conclusion can be drawn that *C. pallida* may have an analogous mode of life and be likewise parasitic. The results are therefore strongly indicative that *C. pallida* is engaged within a parasitic relationship with *A. apus*, and should therefore have a clear detrimental effect upon it. This conclusion is justified because the population dynamics demonstrated by a specific species provide a good indication as to its life-style.

The higher levels of prevalence, aggregation and parasite load, plus the short term variations in abundance discovered here strongly suggest that the previous investigations studying the effect of *C. pallida* on swifts may have underestimated the extent of parasitic pressure. A mean measure of parasite load may provide a more realistic impression of parasite load and pressure. Using more accurate measures of parasite pressure may lead to the elucidation of clear effects, not apparent in these previous studies.

The decline in population size over time indicates that parasitic effects should be most apparent early during swift reproduction, particularly when nestlings are young. Thus study of nestling growth and development may be particularly productive in establishing parasitic costs, as altricial nestling growth is at its most rapid during the initial stages of development.

3.8: CHAPTER REFERENCES

ANDERSON, R.M. and MAY, R.M. (1978). Regulation and stability of host-parasite population interactions. 1 Regulatory processes. *Journal of Animal Ecology*, **47**, 219-247.

BEQUAERT, J.C. (1953). The Hippoboscidae or Louse Flies (Diptera) of mammals and birds Part I. Structure, physiology and natural history. *Entomologica Americana*, **32**, 1-209.

BIZE, P., ROULIN, A., BERSIER, L.F., PFLUGER, D. and RICHNER, H. (2003). Parasitism and developmental plasticity in Alpine Swift nestlings. *Journal of Animal Ecology*, **72**, 633-639.

BIZE, P., ROULIN, A. and RICHNER, H. (2004a). Parasitism, developmental plasticity

- and bilateral asymmetry of wing feathers in Alpine Swift (*Apus melba*) nestlings. *Oikos*, **106**, 317-323.
- BIZE, P., ROULIN, A., TELLA, J., BERSIER, L.F. and RICHNER, H. (2004b). Additive effects of ectoparasites over reproductive attempts in the long-lived alpine swift. *Journal of Animal Ecology*, **73**, 1080-1088.
- BIZE, P., ROULIN, A., TELLA, J. and RICHNER, H. (2005). Female-biased mortality in experimentally parasitized alpine swift (*Apus melba*) nestlings. *Functional Ecology*, **19**, 405-413.
- BÜTTIKER, W. (1944). Die Parasiten und Nestgäste des Mauerseglers (*Micropus apus* L.). *Der Ornithologische Beobachter*, **41**, 25-35.
- CAMPBELL, T.W. (1988). *Avian hematology and cytology*. Iowa State University Press, Ames, Iowa.
- CLAYTON, D.H. (1991). The influence of parasites on host sexual selection. *Parasitology Today*, **7**, 329-334.
- CLAYTON, D.H. and MOORE, J. (1997). *Host-parasite evolution: General principles and avian models*. Oxford University Press, New York.
- HUTSON, A.M. (1981). The population of the Louse Fly, *Crataerina pallida* (Diptera, Hippoboscidae) on the European swift, *Apus apus* (Aves, Apodidae). *Journal of Zoology London*, **194**, 305-316.
- KEMPER, H. (1951). Beobachtungen an *Crataerina pallida* Latr Und *Melophagus ovinus* (Diptera, Pupipara). *Zeitschrift für Hygiene (Zoologie)*, **39**, 225-259.
- LACK, D. (1956). *Swifts in a tower*. Methuen Publishing, London.
- LEE, P.L.M. and CLAYTON, D.H. (1995). Population biology of swift (*Apus apus*) ectoparasites in relation to host reproductive success. *Ecological Entomology*, **20**, 43-50.
- LOYE, J.E. and ZUK, M. (1991). *Bird-parasite interactions: Ecology, evolution and behaviour*. Oxford University Press, Oxford, UK.
- MARSHALL, A.G. (1981). *The ecology of ectoparasitic insects*. Academic press, London.
- MCCLURE, H.E. (1984). The occurrence of Hippoboscid flies on some species of birds in southern California. *Journal of Field Ornithology*, **55**, 230-240.
- MØLLER, A.P. (1997). Parasitism and the evolution of host life history. In: CLAYTON, D.H., MOORE, J. (eds.). *Host-parasite evolution: General principles, avian models*. Oxford University Press, Oxford, UK.
- MØLLER, A.P., ALLANDER, K. and DUFVA, R. (1990). Fitness effects of parasites

- on passerine birds: a review. In: BLONDEL, J., GOSLER, A., LEBRETON, J. and MCCLEARY, R.H. (eds.). *Population biology of passerine birds: an integrated approach*. Springer-Verlag, Berlin, Germany.
- MØLLER, A.P. (1989). Parasites, predators and nest boxes: facts and artefacts in nest box studies of birds. *Oikos*, **56**, 421–423.
- SOUTHWOOD, T.R.E. (1978). *Ecological methods, with particular reference to the study of insect populations*. Chapman and Hall, London.
- SUMMERS, R.W. (1975). On the ecology of *Crataerina hirundinis* (Diptera; Hippoboscidae) in Scotland. *Journal of Zoology*, **175**, 557-570.
- TELLA, J.L. and JOVANI, R. (2000). Sources of variability in aggregation and sex ratios of *Crataerina melbae* (Diptera: Hippoboscidae) among adult colonial Alpine Swifts. *Journal of Parasitology*, **86**, 933-938.
- TOMPKINS, D.M., JONES, T. and CLAYTON, D.H. (1996). Effect of vertically transmitted ectoparasites on the reproductive success of swifts (*Apus apus*). *Functional Ecology*, **10**, 733-740.
- WEITNAUER, E. (1947). Am Neste des Mauerseglers *Apus apus apus* (L.). *Der Ornithologische Beobachter*, **44**, 133-182.
- WOOD, M. (1983). A study of hippoboscid flies on house finches. *North American Bird Bander*, **8**, 102-103.

**CHAPTER FOUR:
INTER-NEST DISPERSAL BY THE
ECTOPARASITIC LOUSE FLY *C. PALLIDA***

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CHAPTER ABSTRACT	4.2
INTRODUCTION	4.3
METHOD	4.4
RESULTS	4.5
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DISCOVERY OF INTER-NEST DISPERSAL BY AN ECTOPARASITIC LOUSE FLY, *CRATAERINA PALLIDA*

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4.1: CHAPTER AIMS

The aim is to investigate the mode and extent of *C. pallida* parasite transmission. The specific objective is to:

- Examine whether movement of *C. pallida* adults between *A. apus* nests occurs.

A method involving the marking and subsequent observation of individual adult *C. pallida* will be developed in order to fulfil this objective. *C. pallida* adults from selected nests will be marked. Adjoining nests will then later be examined for the presence of marked *C. pallida* originating from other nests. This would successfully demonstrate that *C. pallida* movement occurs between nests.

The rationale behind this investigation is that the level of *C. pallida* movement between host nests may account for the lack of parasitic effect previously demonstrated by this species. The mode and extent of transmission between hosts greatly influences the level of virulence parasites express. Parasites which move vertically, that is solely between parent and offspring, exhibit typically lower levels of virulence. Where a parasite uses host offspring as further hosts, reducing host reproductive success would lower a parasites own reproductive chances. The assumed vertical nature of adult *C. pallida* transmission has been used to account for the lack of virulence shown by this parasite.

However, the exact nature of *C. pallida* transmission remains unstudied. Evidence that movement of *C. pallida* between nests does not occur would help substantiate the hypothesis that reduced virulence has evolved due to the vertical nature of its dispersal. Evidence for horizontal transmission would mean some other explanation for the lack of detrimental effect would have to be made.

4.2: CHAPTER ABSTRACT

The dispersal of ectoparasitic Louse Flies *Crataerina pallida* (Diptera; Hippoboscidae), between nests of their Common Swift *Apus apus* (Aves; Apodidae) hosts is reported for the first time. Adult flies were marked and the presence in other nests determined. Over ten percent of marked flies were found in nests other than those in which they were originally marked. This indicates that such dispersal is frequent. As the supposed lack of dispersal of this parasite between unrelated hosts has been used to account for the lack of effect it has upon hosts, this discovery has important implications for understanding of this host-parasite system. New explanations accounting for its apparent lack of virulence may be required.

4.3: INTRODUCTION

Parasite virulence is related to the extent and ease of parasite dispersal between hosts (Anderson and May 1982, Ewald 1994). Easy dispersal between hosts allows parasites to exhibit high levels of virulence as parasite fitness is not related to host fitness or reproductive success. Therefore knowledge about parasitic dispersal is required for a good understanding of the functioning of host-parasite systems to be developed.

Previous investigations have found no negative effect of the Hippoboscid Louse Fly *Crataerina pallida* Latreille 1812 (Diptera; Hippoboscidae), an haematophagous nest ectoparasite, on its Common Swift *Apus apus* Linnaeus 1758 (Aves; Apodidae) hosts (Lee and Clayton 1995, Tompkins *et al.* 1996). This is surprising as the literature review in chapter 2 showed that Louse Flies possess all the features of being a pugnacious parasite and the study conducted in chapter 3 shows that they have population structures in accordance with those seen by parasitic species. This lack of parasitic virulence has been accounted for as being due to the lack of horizontal transmission of parasites between non-related hosts (Lee and Clayton 1995).

Louse Flies have atrophied wings, and thus movement between nests is believed to be limited (Walker and Rotherham 2010). As Louse Fly success is thought to be dependant on successful host reproduction a reduction in virulence would be advantageous to parasites. However, observation of related species indicates horizontal transmission may occur (Bize 2004). Thus an investigation of the mode and extent of Louse Fly dispersal was considered pertinent.

4.4: METHOD

A preliminary study to investigate the movement of marked adult Louse Flies was conducted to find evidence for inter-nest dispersal. The research was conducted at a swift nesting colony situated within a roadway bridge spanning the Bigge Reservoir at Olpe, Germany. This site is described in detail elsewhere (Walker *et al.* 2009). In 2009, 38 breeding pairs nested here, producing 30 broods of young and 74 nestlings.

A total of 76 adult Louse Flies were marked between the 12th and 18th of June 2009. Flies from individual nests were all marked identically on their atrophied wings using acrylic paint. Through the use of different colours and through marking either left or right wings, flies from separate nests could be identified. Trials in 2008 successfully showed that marking was permanent and had no detrimental effect on parasites. Trial markings using numbered apiary discs, which would have allowed individual marking of adults, proved ineffective (Photograph 1). Photograph 1 shows one adult marked with one such apiary tag. As can be seen the large size of these tags hindered louse fly movement and eventually led to louse fly death so their use was discontinued. Seven nests, containing a total of 13 nestlings (range in brood size 0 to 3) were used. No nestlings died during the period of Louse Fly marking and the subsequent examination of nests. The average age of nestlings on the day of marking was 10.8 SD \pm 2.54 days (range 2 to 10 days of age). Nests are typically widely separated from each other (Mean distance between nests = 5.30 metres \pm 48 metres, Range 1.07-19.10 metres). *C. pallida* are closely associated with nests and have not been observed at distances greater than four metres away from nests (Author, personal observation). Thus self-mediated dispersal of the flightless *C. pallida* is unlikely. Parasite numbers and movement between nests was studied on the 15 days post marking.

4.5: RESULTS

Of 76 parasites originally marked (mean per nest 10.86 \pm 5.56), 9 were found in nests other than where they had originally been marked, clearly indicating that inter-nest movement had occurred (Table 1). Such dispersal occurred at 3 of the 7 nests where parasites were marked. Thus 11.84% of marked adults were found to transfer between nests over the 15 days studied and dispersal was seen from 42% of nests where parasites were originally marked.

Figure 1 shows the total number and number of marked parasites seen in nests over the 15 days post marking. *C. pallida* moves between nests and nestling and adult hosts in order to feed. Thus unmarked *C. pallida* were seen at nests as a result of returning to nests from hosts post feeding. Likewise the number of marked *C. pallida* seen post marking was low, due to movement of marked flies onto hosts and thus their consequent disappearance from nests. Both the total parasite population and number of marked flies declined over time, in line with general trends for *C. pallida* populations seen in previous seasons (Walker and Rotherham 2010). Despite close examination no dead flies were found at nests.

More males, 41 (Mean per nest = 4.29 ± 1.70), than females, 35 (Mean per nest = 6.86 ± 4.71), were initially marked (Sex ratio = 54: 46). Despite there being significantly more males than females within the total nest population on the day of marking and the subsequent 15 days (Wilcoxon Rank Test: $W = -130$, $n = 16$, $z = 3.35$, $P < 0.01$), there was no significant difference in the sex of flies marked initially or marked flies subsequently seen at nests (Wilcoxon Rank Test: $W = -26$, $n = 16$, $z = 3.54$, $P = 0.18$). However eight of the nine dispersed flies were female, indicating that this sex is more likely to disperse between nests.

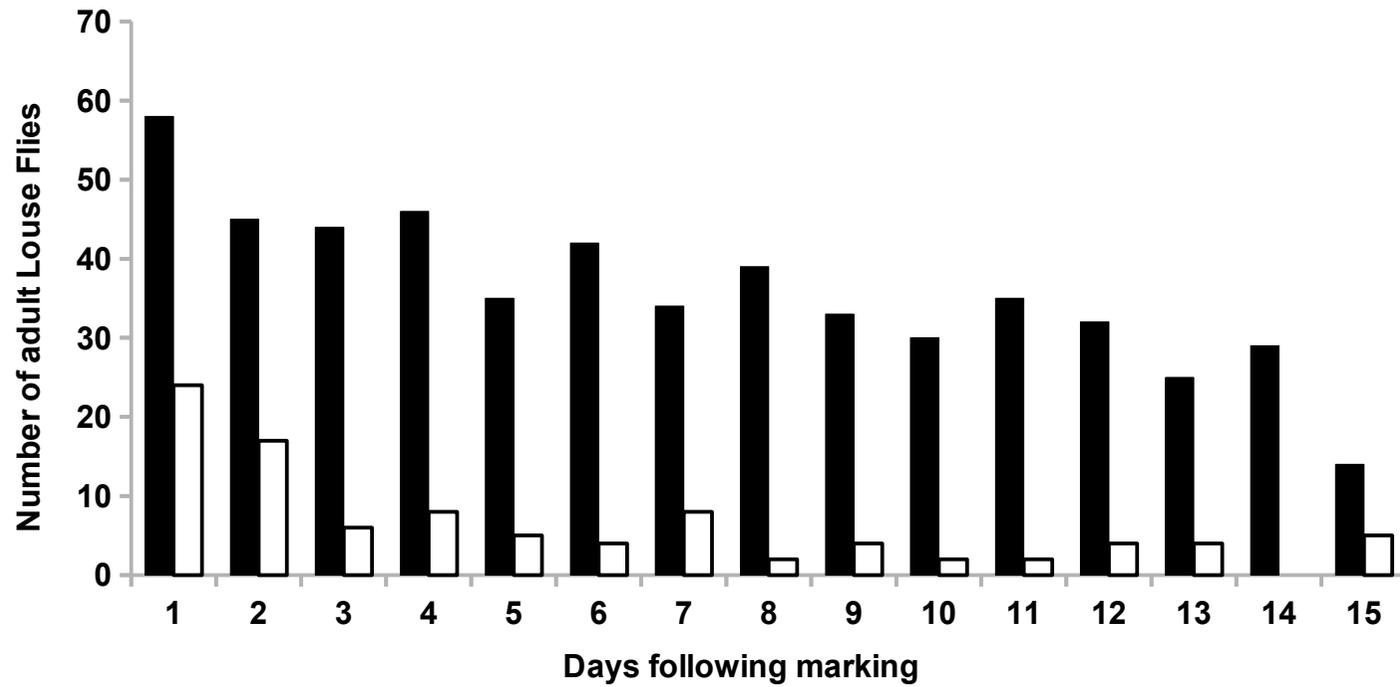
Table 1: The number of *C. pallida* marked and subsequently found in nests other than where originally marked for each of the 7 nests studied. The number of males and females respectively is provided in brackets.

Nest	Number of <i>C. pallida</i> initially marked	Number later found in nests other than where originally marked
1	6 (2:4)	2 (0:2)
2	22 (16:6)	4 (0:4)
3	13 (6:7)	0
4	10 (2:8)	0
5	11 (3:8)	0
6	6 (3:3)	3 (1:2)
7	8 (4:4)	0

Photograph 1: Initial attempts to mark *C. pallida* adults with numbered apiarist marking discs failed. Instead painted marks of different colour were placed upon the atrophied wings.



Figure 1: The numbers of marked and unmarked *C. pallida* adults seen at the 7 nests studied on each of 15 days subsequent to marking. The number of unmarked *C. pallida* adults is represented as black bars. Marked *C. pallida* number is represented by the white bars.



4.6: DISCUSSION

This is the first reported discovery that *C. pallida* disperses between adult hosts and host nests. A notable number of marked adults were found to have moved between nests thus indicating that dispersal between nests occurs. The discovery of such dispersal has important implications for the understanding of this host-parasite system as the assumed lack of such dispersal has been used to account for the lack of detrimental effect this species exerts upon hosts.

In the only other quantitative study of Hippoboscid dispersal, inter nest movement was rare. Adult *C. hirundinis*, a Louse Fly parasite of the House Martin *Delichon urbica*, were marked and dispersal studied (Summers 1975). Only 6 of 450 marked flies moved between nests. Movement occurred only between nests situated closely together and thus dispersal through self locomotion could not be excluded (Summers 1975). However, recent anecdotal observations of another Hippoboscid, *C. melbae*, a nest ectoparasite of the Alpine Swift, report high levels of parasite dispersal (Bize 2004). The results presented here support this observation and suggest that movement by *C. pallida* is more frequent than previously thought. If this is the case new explanations for the observed lack of parasitic virulence are required.

Movement of the flightless Louse Flies may be mediated through physical contact between adult swifts. Such contact was reported in chapter 2. The true level of dispersal is probably even greater than that observed here as swifts are more gregarious before incubation begins but become increasingly sedentary as breeding is initiated (Lack 1956). Here parasitic movement only post incubation could be quantified. Adult visitation of foreign nest sites could be another mechanism by which Louse Flies potentially move between nests as explained in chapter 2. Inter-nest dispersal may explain how *C. pallida* colonizes new and vacant nest sites, previously how this occurred was unclear as adult swifts return from migration parasite free (Zumpt 1966).

The low proportion of marked *C. pallida* seen following marking suggests that the nest population of parasites makes up only a fraction of the total amount of parasitism to which hosts are exposed. Previous studies have examined and quantified solely the nest populations in the calculation of the hosts exposure to parasitic pressure. Parasites feeding temporarily on nestling or adult hosts have not been considered in such counts.

Thus such studies may have underestimated or miscalculated the true level of parasitic pressure faced by hosts. This may account for the apparent lack of effect this parasite has on hosts observed in previous studies.

The results indicate that female *C. pallida* may more readily disperse between nests than males. Gravid females could gain significant fitness benefits by depositing larvae at uncolonised nests or those with lower intra-specific competition. There is good anecdotal evidence that nests may be abandoned once parasitism levels become too high (G. Candelin: personal communication), which would favour such dispersal to sites with lesser competition.

Although limited the discovery of inter-nest dispersal here reported is important as it is the first report that such movement occurs. Further investigation of *C. pallida* movement and populations is required. More detailed study, with a larger number of parasites being marked from a greater number of nests is required to confirm such movement and discover its true extent. The sensitivity of adult swifts during breeding and the limited number of nests available for study hindered marking at additional nests. Swifts colonial nesting sites are typically difficult to study and those that are accessible are often small in size, limiting such research. Pooling of data from a number of years may provide additional data. Further research could extend the scope of this study by individually marking adults, allowing the true size of nest plus host population sizes to be established. The relation of nest parasite population size to the level of parasitic pressure experienced is required to gauge the effectiveness of previous studies investigating parasitic virulence.

Despite the limited nature of the results presented here, the discovery and reporting of such dispersal is important in stimulating further study and a re-examination of this and other similar host-parasite systems.

4.7: CHAPTER SUMMARY

Movement of *C. pallida* adults between *A. apus* nests was discovered. Marked *C. pallida* adults were successfully found in nests other than those in which they were originally marked. This discovery has important implications for the understanding of this host-parasite relationship.

The discovery of marked *C. pallida* in nests other than those they originated from, implies that *C. pallida* can move between nests and thus that inter-nest dispersal and horizontal transmission of *C. pallida* adults occurs. Thus new potential hosts are easy to access, meaning that there is less selection pressure on parasites to reduce the levels of virulence they exhibit. Previously such movement of *C. pallida* was not thought possible.

Marked parent adults could only have dispersed upon adult swifts. Transmission must occur either through physical contact between individual adult swifts or through adults visiting other swift nests. The successful demonstration that horizontal transmission occurs, and probably at quite high levels, means that some other factor accounting for its lack of pathogenicity must be formulated. Further research should quantify the exact extent and mode of *C. pallida* movement between nests.

4.8: CHAPTER REFERENCES

- ANDERSON, R.M. and MAY, R.M. (1982). Coevolution of hosts and parasites. *Parasitology*, **85**, 411-26.
- BIZE, P., ROULIN, A. and RICHNER, H. (2004). Parasitism, developmental plasticity and bilateral asymmetry of wing feathers in Alpine Swift, *Apus melba*, nestlings. *Oikos*, **106**, 317-323.
- EWALD, P.W. (1994). *Evolution of infectious diseases*. Oxford University Press, New York.
- LACK, D. (1956). *Swifts in a tower*. Methuen Publishing, London.
- LEE, P.L.M. and CLAYTON, D.H. (1995). Population biology of swift (*Apus apus*) ectoparasites in relation to host reproductive success. *Ecological Entomology*, **20**, 43-50.
- SUMMERS, R.W. (1975). On the ecology of *Crataerina hirundinis* (Diptera; Hippoboscidae) in Scotland. *Journal of Zoology, London*, **175**, 557-570.
- TOMPKINS, D.M., JONES, T. and CLAYTON, D.H. (1996). Effect of vertically

transmitted ectoparasites on the reproductive success of Swifts (*Apus apus*). *Functional Ecology*, **10**, 733-740.

WALKER, M.D., ROZMAN, J. and WITTE, K. (2009). Brutkolonie des Mauerseglers (*Apus apus*) in einer Autobrücke. *Vogelwarte*, **47**, 41-43.

WALKER, M.D. and ROTHERHAM, I.D. (2010). Characteristics of *Crataerina pallida* (Diptera: Hippoboscidae) populations, a nest ectoparasite of the common swift, *Apus apus* (Aves: Apodidae). *Experimental Parasitology*, **126**, 451-455.

ZUMPT, F. (1966) The arthropod parasites of vertebrates in Africa south of the Sahara. 3 Insecta excl. Phthiraptera. *Publications of the South African Institute for Medical Research*, **13**, 1-283.

**CHAPTER FIVE:
HOST SELECTION BY THE LOUSE FLY**

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HOST SELECTION BY THE LOUSE FLY

The contents of this chapter were accepted for publication by the *Cambridge Journal of Parasitism* and *Journal of Wildlife Disease* following peer review, but were not published due to administrative problems. The article in this form has been submitted to *Experimental Parasitology*.

5.1: CHAPTER AIMS

This chapter aims to determine whether there are intra-brood differences in the pressure of parasitism faced by nestling *A. apus* from *C. pallida*. The specific objectives are to:

- Discover whether there are differences in the numbers of *C. pallida* adults feeding from different nestlings within broods.
- Assess whether there are differences in the abundance of male and female *C. pallida* adults on different nestlings within broods. Formulate possible explanations for accounting for such differences.

These objectives are pertinent as differences in the numbers and sex of *C. pallida* adults on different nestlings might be affecting and accounting for the lack of parasitic effects seen. Differences in the numbers of *C. pallida* on different nestlings would be indicative that this insect preferentially selects particularly nestlings within each brood over others. Parasites might be preferentially choosing those nestlings either able to offer them the most resources or with the lowest level of resistance to their parasitism. Should nestlings best able to overcome the negative effects of parasitism be chosen as hosts over others, this might be masking the detrimental effects of parasitism.

Studying differences in the number of different sexes of *C. pallida* on offspring is of interest, as the costs of parasitism from male and female adult *C. pallida* may vary. Thus, although different nestlings might suffer infestation from similar numbers of *C. pallida*, differences in the sexual composition of these parasites may mean the costs faced are different. This may be obscuring the expected detrimental effects of parasitism.

This topic is worthy of study as preferential host selection by parasite has rarely been

considered as a factor influencing parasitic effect. This has been seldom studied in any host-parasite system. This is the first such study examining intra-brood differences in parasitism by *C. pallida* and examining the possibility of host selection by this species.

5.2: CHAPTER ABSTRACT

Preferences by parasites for particular hosts may influence the parasitic costs evident in host-parasite systems. No detrimental effect of Louse Fly *Crataerina pallida* parasitism has been found on Common Swift *Apus apus* nestling hosts. Host selection choices may be mediating the effect this parasite has and account for this apparent avirulence. Two aspects of parasite host selection were studied at a breeding colony of Common Swifts during 2008;

- Intra-brood differences in *C. pallida* parasitism.
- Sexual differences in *C. pallida* parasitism between nestlings.

Greater mean abundances of parasites were seen on higher than lower ranking nestlings within broods of both two and three chicks. Greater proportions of females were present upon higher ranking than lower ranking nestlings. Proportions of females were greater on nestlings than at nests. These results indicate that host selection may be occurring and this may account for the previous lack of parasitic virulence reported.

5.3: INTRODUCTION

Studies of host-parasite systems have often centred on host biology, while the life-history traits of parasites engaged in such inter-specific relationships have often been neglected (Combes 2001). Parasite, as well as host, life-history traits should occur at some optimum that maximises biological fitness (e.g. Poulin and Combes 1999, Combes 2001). Such traits may be important in determining parasitic virulence. Host selection is one such parasitic life-history trait. Parasites are expected to choose those hosts which provide the greatest returns at least cost. Trade-offs between host condition, resource availability and host immunity may mediate the host selection decisions parasites make (reviewed by: Sheldon and Verhulst 1996, Norris and Evans 2000). However, knowledge about parasitic host selection choices remains poor.

One example where parasite host selection choices may be affecting a host-parasite relationship occurs between the haematophagous ectoparasitic Louse Fly, *Crataerina pallida* Latreille (Insecta: Hippoboscidae), and its host the Common Swift, *Apus apus* Linnaeus (Aves: Apodidae). No detrimental effect of *C. pallida* parasitism on nestling hosts has been identified (Lee and Clayton 1995, Tompkins *et al.* 1996). Host selection choices by *C. pallida* may be mediating or obscuring the expected heavy costs such parasitism is expected to incur.

Two aspects of parasite host selection choice were studied. Firstly, intra-brood differences in the abundance of *C. pallida* on particular nestling hosts were investigated. *C. pallida* may be selecting nestlings of a particular rank preferentially. Sibling nestlings can vary considerably in size and resource availability as can be seen in photograph 1 which shows two nestling siblings from a single nest. Despite being only a day older than its younger sibling was considerably larger. Studies have shown that nestling resistance to parasitism varies according to nestling rank and immunology (Christe *et al.* 1998, Roulin *et al.* 2003). If preferential selection for nestlings best able to resist parasitism occurs no costs of parasitism may be apparent if all nestlings within a brood are considered together in investigations examining parasitic costs.

Secondly, sexual differences in *C. pallida* parasitism were studied. Females remove more resources from hosts than males, thus differences in parasitism between the sexes could strongly influence the expression of parasitic costs. *C. pallida* is pupiparous, with

larvae developing internally and the physiological demands such parental care entails probably accounts for the increased nutritional requirements that females have. The higher feeding demands of female *C. pallida* may result in a greater impact of female parasitism than that of an equivalent number of males (Lehane 2005). However, previous studies examining the effect *C. pallida* has on hosts have not considered what effect differences in sex ratios might be having on the parasitic costs observed. *C. pallida* populations are known to be heavily female biased (Walker and Rotherham 2010a). As female parasitism has a potentially greater impact, females would be expected to exhibit stronger host selection choices.

Whether parasites adaptively select certain hosts over others remains contentious. The possible factors influencing and mediating such choices are complex and often contradictory. Trade-offs between host condition and host immunity may be occurring (Sheldon and Verhulst 1996, Norris and Evans 2000). However other factors such as host availability, and the specific life-history features of the host species involved in each host-parasite relationship are complicating factors meaning much further study is required. Species specific traits may mean an examination of individual host-parasitic systems is necessary to fully understand the functioning of each system.

Photograph 1: Siblings from a nest in OL-K6. Despite there only being a days difference in age, there is considerable difference in nestling size and development. Such differences may be facilitated through parasite host selection choices.



5.4: METHODS

Study Species: *C. pallida* is an obligate nest ectoparasite of the swift. Adult Louse Flies feed from hosts approximately once every five days removing a mean of 60 mg of blood on each occasion (Kemper 1951). This is expected to result in significant detrimental costs to the hosts (Lee and Clayton 1995). *C. pallida* life-history has been reviewed by Walker and Rotherham (2010b).

The Common Swift hosts are specialist avian aerial insectivores. Breeding commences each spring at colonial nesting sites following the return of adults from the overwintering grounds in southern Africa (Lack 1956). Common Swifts exhibit high mate and nest site fidelity (Weitnauer 1947, Lack and Lack 1951). Nestling development is highly time constrained and strongly weather dependant, with nestlings having to be fully capable of flight upon fledging at approximately only 35 days of age. Thus the additional costs that parasitism may incur and its consequences are expected to be particularly great in this species.

Study Site: The study was conducted during the swift breeding season of 2008 at a nesting colony situated within a road bridge close to the German town of Olpe (51° 04' 00" N, 07° 81' 00" E). Thirty-eight pairs of swifts bred at this site in 2008 with a total of 89 nestlings hatching of which 38 fledged successfully. High rates of nestling mortality are usual in this species (Lack and Lack 1951). Nestlings were weighed daily using electronic scales accurate to 0.01 grams (Ohaus, Scout Pro). Hatching asymmetry occurs in swifts, with the earlier hatching nestlings being of greater weight than later hatching siblings. Nestling weight is known to be a reliable and consistent indicator of nestling rank, with intra-brood weight hierarchies remaining constant once established (Weitnauer 1947, Lack 1956). Marking of nestlings using tippex (Trade-mark) and different colours of nail vanish confirmed that nestling weight differences between nestlings remained constant and could be used to accurately determine nestling rank throughout the nestling period.

Louse Fly abundance on hosts: *C. pallida* populations were quantified on a daily basis and the number and sex of adult parasites on each nestling and within each nest was determined. This followed the methods outlined by Kemper (1951) and Walker and Rotherham (2010b). Broods with a single nestling were excluded from subsequent

analyses. Bize *et al.* (2008), studying a related host-parasite system, that between the Alpine Swift *Apus melba* (Aves: Apodidae) and its Louse Fly *C. melbae* (Insecta: Hippoboscidae), classified nestlings as ‘senior’ or ‘junior’ and calculated the mean number of *C. pallida* parasitizing on each. This method was refined and extended by considering broods of two and three nestlings separately and each nestling individually.

Data was analysed from approximately weekly intervals throughout the swift breeding season, on the 21st and 28th of June, and the 5th and 10th of July. These dates also, rather practically, closely corresponded to average nestling ages of approximately 15, 20, 25 and 30 days of age (21st of June, mean = 16.12 ± 1.92 ; 28th of June, mean = 21.94 ± 3.30 ; 5th of July, mean = 23 ± 6.78 , 10th of July, mean = 26.70 ± 6.87). Studying *C. pallida* populations at such discrete periods of the nestling period allows an examination of general trends throughout the swift breeding season within the parasite population to be established. *C. pallida* feed once every five days (Kemper 1951) so examining *C. pallida* host selection at such intervals corresponds to the feeding cycle of individual parasites. The number of fledglings and available nests dropped rapidly from the 5th of July onwards due to nestling fledging. Fledging of nestlings occurs once they reach 35 days of age.

The aggregated nature of *C. pallida* populations meant that statistical analyses were conducted using non parametric Mann-Whitney and Friedman testing. Two way repeated measures ANOVA testing was also conducted despite the aggregated nature of populations to allow comparison with a similar study by Bize *et al.* (2008). In addition such testing allows examination of the interaction of parasite abundance on separate dates and between individual nestlings.

Louse Fly sex determination: The sex of *C. pallida* adults parasitizing nestlings was recorded at regular intervals from the 28th of June onwards. Whether the sex ratio of *C. pallida* populations seen on individual nestlings and at individual nests was as expected compared to the sex ratio seen overall at all nests at the colony was examined with Fischer exact test analyses for the dates; the 28th of June, and the 5th, and 10th of July.

5.5: RESULTS

***C. pallida* parasite abundance upon nestlings of different rank:**

Table 1 summarizes parasitic abundance and number of broods of each size on each date examined. Tables 2 and 3 provide the *C. pallida* abundances at broods with two and three nestlings, and show the total and mean number of parasites found on each nestling, in the nest, and in total. Figures 1 and 2 illustrate mean abundance of *C. pallida* parasites found on each rank of nestling in broods containing two and three nestlings. Nestlings were 16 ± 3.31 days old when first parasitized (range 10 to 30 days of age). There was no significant difference in the age at which nestlings of different rank were first parasitized (Kruskal-Wallis test, $\chi^2 = 0.905$, d.f. = 2, $P = 0.90$). Abundances fell over time fitting what is known of *C. pallida* biology (Walker and Rotherham 2010a, Walker and Rotherham 2010 b).

There were higher mean parasite abundances on first than second ranking nestlings in broods with two nestlings (Table 2), however this difference was not significant on the dates examined (28th June: $U = 16.3$, $z = 0.08$, $P = 0.47$; 5th July; $U = 165$, $z = 0.44$, $P = 0.33$; 10th of July, $U = 171$, $z = -0.61$, $P = 0.27$). There were significantly greater numbers of parasites at nests than on nestlings (Friedmans Test, $\chi^2 = 6.00$, d.f. = 2, $P = 0.04$). For broods of three nestlings there were greater mean abundances of parasites on first than second ranking nestlings on two dates examined, and upon second than third ranking nestlings on all dates. However no significant difference in the total number of parasites observed on the four occasions on each nestling (Table 3) (Friedmans Test, $\chi^2 = 2.38$, d.f. = 2, $P = 0.30$). As for broods of two nestlings there were significantly more *C. pallida* in the nest than on nestlings (Friedmans Test, $\chi^2 = 8.63$, d.f. = 3, $P = 0.03$).

Two-way factor ANOVA analyses showed that there were significantly more *C. pallida* parasites on first ranking nestlings within broods containing two nestlings ($F = 4.93$, $P \leq 0.01$). There was a significant difference between the mean number of *C. pallida* parasites seen on nestlings in broods with three nestlings, with first ranking nestlings having most parasites ($F = 14.63$, $P \leq 0.01$). However, there were no differences between different nestling ages ($F = 0.63$, $P = 0.54$) and no interaction between age and date ($F = 0.75$, $P = 0.62$).

Sex ratio differences in Louse Flies parasitism: Tables 4 and 5 provide data on the sex ratio of *C. pallida* on nestlings within broods of two and three nestlings respectively. On the 28th of June there were 61 male (mean per nest = 1.74 ± 1.38) and 103 female parasites (mean = 2.94 ± 3.00) (overall sex ratio = 0.41 males: 0.59 females). On the 5th of July there were 29 males (mean = 0.97 ± 0.96), and 94 females (mean = 3.14 ± 3.25) (sex ratio = 0.30: 0.70). On the 10th of July there were 29 males (mean = 1.12 ± 0.86) and 49 females (mean = 1.88 ± 1.84) (Sex ratio = 0.43: 0.57).

There were greater numbers of females on first than second ranking nestlings for broods with two nestlings, but this difference was significant on only the 10th of July ($U = 270.5$, $z = -1.47$, $P = 0.07$). There were significantly more females on nestlings than within the nest over the three dates (Friedmans Test, $\chi^2 = 4.67$, d.f. = 2, $P = 0.09$). Similarly there were more females than males on nestlings than at the nest in broods with three nestlings but this was not significant (Friedmans Test, $\chi^2 = 7.3$, d.f. = 3, $P = 0.63$). There was no significant difference in the number of females between individual nestlings in broods with three nestlings.

Two factor repeated measures ANOVA for broods of two nestlings, with date as the repeated measure and nestling as factor showed that there were significantly more females on first ranking nestlings than their smaller siblings ($F = 3.38$, $P \leq 0.05$). There was however no significant difference in the number of males between nestlings ($F = 1.21$, $P = 0.30$) There was no difference between dates ($F = 0.18$, $P = 0.67$) and no significant interaction between the number of males and date ($F = 5.25$, $P = 0.90$) or of females and date ($F = 0.22$, $P = 0.80$). A similar pattern was seen in broods with three nestlings. First ranking nestlings had significantly more females than second and third ranking nestlings ($F = 3.38$, $P \leq 0.05$), but not males ($F = 0.42$, $P = 0.67$). There was an effect of date upon male *C. pallida* ($F = 4.23$, $P \leq 0.02$) but not on female population size between nestlings ($F = 0.18$, $P = 0.67$). There was no significant interaction between factors and repeated measures ($F = 0.22$, $P = 0.80$).

Table 1: Summary of number of broods, number of broods of each size, total parasite abundance and mean parasite abundance on the four dates considered.

Date	Total number of broods	Number of nestlings of each rank			Total parasite abundance	Mean parasite abundance per brood (SD)
		1	2	3		
21 st June	24	2	10	12	208	08.67 ± 3.62
28 th June	35	2	14	19	171	4.89 ± 3.74
5 th July	30	5	21	4	130	4.34 ± 3.62
10 th July	26	8	15	3	78	3.00 ± 1.97

Table 2: The numbers of *C. pallida* parasites found on each nestling and at the nest, plus the total population including those in the nest and on nestlings, for broods containing two nestlings, on four dates at approximately weekly intervals throughout the swift breeding season. The mean number parasitizing each per nestling or nest is provided with the standard deviation in brackets.

Date	Total nest population			Nestling 1			Nestling 2			Nest only		
	Total	Male	Female	Total	Male	Female	Total	Male	Female	Total	Male	Female
21st of June (<i>n</i> = 10)	57			12			3			42		-
	(3.80 ±	-	-	(1.2 ±	-	-	(0.3 ±	-	-	(4.2 ±	-	
	3.09)			1.40)			0.48)			3.55)		
28th of June (<i>n</i> = 14)	79	24	55	7	3	4	5	1	4	67	20	47
	(5.64 ±	(1.71 ±	(3.95 ±	(0.50 ±	(0.21 ±	(0.29 ±	(0.36 ±	(0.07 ±	(0.29 ±	(4.79 ±	(1.43 ±	(3.36 ±
	4.45)	4.44)	1.14)	0.47)	0.00)	0.43)	0.47)	0.76)	0.27)	3.79)	0.00)	1.16)
5th of July (<i>n</i> = 21)	90	21	69	24	1	23	25	2	23	41	16	25
	(4.23 ±	(1.04 ±	(3.34 ±	(1.19 ±	(0.15 ±	(1.04 ±	(0.96 ±	(0.09 ±	(1.09 ±	(2.19 ±	(0.73 ±	(1.46 ±
	3.78)	0.99)	3.43)	1.43)	0.46)	1.43)	1.58)	0.30)	1.67)	2.43)	0.87)	2.04)
10th of July (<i>n</i> = 15)	44	18	26	8	0	8	10	5	5	26	13	13
	(2.94 ±	(1.2 ±	(1.74 ±	(0.54 ±	(0.00)	(0.54 ±	(0.67 ±	(0.34 ±	(0.34 ±	(1.74 ±	(0.87 ±	(0.87 ±
	1.84)	1.04)	1.71)	0.74)		0.74)	0.72)	0.49)	0.49)	1.03)	0.99)	0.99)

Table 3: The numbers of *C. pallida* parasites found on each nestling and at the nest, plus the total population including those in the nest and on nestlings, for broods containing three nestlings, on the 28th of June, 5th of July and the 10th of July. The mean number parasitizing each per nestling or nest is provided with the standard deviation in brackets.

Date	Total nest population			Nestling 1			Nestling 2			Nestling 3			Nest only		
	Total	Male	Female	Total	Male	Female	Total	Male	Female	Total	Male	Female	Total	Male	Female
21st of June (n = 12)	62 (5.17 ± 3.01)	-	-	17 (1.42 ± 1.44)	-	-	13 (1.08 ± 1.31)	-	-	8 (0.67 ± 0.98)	-	-	24 (2.18 ± 1.54)	-	-
28th of June (n = 18)	61 (3.68 ± 2.34)	31 (1.74 ± 1.52)	30 (1.74 ± 1.52)	10 (0.55 ± 0.77)	4 (0.22 ± 0.43)	6 (0.33 ± 0.56)	16 (0.88 ± 1.18)	9 (0.5 ± 0.86)	7 (0.39 ± 0.69)	4 (0.22 ± 0.54)	1 (0.05 ± 0.24)	3 (0.17 ± 0.39)	31 (2.61 ± 0.67)	17 (0.93 ± 1.30)	14 (0.79 ± 1.22)

Date	Total nest population			Nestling 1			Nestling 2			Nestling 3			Nest only		
	Total	Male	Female	Total	Male	Female	Total	Male	Female	Total	Male	Female	Total	Male	Female
5th of July (n = 4)	11 (2.25 ± 0.96)	3 (0.75 ± 0.57)	8 (2.00 ± 0.96)	0 (0.00)	0 (0.00)	0 (0.00)	3 (0.75 ± 0.15)	1 (0.25 ± 0.5)	2 (0.5 ± 1.00)	3 (0.75 ± 0.5)	1 (0.25 ± 0.5)	2 (0.5 ± 0.58)	5 (1.25 ± 0.96)	2 (0.5 ± 0.56)	3 (0.75 ± 0.5)
10th of July (n = 3)	10 (3.34 ± 3.21)	4 (1.34 ± 0.58)	6 (2.00 ± 2.65)	2 (0.67 ± 1.15)	0 (0.00)	2 (0.67 ± 1.15)	1 (0.34 ± 0.58)	1 (0.34 ± 0.58)	0 (0.00)	0 (0.00)	0 (0.00)	0 (0.00)	7 (2.34 ± 2.52)	3 (1.00 ± 1.00)	4 (1.34 ± 1.54)

Table 4: The sex ratio of *C. pallida* adults parasitizing nestlings of different rank and within the nest, for broods containing two nestlings.. The observed sex ratio is tested against that expected given that observed at the entire colony upon each date using the Fischer Exact Test. *P*, are provided in brackets. * equals significant level of probability.

DATE	TOTAL	NESTLING			NEST ONLY
		1	2	3	
28 th June/ 20 days of age (<i>n</i> = 14). Colony sex ratio: 37:63	30: 69 (0.50)	43:57 (1.00)	20:80 (1.00)	-	30: 70 (0.46)
5 th of July/ 25 days of age (<i>n</i> = 21). Colony sex ratio: 24:76	23:77 (1.00)	4:96 (0.09)*	8:92 (0.25)	-	39:61 (0.23)
10 th of July/ 30 days of age (<i>n</i> = 15). Colony sex ratio: 37:63	40:60 (0.83)	0:100 (0.20)	50:50 (1.00)	-	50:50 (0.58)

Table 5: The sex ratio of *C. pallida* adults parasitizing nestlings of different rank and within the nest, for broods containing three nestlings.. The observed sex ratio is tested against that expected given that observed at the entire colony upon each date using the Fischer Exact Test. *P*, are provided in brackets. * equals significant level of probability.

DATE	TOTAL	NESTLING			NEST ONLY
		1	2	3	
28 th June/ 20 days of age (<i>n</i> = 18). Colony sex ratio: 37:63	50:50 (0.16)	40:60 (1.00)	56: 44 (0.47)	25:75 (1.00)	55:45 (0.20)
5 th of July/ 25 days of age (<i>n</i> = 4). Colony sex ratio: 24:76	27: 73 (1.00)	-	33:67 (1.00)	33:66 (1.00)	40:60 (0.58)
10 th of July/ 30 days of age (<i>n</i> = 3).Colony sex ratio: 37:63	40:60 (1.00)	0:100 (1.00)	100:0 (1.00)	-	43: 57 (1.00)

Figure 1: Do *C. pallida* adults preferentially parasitize first ranking nestlings in broods with two chicks? Mean *C. pallida* adult abundance on nestlings of different rank within broods of two nestlings. First ranking nestlings as black bars, second ranking nestlings as white bars. Standard deviation shown as error bars.

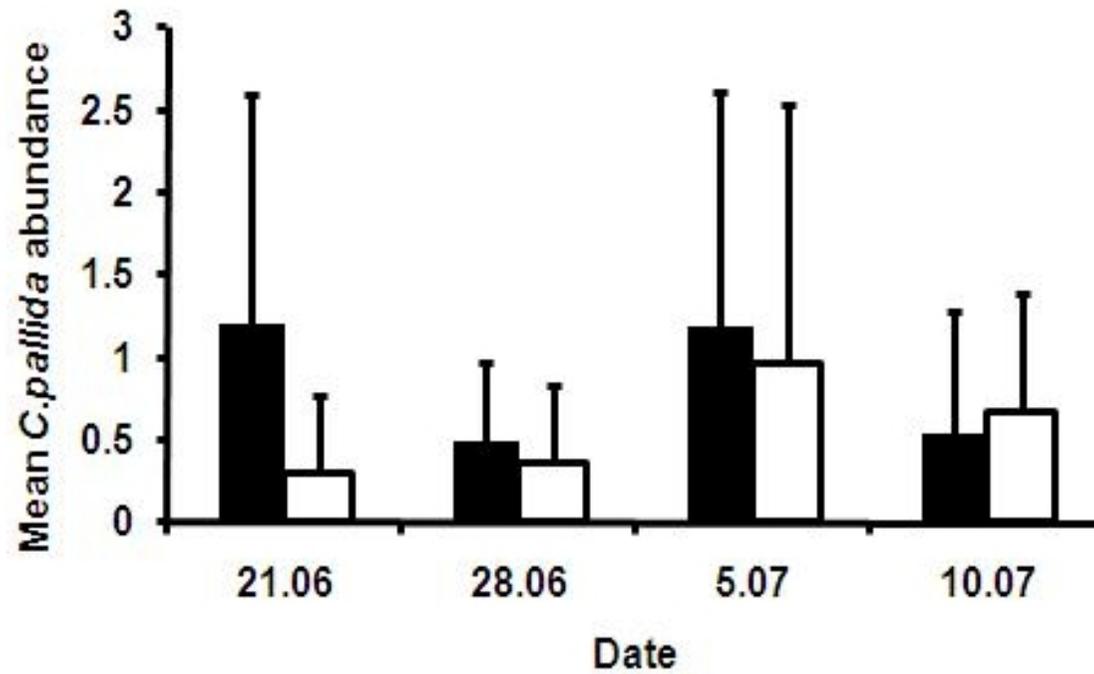
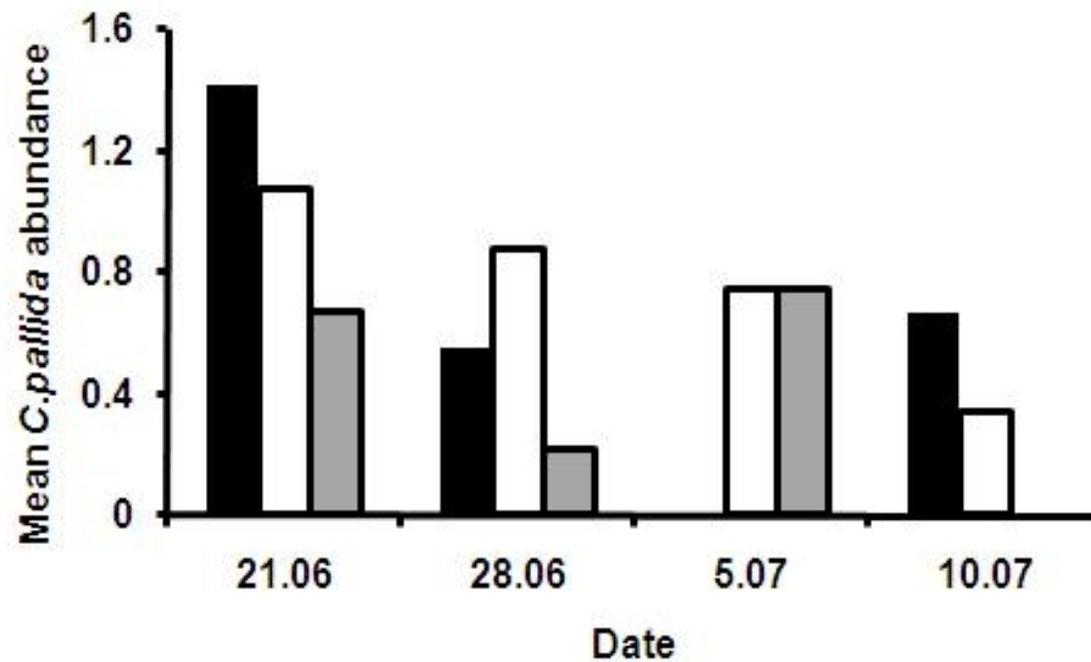


Figure 2: Do *C. pallida* adults preferentially parasitize nestlings of a higher rank in broods with three chicks? Mean *C. pallida* adult abundance on nestlings of different rank within broods containing three nestlings at different ages. First ranking nestlings in black bars, second ranking nestlings as white bars and third ranking nestlings in grey.



5.6: DISCUSSION

Differences in *C. pallida* abundances on nestlings of different rank:

Generally, there were greater mean abundances of parasites upon higher ranking nestlings than their lower ranking siblings within broods of both two and three nestlings. This is the first time that such preferences have been shown within this host-parasitic system. Preferences for larger nestlings has been previously demonstrated (Valera *et al.* 2004). Conversely, other studies show parasite preferences for weaker hosts with decreased immune responses (Wakelin 1996, Roberts *et al.* 2004). Studies on a related system to this, that between *A. melba* and *C. melbae*, found senior siblings were favoured (Roulin *et al.* 2003), or that parasites distributed themselves equally between hosts (Bize *et al.* 2008).

Factors mediating parasite host selection are complicated with trade-offs between the nutritional resources available to parasites and nestling immunocompetence occurring (Lochmiller and Deerenberg 2000). Nestling rank has been found to be a good surrogate for nestling condition, availability of resources for parasites and nestling immunity (Råberg *et al.* 2003, Roulin *et al.* 2003). First ranking nestlings offer more resources for potential parasites, but conversely are better able to fight off parasite challenges (Christe *et al.* 1998).

The preference for higher ranking nestlings discovered in this study may account for the apparent avirulence of *C. pallida*. Negative effects may be being obscured if the burden of parasitism is being carried predominately by higher ranking nestlings as these are best able to overcome costs, which are thus not apparent. These selection tendencies may lessen pressure on lower ranked nestlings. Parasites may be causing costs, but these may simply be being obscured due to them occurring only upon those hosts best able to surmount them.

Selecting the host most able to tolerate the effects of its parasitism may be an active strategy by *C. pallida* to increase its fitness. *C. pallida* reproductive success is dependent upon the reproductive success of its host. Further research should consider the possibility of intra-brood differences in parasitism as opposed to considering all nestlings within a nest together. Factors affecting parasite choices should also be studied, for example although differences in feather development between siblings are

small, differences being most apparent in nestling mass, it may be that parasites prefer the slightly more feathered older siblings as hosts than the siblings and be using this as a cue influencing their choices. Examination of the correlation between parasite abundance and nestling rank may lead to the discovery of distinct differences in the expression of parasitic costs.

Sexual differences in host selection: Greater proportions of females than males were seen on higher ranking than lower ranking chicks and also upon chicks than at the nests. The proportion of males was greatest within the nests. This is the first time that such sexual differences in host selection by parasites have been demonstrated within this or similar systems.

This may result from females feeding more frequently than males due to the increased food demands that they have. Females take larger blood meals than males as the physiological demands of larval production mean females require more resources (Kemper 1951). The higher proportions of female *C. pallida* seen on higher ranking nestlings may be a reflection that these nestlings are able to offer the greatest nutritional resources. Remaining in the nest may be the best strategy for males as the risk of removal from the nest or of injury by the host is lower. Increased opportunity to mate may occur in the nest. Gravid females may remain on nestlings as they offer a method of dispersing between nests and colonising new nest sites.

The results of this investigation into host selection may tie in with the presence of mating clusters observed in chapter 6. The differences in host selection observed may explain the presence of mating clusters at the nest documented in chapter 6, as males may remain at the nest in order to participate in mating competition. Females carried on nestlings which move between nests or fledge may be carried phoretically to new nest sites, and thus their offspring may experience sites with less intra-specific competition.

Previous studies have not considered sex related differences in costs of parasitism, instead considering the costs of male and female parasitism as being equal. This may have caused the burden of parasitism to be falsely estimated or quantified and thus lead to the making of false assumptions about parasite virulence. Further investigation looking for virulent effects of this parasite should consider these aspects.

General discussion: Host selection choices by parasites may be mediating the costs of parasitism and account for avirulence observed in other studies. Investigating the interactions between host immunity and host resource availability in influencing such choices are logical next steps of study. A previous study which found a lack of virulence by this parasite concluded that it was due to the vertical nature of parasitic dispersion, with parasites assumed to be mostly transferred from parent to offspring. However, host selection may also be a mechanism by which parasitic effect could be reduced. The results of this study therefore offer another possible explanation for the results seen by Lee and Clayton (1995).

This investigation shows that the species specific life-history traits of the partners engaged within a host-parasitic interaction must be considered when examining parasite host selection choices. Further research is needed to determine why preferential host selection is occurring, the factors mediating it and its influence on parasitic pathogenicity.

5.7: CHAPTER SUMMARY

Intra-brood differences in *C. pallida* parasitism were observed. It was found that greater abundances of *C. pallida* were present upon the largest and highest ranking nestlings within broods. The proportion of females upon nestlings was discovered to be greater than that seen in nests.

These results indicate that parasites might preferentially be selecting those hosts most able to fulfil their needs and therefore offering them the best levels of fitness. This conclusion may account for the lack of perceived costs nestlings face as a result of parasitism. Higher ranking nestlings are those of the largest size, with most resources to offer and the greatest levels of immunity. They may thus be better able to resist and counter the expected costs experienced through parasitism than their weaker siblings. This may be obscuring the costs of parasitism.

Parasitism by female *C. pallida* parasites is expected to be more costly than that by males. That greater abundances of females are seen on nestlings than at nests, indicates that females feed more than males to fulfil these needs and may express stronger host selection preferences. Further studies examining parasitic virulence should quantify the

numbers of each sex of *C. pallida* adults at nests to correctly assess the parasitic pressures experienced by each brood. This may result in costs due to *C. pallida* parasitism becoming apparent.

This is the first time evidence of intra-brood differences in parasite abundance and sex have been examined. It is the first evidence indicating that parasite preferences for certain hosts may be occurring. This investigation again shows the need for more parasite centred research as opposed to simply concentrating on host biology. A closer examination of parasite traits is needed before host-parasitic systems can be understood. The study demonstrates that parasites will exhibit features, such as host selection, which provide them with the maximum levels of fitness.

5.8: CHAPTER REFERENCES

BIZE, P., JEANNERET, C., KLOPFENSTEIN, A. and ROULIN, A. (2008). What makes a host profitable? Parasites balance host nutritive resources against immunity. *American Naturalist*, **171**, 107-118.

CHRISTE, P., MØLLER, A.P. and DE LOPE, F. (1998). Immunocompetence and nestling survival in the house martin: the tasty chick hypothesis. *Oikos*, **83**, 175-179.

COMBES, C. (2001). *Parasitism: the ecology and evolution of intimate interactions*. University of Chicago Press, Chicago.

LACK, D. and LACK, E. (1951). The breeding biology of the swift, *Apus apus*. *Ibis*, **93**, 501-546.

LACK, D. (1956). *Swifts in a tower*. Methuen publishing, London.

LEE, P.L.M. and CLAYTON, D.H. (1995). Population biology of swift (*Apus apus*) ectoparasites in relation to host reproductive success. *Ecological Entomology*, **20**, 43-50.

LEHANE, M. J. (2005). *The biology of blood-sucking in insects*. Cambridge University Press, Cambridge.

LOCHMILLER, R.L and DEERENBERG, C. (2000). Trade-offs in evolutionary immunology: just what is the cost of immunity? *Oikos*, **88**, 87-98.

KEMPER, H. (1951). Beobachtungen an *Crataerina pallida* Latr. und *Melophagus ovinus* L. (Diptera, Pupipara). *Zeitschrift für Hygiene (Zoologie)*, **39**, 225-259.

NORRIS, K. and EVANS, M.R. (2000). Ecological immunology: life-history trade-offs and immune defence in birds. *Behavioural Ecology*, **11**, 19-26.

POULIN, R. and COMBES, C. (1999). The concept of virulence: interpretations and

- implications. *Parasitology Today*, **15**, 474-475.
- RÁBERG, L., STJERNMAN, M. and HASSELQUIST, D. (2003). Immune responsiveness in adult blue tits: heritability and effects of nutritional status during ontogeny. *Oecologia*, **136**, 360-364.
- ROBERTS, M.L., BUCHANAN, K.L. and EVANS, M.R. (2004). Testing the immunocompetence handicap hypothesis: a review of the evidence. *Animal Behaviour*, **68**, 227-239.
- ROULIN, A., BRINKHOF, M.W.G., BIZE, P., RICHNER, H., JUNGI, T.W., BAYOUX, C., BOILEAU, N. and BURNLEAU, G. (2003). Which chick is tasty to parasites? The importance of host immunology vs. parasite life history. *Journal of Animal Ecology*, **72**, 75-81.
- SHELDON, B.C. and VERHULST, S.(1996). Ecological immunity: costly parasite defences and trade-offs in evolutionary ecology. *Trends in Ecology and Evolution*, **11**, 317-321.
- TOMPKINS, D.M., JONES, T. and CLAYTON, D.H. (1996). Effect of vertically transmitted ectoparasites on the reproductive success of Swifts (*Apus apus*). *Functional Ecology*, **10**, 733-740.
- VALERA, F., HOI, H., DAROLOVA, A. and KRISTOFIK, J. (2004). Size versus health as a cue for host choice: a test of the tasty chick hypothesis. *Parasitology*, **129**, 59-68.
- WALKER, M.D. and ROTHERHAM, I.D. (2010 a). Population structure of *Crataerina pallida* (Diptera: Hippoboscidae), an obligate parasite of the Common Swift, *Apus apus* (Aves: Apodidae). *Experimental Parasitology*, **126**, 451-455.
- WALKER, M.D. and ROTHERHAM, I.D. (2010 b). The common swift Louse Fly, *Crataerina pallida*: An ideal species for studying host parasite interactions. *Journal of Insect Science*, **10**, 193.
- WAKELIN, D. (1996). *Immunity to parasites: How parasitic infections are controlled*. Cambridge University, Press, Cambridge.
- WEITNAUER, E. (1947). Am Neste des Mauerseglers, *Apus apus apus* (L.). *Der Ornithologische Beobachter*, **44**, 133-182.

**CHAPTER SIX:
OTHER ASPECTS OF *C. PALLIDA*
AND *A. APUS* BIOLOGY**

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DAILY FLUCTUATIONS	6.2
MATE GUARDING AND CLUSTERING	6.3
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OTHER ASPECTS OF *C. PALLIDA* AND *A. APUS* BIOLOGY

The contents of this chapter have been published or have been accepted for publication by the following journals:

- WALKER, M.D. (2009). Daily fluctuations in the numbers of the Louse Fly *C. pallida* (Latreille 1812) (Dip.: Hippoboscidae) seen at Common Swift *A. apus* nests. *Entomologist's Record*, **121** (4), 157-158.)
- WALKER, M.D. and ROTHERHAM, I.D. Previously unreported mate guarding and 'clustering' by a nest ectoparasite. Accepted for publication by *Dipterist's Digest*.
- WALKER, M.D. and ROTHERHAM, I.D. (2010). Temperature Affects Emergence of *Crataerina pallida* (Diptera: Hippoboscidae). *Journal of Medical Entomology*, **47**, 1235-1237.
- WALKER, M.D. and ROTHERHAM, I.D. 'Cool dudes': torpor in Common Swifts? *British Birds*.

6.1: CHAPTER AIMS

This chapter aims to consider other aspects of *C. pallida* and *A. apus* life-history which could possibly influence the effect that this insect has on its hosts. A number of different biological features will be investigated including; short term *C. pallida* population stability, male *C. pallida* mating competition, factors influencing parasite emergence, and temperature regulation in nestling swifts.

The precise objectives of this chapter are to:

- Assess the short term stability of nest-based parasite population sizes and thus make an assessment as to the accuracy of estimates of parasite load used in previous studies looking for effects of parasitism.
- Examine whether competition is likely to occur between male *C. pallida* for mating opportunities and to ascertain what effect this might be having on its distribution and thus parasitism.
- Investigate how temperature affects the rate of emergence of adult *C. pallida* from pupae.
- Study whether there is a decrease in *A. apus* body temperatures during periods of

poor weather conditions.

The stability of populations were examined by counting the abundances of *C. pallida* adults on a daily basis. Evidence for mating competition was sought through nest observation of *C. pallida* behaviour. *C. pallida* emergence will be studied experimentally by placing pupae under different temperature regimes and observing rates of hatching. Host temperatures was measured during periods of poor weather to establish whether they were lower than normal.

These are valid aims as each of these aspects could have a direct influence on the pressure *A. apus* faces from parasitism. The parasitic load; the number of parasites which each host harbours; is of importance in determining the existence of parasitic costs. Previous investigations have assessed parasitic load from only a limited number of population counts. However, should short term fluctuations in *C. pallida* abundance occur this may affect the parasite load observed. Strong mating competition pressures may influence nest based sex ratios and population sizes, likewise affecting parasite load, especially if the extent of male and female resource removal differs. The factors affecting parasite emergence influence *C. pallida* abundance; and are thus of interest. Differences in parasite load may occur if rates of male and female insects emergence vary under different conditions. Also an examination of emergence provides an indication of the level of synchrony in the relationship between *C. pallida* and *A. apus*. Investigating whether hosts exhibit lower temperatures during poor weather could indicate that hosts actively lower metabolic rate to save energy in response to environmental stresses such as parasitism thus mediating these costs.

6.2: DAILY FLUCTUATIONS IN THE NUMBERS OF LOUSE FLIES

The Louse Fly *C. pallida* (Latreille 1812) (Diptera: Hippoboscidae) is a blood sucking nest parasite of the Common Swift *A. apus* (Linnaeus 1758) (Aves: Apodidae). Louse Flies are closely associated with their hosts nests, moving onto the adult and nestling swifts approximately once every five days in order to feed (Kemper 1951).

No effect of Louse Fly parasitism upon the host has been found (Lee and Clayton 1995, Tompkins *et al.* 1996). This could be because the levels of parasite abundance seen did not truly reflect this parasites true population size. Parasite counts were made on only a

few occasions. The stability of Louse Fly numbers at nests over time is unknown.

Common Swifts have established a nesting colony within a road bridge which spans the Bigge Reservoir close to the German town of Olpe (51° 04' 00" N, 07° 81' 00" E). The number of Louse Flies in each swift nest was counted on a regular basis. A summary of the Louse Fly population observed at this site and the quantification of basic population parameters was made in chapter 3.

Surprisingly the number of Louse Flies seen at individual nests rarely remained constant between days. Sometimes even great fluctuations in Louse Fly number occurred per nest from one day to the next. This is best shown by considering individual nests. For example at nest OL-K5-72 the number of Louse Flies seen on the 12th of June was 27. The day after it had dropped to 12. It dropped to 6 on the 14th of June, only to increase to 23 on the 15th of June. It fell again to 12 on the 16th. Another example was DR-K6-228 where great fluctuations occurred. At this nest on the 25th of June the number of Louse Flies seen was 20. On the day after, the 26th of June, it had dropped to 15. While on the 27th it had again increased to 20. Thereafter the number seen began to fall, being 18 on the 28th, 15 on the 29th and 5 on the 30th.

Considering all 47 swift nests there were 26 separate occasions where the population of Louse Flies changed by 5 or more over a single 24 hour period at single nests. On 6 of these occasions Louse Fly numbers increased, but decreases in Louse Fly numbers were more common occurring 20 times. There were 5 instances where Louse Fly populations changed by more than 10 from one day to the next. Such fluctuations were most prominent at nests with the highest numbers of parasites, but even at nests with fewer Louse Flies the number seen from day to day rarely remained constant but simply did not fluctuate by as large a range.

I believe that the reason for these fluctuations is that Louse Flies move alternately between the nests and the adult swifts as and when they feed. A decrease in adult Louse Fly populations in the nest may mean that more are to be found on the adult swifts. The changes in the nest population size are unlikely to be caused by death of adult Louse Flies or by hatching of new adults. Although the life-cycle of this parasite is not well known it is unlikely that large numbers of Louse Flies would die or hatch out over such short periods of time.

The observation of these fluctuations complement the results of Louse Fly population parameters made in chapter 3. Initial investigation of populations showed that populations declined in size over time, exhibited heavy sexual bias, and that both prevalence and parasite load were high. A closer examination of Louse Fly populations at the nest level allowed a more detailed examination of these traits and identified the presence of nest population fluctuations at the nest based level. Thus these results extend the results of chapter 3.

These fluctuations have important implications for studies investigating the effects of parasitism in this host-parasite system. Single or a small number of Louse Fly population counts, on either the adult hosts or in the nests, may not reflect the true level of parasitism these hosts are exposed to. The abundance of parasites should be studied over many occasions to gain a more realistic view of parasitic abundance. This observation shows the difficulty of estimating the true level of parasitism experienced by wild birds and the importance of studying parasite life-history before attempting to understand the functioning of host-parasite systems.

6.3: PREVIOUSLY UNREPORTED MATE GUARDING AND 'CLUSTERING' BY A NEST ECTOPARASITE

We report the discovery of mate guarding and the formation of concentrated aggregations of males into 'clusters' or 'mating balls' by Louse Flies, *Crataerina pallida* (Diptera: Hippoboscidae) Latreille 1812, a parasite of Common Swifts, *Apus apus* (Aves: Apodidae) Linnaeus 1758. *C. pallida* is a obligate haematophagous nest ectoparasite of swifts (Kemper 1951, Bequaert 1953, Walker and Rotherham 2010a, Walker and Rotherham 2010b). However due to the difficulties of accessing swift colonial nesting sites there is a paucity of knowledge about this parasite, and particularly about its reproductive habits (Marshall 1981).

A Common Swift nesting colony situated beneath a roadway bridge spanning the Bigge Reservoir at Olpe in Germany (51° 04' 00" N, 07° 81' 00" E), offered a unique opportunity to study this species further. This colony comprised 38 breeding pairs of swifts in 2008 and 30 breeding pairs in 2009. Nests were visited on a daily basis throughout the swift breeding season and *C. pallida* populations observed. Particular attention was paid to parasite mating behaviour. This parasite is closely associated with

the host nests, with mating occurring on the nest rim or in direct proximity to the nest rather than upon hosts directly.

Here the first report of mate guarding by males of this species is reported. Although mating is often ephemeral, males would frequently remain situated positioned over females for much longer periods of time post copulation. Typically such waiting lasted approximately five to ten minutes in length, but on one occasion was observed to continue for approximately 20 minutes.

In addition, large aggregations of *C. pallida* adults, with parasites present in ball-like 'clusters', were observed frequently at nests. Photograph 1 shows one such ball like mass of parasites at one nest, (Nest: DR-K6-231), observed on the 14th of June 2008. This is the first time such congregations and aggregations of this parasites have been seen and reported. An example of one such mating cluster can be seen in photograph 1. Close examination showed such aggregations to be comprised predominately of males centred around a single or small numbers of females.

Although anecdotal, these reports indicate the presence of strong mating competition in this species, with males contesting fiercely for access to female copulation. Such strong mating competition may be expected. *C. pallida* is viviparous, with larvae developing singly in-uterus before being deposited at the 4th in-star stage. So although *C. pallida* populations are heavily female biased for much of their active life-cycle, female reproduction is limited and thus females are likely to be a limited resource for males. In addition, at emergence from winter diapause population sex ratios are equal (Bequaert 1953). Female preponderance only occurs later due to heavy male mortality, possibly as a direct consequence of severe mate competition. Males remaining positioned over females post mating may be ensuring paternity and thus be increasing their own fitness. Likewise the formation of 'clusters' of parasites may occur due to the males actively competing for females.

The observation of mating competition and apparently of mating clusters composed predominately of male Louse Flies may explain the host selection differences observed in chapter 5. Here, nest based populations were found to be more male biased than the population of parasites observed in nestlings. It could well be that males prefer to

remain in the nest to participate in mating clusters and enhance their chances of reproductive success, and thus a greater preponderance of females is seen on hosts.

The possible presence of mating competition has implications for the functioning of this host-parasite system. As the males and females remove different amounts of resources from hosts (Kemper 1951), and therefore cause different levels of costs to hosts, this may be influencing the effect this parasite has on hosts. Previous studies have found no effect of parasitism by this species on hosts (Tompkins *et al.* 1996).

Photograph 1: Mating cluster observed at nest DR-K6-231 on the 14th of June, 2008.



Photograph 2: Adult *C. pallida* can clearly be seen in this nest of newly hatched nestlings.



6.4: TEMPERATURE AFFECTS EMERGENCE OF HIPPOBOSCID LOUSE FLIES, *CRATAERINA PALLIDA*.

Abstract: Despite knowledge of parasite biology being essential for host-parasitic system functioning to be understood, the life-histories of many parasites remain little studied. One example being the Hippoboscid Louse Fly, *Crataerina pallida*, a nest ectoparasite of the Common Swift, *Apus apus*. The factors influencing adult parasite emergence remain unclear. Whether temperature affects emergence was studied by exposing overwintering pupae to differing temperature regimes. At higher temperatures greater numbers of adults emerged. This indicates that adult hatching is temperature mediated and may be enhanced by host presence. The relationship between *C. pallida* and their hosts is thus close.

Introduction: There is often a paucity of knowledge about parasite biology, despite such information being essential for the functioning of host-parasite systems to be understood (Clayton 1991). One example is the Louse Fly *Crataerina pallida* Latreille (Diptera: Hippoboscidae), a haematophagous nest ectoparasite of the Common Swift, *Apus apus* Linnaeus (Aves: Apodidae), about which little is known. *Crataerina pallida* is pupiparous; larval development occurs internally before deposition of 4th in-star larvae which pupate and overwinter in this form (Bequaert 1953). No detrimental effect of parasitism has been found on hosts (Lee and Clayton 1995, Tompkins *et al.* 1996). The expected costs resulting from such parasitism may be being obscured or mediated by unknown aspects of its biology.

The timing of parasite emergence is important in influencing the parasitic pressure hosts experience and thus the costs they may bear. *Crataerina pallida* populations fall gradually as the swift breeding season progresses. Thus the factors affecting the timing of their emergence are of pertinence in understanding the level of parasite virulence observed. Whether temperature influences the timing of emergence was investigated. The number and sex of *C. pallida* adults emerging from pupae experiencing different temperature regimes was examined. Adult emergence at particular temperatures may indicate possible cues initiating emergence and indicate the closeness and dependency of the relationship between the parasite and its host.

Materials and Methods: Pupae were collected from a Common Swift nesting colony situated beneath a roadway bridge spanning the Bigge Reservoir situated at Olpe, Germany (51° 04' 00" N, 07° 81' 00" E). Pupae were collected over several days in October 2007 and placed under experimental treatments from November the 2nd. The total number of *C. pallida* pupae at the bridge at this time was 748, which were distributed between 48 nests (mean per nest = 20.33 ± 13.69 , range 0-66 per nest). 183 pupae were collected from a total of 9 nests (Mean = 19.22 ± 13.86 , range = 2-44) and used in the subsequent experiment. These pupae were selected as the destruction of the nests where they originated was expected to occur as a result of subsequent building work.

Of the original 183 pupae collected 14 were destroyed through handling. The remaining pupae were randomly allocated into four groups, each containing 41 pupae. Pupae were placed on filter paper in petri dishes, five pupae per dish. Pupae were then placed under one of four different temperature regimes, each with the intention of simulating different conditions. One group remained at the bridge, and was placed upon filter paper within petri dishes as for the other treatments. These dishes were kept at one end of the bridge in close proximity to nests and experienced the same conditions as pupae present close to nests would. This group acted as a form of 'control' and thus experienced normal conditions (mean temperature = $21.05 \text{ }^{\circ}\text{C} \pm 1.77$, range = 18-27.5 $^{\circ}\text{C}$). The second group was placed within a refrigerator, to simulate 'winter' (mean temperature = $8.33 \pm 2.42 \text{ }^{\circ}\text{C}$, range = 4-14 $^{\circ}\text{C}$). A third group was placed within an incubation cabinet experiencing temperatures typical of 'spring-like' conditions (mean = $22.71 \text{ }^{\circ}\text{C} \pm 1.84$, range = 19-25 $^{\circ}\text{C}$). The final group was placed in a warmer incubating cabinet at temperatures aimed at simulating those experienced by pupae situated within the nest during swift brood incubation. (mean = $34.70 \text{ }^{\circ}\text{C} \pm 9.02$, range = 27-36 $^{\circ}\text{C}$). Automatic data loggers checked the constancy of temperatures experienced within each regime. These recorded temperature every five minutes over five days from the 20th of May; the mean and range of temperatures recorded was calculated. Pupae were examined regularly to quantify the adult emergence until it became clear that emergence had ceased.

Results: Table 1 shows the number and sex of adult *C. pallida* which emerged from each group. Emergence began on the 27th of May 2008 within the 'nest' group of pupae. Within the 'spring' group, hatching began on the 30th of May. Emergence within the 'control' bridge group of pupae began on the 6th of June.

Most adults appeared from those pupae within the 'nest' regime which experienced the highest temperatures. No adult emergence resulted from the pupae kept refrigerated in the 'winter' simulated group. Intermediate levels of emergence were seen from pupae in the other two temperature regimes. Using the 'control' group as a standard comparison of normal hatching rates, there were significantly fewer adult emergence's from the 'winter' group ($\chi^2 = 13$, $P < 0.01$), and more from the 'nest' group ($\chi^2 = 13.71$, $P < 0.01$). There was no significant difference in the number hatching from the 'spring' group or in the number of males and females hatching either overall or within any group.

Discussion: The higher the temperature experienced the greater the number of adult *C. pallida* which hatched from pupae, with the greatest number appearing amongst pupae experiencing temperatures that would be experienced within nests during swift incubation. These results indicate that *C. pallida* hatching is temperature mediated, with raised temperatures promoting adult emergence. However emergence is not dependent on swift presence, as hatching occurs under typical spring like conditions, which would be experienced whether hosts were present or not. Swifts may facilitate *C. pallida* emergence as hatching is greatest at temperatures encountered during host presence.

Emergence rates of adults from pupae kept at 'spring-like' temperatures and under 'control' conditions at the bridge were broadly similar in magnitude. The difference seen between these two groups in hatching may be due to differences in humidity or in the number of times certain temperatures were reached in each treatment. Emergence may be triggered once certain minimum temperatures are reached.

This study raises many related potential avenues of further investigation. Bequart (1951) cited that populations exhibited equal sex ratios. However, this has not been investigated further. Determining the sex ratio over the entire season at individual nest sites and at whole colonies would be interesting. Males appear to emerge earlier than females. This needs further investigation as this may affect the parasitic efficacy of this

species. Females are likely to pose a greater cost to hosts than males as they may remove more resources more often. Males may be emerging earlier in order to engage in male mating competition. Also, an investigation into the lifespan of Louse Flies is needed. Differences in lifespan between males and females may likewise influence parasitic effect.

These results may explain some features of *C. pallida* populations observed earlier in this discussion. Should emergence of male and female pupae differ, this may account for the differences in sex ratios observed in nest populations seen in chapter 3, or the differences in host selection by the two sexes observed in chapter 6. Thus an examination of sex based differences in emergence should be considered.

Table 1. The number and sex of adult *C. pallida* emerging under each temperature regime.

Regime	Treatment Size	No. Hatching (% pupae number)	Males (% emerged adults)	Females (% emerged adults)
Bridge: 'Control'	41	13 (32.5)	8 (61.54)	5 (31.71)
Circa 25 °C : 'Spring'	41	19 (45)	10 (55.56)	9 (47.37)
Circa 35 °C : 'Nest'	41	28 (70)	13 (46.43)	15 (58.29)
Refrigerated: 'Winter'	41	0 (0)	0 (0)	0 (0)
Total all regimes	164	60 (36.59)	31 (51.63)	29 (49.15)

The results indicate that the relationship between *C. pallida* and swifts is close. *C. pallida* adult emergence appears synchronized with host arrival as it is timed to occur at temperatures experienced at this season. Parasite hatching must occur in conjunction with swift presence as unfed *C. pallida* have a lifespan of only approximately five days (personal observation). There are therefore strong selective pressures promoting synchrony of hatching and host arrival and the development of mechanisms for accurately predicting swift arrival by *C. pallida*.

These results mirror anecdotal reports about parasite emergence (Popov 1965). Hatching of *C. pallida* has been found to occur once pupae were placed upon a heated radiator (Kemper 1951). *C. pallida* emergence is reported to coincide with swift arrival and commencement of swift breeding (Weitnaeuer 1947, Lack 1956). The results demonstrate the synchrony of swift and *C. pallida* life-cycles and how increasing dependency upon hosts may develop that may lead to a consequent reduction in parasite virulence. Further study examining the number of adults emerging from pupae at each nest could be conducted. Also the exact cues initiating emergence may be studied. Hatching may occur once a particular 'trigger' temperature is reached or when temperatures remain above a minimum for a certain duration. Host olfactory or sensory cues also may enhance hatching success.

6.5: 'COOL DUDES': TORPOR IN COMMON SWIFTS ‘

Maintaining a constantly high body temperature is energetically costly for warm-blooded birds and any mechanism that reduces the substantial costs entailed should be favoured. One way is to lower temperatures and, in extreme cases, to enter a form of torpor or 'hibernation'. Hibernation as a strategy to save energy during the winter months is a well-known mammalian strategy but, apart from isolated examples, was not thought to be common in birds. However, recent research has indicated that it might be more widespread than previously thought (McKechnie and Lovegrove 2002).

There are anecdotal reports of Common Swift *Apus apus* entering torpor during periods of cold weather (e.g. Lack 1956), while young swifts kept in cool conditions were able to lower their temperatures without apparent detrimental effect (Koskimies 1948). Moreover, nestling swifts are reported to be resistant to a level and duration of cooling to which other altricial nestlings quickly succumb. Swifts rely on an unpredictable food

source (aerial insects), the abundance of which is heavily dependant upon ambient temperature, and so the ability to lower energy demands during poor weather would be of particular benefit.

Here an anecdotal report of torpor in swifts and of the remarkable ability of nestlings to resist cooling is reported. We hope that this will stimulate more systemic study of this phenomenon. On a number of occasions where adults had temporarily deserted nests and left broods exposed, nestlings with extremely low temperatures were recorded. Nestling temperatures were measured with a hand-held probe thermometer, accurate to within 0.1°C, which was placed beneath the fold of skin under their hind leg in close proximity to the body. This proved the most practical place at which to take such a measurement in such small nestlings and provided a good indication of nestling temperature.

On the 17th of June 2008 the temperatures of twelve nestlings from five different broods were measured. Nestlings exhibited reduced temperatures in two broods. At one nest the three nestlings present, which were aged seven, eight and nine days of age, had temperatures of 15.5, 15.6 and 19.3°C respectively. All these nestlings survived this level of extreme cooling with no ill effect. At another nest on the same day the three ten day old nestlings present had temperatures of 18.4, 18.8 and 19.3°C and likewise survived this cooling with no negative effect. The ambient temperature was 16.1°C. At the three other broods where nestling temperatures were measured on this day, nestlings had temperatures of the normally observed levels, ranging from 33.5 to 36°C whether brooded or not. The average temperature of nestlings not exhibiting reduced temperatures was 33.7°C.

Numerous other instances of nestlings exhibiting reduced temperatures were observed at this site during this summer. For example on the 19th of June, two nestlings from one brood had temperatures of 20.1 and 20.6°C. This is in comparison to a mean temperature for the other ten nestlings measured on this day of 36.5°C (ranging from 34 to 38.2°C). On the 20th of June two nestlings had temperatures of 20 and 20.1°C, while three others measured had temperatures of 35.7; 37.8; and 38.4°C. And on the 13th of June, on a particularly cold day, ten of the nineteen nestlings measured had temperatures below 25°C.

Two possible instances of adult swift ‘torpor’ were observed during 2007, a summer which was characterized by cool temperatures and high rainfall. On both occasions the adults appeared to be asleep and showed no response to human presence. This is unusual as swifts typically leave immediately when human presence within the bridge is apparent. On being touched, the swifts appeared to awaken, but remained docile and ‘dozy’ for several minutes before apparently fully recovering and leaving. Unfortunately, it was not possible to measure the temperatures of these birds.

The ability of swifts to alter body temperature and endure extreme cooling is of great potential interest. It demonstrates a method by which this species may save energy. A reduction in body temperature and the associated metabolic rate will bring substantial energetic savings. This is of possible importance in ensuring the survival and success of nestlings within this species. Common Swift nestling development is extremely constrained due to environmental pressures such as weather, food abundance, and parasitism. Any mechanism facilitating nestling survival may mediate these costs and ensure survival.

6.6: CHAPTER SUMMARY

A number of interesting discoveries concerning *C. pallida* ecology and life-history were made. Considerable fluctuations in the nest based population size of *C. pallida* over short periods of time were discovered. Evidence for mating competition was observed and documented for the first time. Emergence of parasites was found to be temperature related with rates of hatching being elevated at higher temperatures. The possible use of facultative heterothermy in nestlings was identified.

These discoveries have implications for studies examining the parasitic effect of *C. pallida*. The observed short term fluctuations in *C. pallida* populations may influence nest parasitic pressure. The presence of mating competition and the formation of male mating clusters may influence parasite population sizes and likewise parasite load. The effect of temperature on adult emergence indicates that the relationship between *C. pallida* and *A. apus* is close and likely to be parasitic in nature. The possible ability of nestlings to facultatively lower body temperature offers a mechanism by which nestlings could mediate the costs of additional environmental stresses such as parasitism.

This is the first time such short term fluctuations in nest populations and evidence for mating competition have been described. The results examining *C. pallida* emergence confirm previous anecdotal reports, but this is the first empirical examination. This is the first description of lowered swift temperatures under natural conditions. These results should be considered in further examinations of the effect *C. pallida* has on hosts as they are likely to affect the parasite loads observed. The results show how parasite and host life-history may affect parasite abundance.

6.7: CHAPTER REFERENCES

Population Fluctuation References

LEE, P.L.M. and CLAYTON, D.H. (1995). Population biology of swift (*A. apus*) ectoparasites in relation to host reproductive success. *Ecological Entomology*, **20**, 43-50.

KEMPER, H. (1951). Beobachtungen an *C. pallida* Latr. und *Melophagus ovinus* L. (Diptera, Pupipara). *Zeitschrift für Hygiene (Zoologie)*, **39**, 225-259.

TOMPKINS, D.M., JONES, T. and CLAYTON, D.H. (1996). Effect of vertically transmitted ectoparasites on the reproductive success of Swifts (*A. apus*). *Functional Ecology*, **10**, 733-740.

Mating Cluster References

BEQUAERT, J.C. (1953). The Hippoboscidae or Louse flies (Diptera) of mammals and birds. Part I. Structure, physiology and natural history. *Entomologica Americana*, **32**, 1-209.

MARSHALL, A.G. (1981). *The Ecology of ectoparasitic insects*. Academic Press, London.

KEMPER, H. (1951). Beobachtungen an *C. pallida* Latr. und *Melophagus ovinus* L. (Diptera, Pupipara). *Zeitschrift für Hygiene (Zoologie)*, **39**, 225-259.

TOMPKINS, D.M., JONES, T. and CLAYTON, D.H. (1996). Effect of vertically transmitted ectoparasites on the reproductive success of Swifts (*A. apus*). *Functional Ecology*, **10**, 733-740.

WALKER, M.D. and ROTHERHAM, I.D. (2010a). The common swift louse fly, *Crataerina pallida*: An ideal species for studying host parasite interactions. *Journal of Insect Science*, **10**, 193.

WALKER, M.D. and ROTHERHAM, I.D. (2010b). Characteristics of *Crataerina pallida* (Diptera: Hippoboscidae) populations; a nest ectoparasite of the common swift,

Apus apus (Aves: Apodidae). *Experimental Parasitology*, **126**, 451-455.

Emergence References

BEQUAERT, J.C. (1953). The Hippoboscidae or Louse flies (Diptera) of mammals and birds. Part I. Structure, physiology and natural history. *Entomology Americana*, **32**, 1-209.

CLAYTON, D.H. (1991). The influence of parasites on host sexual selection. *Parasitology Today*, **7**, 329-334.

KEMPER, H. (1951). Beobachtungen an *Crataerina pallida* Latr. und *Melophagus ovinus* L. (Diptera, Pupipara). *Zeitschrift für Hygiene (Zoo.)*, **39**, 225-259.

LACK, D. (1956). *Swifts in a tower*. Methuen publishing, London.

LEE, P.L.M. and CLAYTON, D.H. (1995). Population biology of swift (*A. apus*) ectoparasites in relation to host reproductive success. *Ecological Entomology*, **20**, 43-50.

POPOV, A.V. (1965). The life-cycle of the Louse Flies *Lipoptena cervi* L. and *Stenopteryx hirundinis* L. (Diptera, Hippoboscidae). *Ent. Obozr.*, **44**, 573-583.

TOMPKINS, D.M., JONES, T. and CLAYTON, D.H. (1996). Effect of vertically transmitted ectoparasites on the reproductive success of Swifts (*A. apus*). *Functional Ecology*, **10**, 733-740.

WEITNAUER, E. (1947). Am Neste des Mauerseglers, *A. apus apus* (L.). *Ornithological Beobachter*, **44**, 133-182.

Host Temperature References

KOSKIMIES, J. (1948). On temperature regulation and metabolism in the Swift *micropus a. apus* L., during fasting. *Experientia*, **4**, 274-276.

LACK, D. (1956). *Swifts in a tower*. Methuen publishing, London.

MCKECHNIE, A.E. and Lovegrove, B.G. (2002). Avian facultative hypothermic responses. *Condor*, **104**, 705-724.

SECTION B:
INFLUENCE OF *C. PALLIDA* ON *A. APUS*

**CHAPTER SEVEN:
COMMON SWIFT BREEDING SUCCESS AND LOUSE
FLY ABUNDANCE**

CHAPTER AIMS	7.1
CHAPTER ABSTRACT	7.2
INTRODUCTION	7.3
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DISCUSSION	7.6
CHAPTER SUMMARY	7.7
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COMMON SWIFT BREEDING SUCCESS AND LOUSE FLY ABUNDANCE

The contents of this chapter were published in a similar format as:

- WALKER, M.D. and ROTHERHAM, I.D. (2010). The breeding success of Common Swifts *Apus apus* is not correlated with the abundance of their Louse Fly *Crataerina pallida* parasites. *Bird Study*, **57**, 504-508.

7.1: CHAPTER AIMS

The aim of this chapter is to examine whether the reproductive success of *A. apus* is related to *C. pallida* abundance. The inter-specific relationship between *C. pallida* and *A. apus* is expected to result in the sub-optimal expression of host life-history traits. The expression of host traits associated with reproductive success are important in influencing lifetime success and are thus especially likely to be related to parasite abundance.

The specific objectives of this chapter are;

- Censuring of *C. pallida* nest populations and calculation of parasitic loads.
- Quantification of *A. apus* life-history parameters of relevance to reproductive success. Parameters to be examined include clutch and brood size, nestling asymptotic size and mass, fledging size and mass, and fledging success.
- Examination of whether there is a correlation between parasite abundance and the parameters studied.

The rationale behind such an initial observational study would be that it could lead to the identification of host life-history traits where the costs caused by parasitism are especially apparent. These traits could then be examined in more detail in a manipulative experimental study. The successful establishment of a relationship between *C. pallida* abundance and *A. apus* reproductive success, with *A. apus* reproductive success being lower in hosts experiencing higher *C. pallida* infestation, would indicate that *C. pallida* causes costs to *A. apus* and is thus parasitic in nature.

7.2: CHAPTER ABSTRACT

Aims: To determine whether parasitism by a haematophagous nest ectoparasite, the Louse Fly *Crataerina pallida* has a detrimental effect on the reproductive success of its Common Swift *Apus apus* hosts. **Methods:** An association between *C. pallida* abundance and various host life-history parameters indicative of host reproductive success were sought. **Results:** No relationship was found between measures of parasite load and clutch size, brood size, length of time required to reach nestling asymptotic weight, the length of time from hatching to fledging, fledging success per nest, fledgling weight, and fledgling size. **Conclusion:** Parasitism has no apparent detrimental effect upon its hosts. Louse Flies may have evolved low levels of virulence or the negative effects expected as a consequence of its parasitism may be expressed on life-history traits other than those studied here.

7.3: INTRODUCTION

An explicit assumption of host-parasite relationships is that parasites cause some cost to their hosts (Poulin 2007). These costs influence host fitness or life-history traits in a variety of ways. Parasites can, for example, increase nestling mortality (Merino and Potti 1995), reduce nestling body mass and growth rates (Brown and Brown 1986, Richner *et al.* 1993), influence clutch sizes (Moss and Camin 1970, Møller 1991), cause an increase in the time nestlings spend in the nest (reviewed by Møller 2005), or increase the amount of provisioning parents must provide (Christe *et al.* 1996). The Louse Fly *Crataerina pallida* Latreille (Diptera: Hippoboscidae), is an obligate haematophagous nest ectoparasite of the Common Swift *Apus apus* Linnaeus (Apodiformes: Apodidae). Louse Flies feed regularly (Kemper 1951) and the cumulative effect of such parasitism should incur considerable costs on host fitness. However, there is no evidence that parasitism has such an impact (Lee and Clayton 1995, Tompkins *et al.* 1996). A limitation of these studies could be that parasite abundance seen at the colony studied, the Oxford University Museum colony (Lack 1956), may not truly reflect natural levels of parasite abundance.

Access to a previously unstudied swift colony provided an opportunity to examine the relationship between swift breeding success and parasitism anew and to attempt to find an effect upon hosts of such parasitism. Parasitic abundances at this site are considerably higher than those seen at Oxford, possibly more closely resembling natural

parasitic levels and distributions. We compared swift breeding success between the years 2007 and 2008 at this colony and the association between parasitic abundance and several important swift life-history traits were investigated.

7.4: METHODS

Study site: The colony was positioned within a concrete highway bridge (51° 04' 00" N, 07° 81' 00" E) spanning the Bigge Reservoir, Olpe, Germany. The bridge was a large concrete structure 372 metres long, 22.3 metres wide and 19 metres above the water surface. A pair of enclosed walkways ran the length of the underside of the bridge. These walkways were divided into eight chambers, each approximately 5 metres wide and 40 metres long. Swifts could access these chambers through ventilation holes with an approximate diameter of 10.5 cm on the floors of the chambers. There were a total of 264 holes at the bridge. The swifts built their nests on the floor of these chambers in close proximity to the entry holes. The colony comprised 38 breeding pairs in 2007; 35 of which produced a total of 75 nestlings. Unfortunately, owing to poor weather only seven nestlings fledged. Nestlings were present from 10th June until 26th July. In 2008 there were 41 breeding pairs, 38 of which produced 89 nestlings, 38 of which fledged. Nestlings were present from 2nd June to 31st July.

Swift nestling measurements: The colony was visited daily during both breeding seasons. Data on the dates of hatching and fledging were recorded. Clutch size could not be determined in 2007. The fledging date was determined as the last day on which a nestling was present at the nest. Nestling weight was measured using electronic scales accurate to 0.01 g (Scout Pro, Ohaus, USA). The asymptote weight was nestling mass on the date on which a nestling reached its maximum weight before subsequently fledging. Weight regression occurs in this species in the days prior to fledging. Nestling size parameters, left wing length (in both 2007 and 2008), and length of the longest left primary feather of nestlings (2008 only), were measured using electronic callipers (Lux-tools, Germany) following the methods outlined by Svensson (1992).

Parasite load: Louse Fly populations were censused regularly throughout the swift breeding period. Following the methods used by Lee and Clayton (1995) and Tompkins *et al.* (1996) the highest number of Louse Flies seen on any single occasion was used as a measure of parasitic intensity for each nest. Parasite numbers can fluctuate on a day-

by-day basis (Walker 2009). This measure allows easy comparison with previous studies.

Data analysis: Statistical analyses were used to investigate relationships between parasite load and life-history traits. Possible differences in breeding and nestling traits between 2007 and 2008 were examined using Mann-Whitney U-tests. The strength of associations between parasite abundance and host traits were gauged using Spearman rank correlation. A general linear model analysis was conducted using parasite load as a dependent and year, brood size, and fledgling number per nest as variables. Data were considered separately for 2007 and 2008. However, owing to the small size of the colony, and in particular the small number of fledglings in 2007, data were additionally pooled across years. Where more than one nestling was present within a single nest, and where appropriate for the analysis conducted, mean values per nestling per nest were calculated and used to avoid pseudo-replication.

7.5: RESULTS

Parasite abundance: The level of parasite abundance at the 35 nests where nestlings hatched in 2007 was 8.94 ± 5.17 adult Louse Flies per nest. At the 38 nests inhabited by nestlings in 2008 mean parasite abundance was 12.05 ± 7.47 . The overall mean parasite abundance over the two years was 10.61 ± 6.64 adult parasites per nest. There was a significant difference in parasite abundance between the years ($U = 460.5$, $z = 1.91$, $P < 0.02$). The overall mean parasite abundance considering only the nests where nestlings fledged from in both 2007 and 2008 was 11.01 ± 6.74 . There was a significant difference in levels of parasitism at nests where fledging occurred between years, with the parasite abundance in 2007 being higher (mean = 12.50 ± 4.41) than in 2008 (mean = 10.76 ± 6.96) ($U = 461.50$, $z = 2.24$, $P < 0.01$). An adult parasite prevalence of over 90%, and parasite pupae prevalence rates of over 70% were observed in both 2007 and 2008.

Clutch and brood size: The mean parasite load for broods and clutches of different sizes is shown in Figures 1 and 2. There was no significant difference in brood sizes between years ($U = 717.50$, $z = -0.044$, $P = 0.33$). There was no significant difference in the parasite load at nests with different clutch sizes in 2008 (one-way ANOVA, $F = 2.28$, d.f. = 3, $P = 0.09$). There was, however, a significant difference in levels of

parasite abundance between broods of different sizes, with smaller broods having more parasites, both in 2007, (one-way ANOVA, $F = 5.02$, d.f. = 3, $P < 0.05$) and in 2008 (one-way ANOVA, $F = 5.66$, d.f. = 4, $P < 0.05$).

Nestling asymptotic mass: There was a significant difference in the asymptotic mass nestlings reached in 2007 (mean = 47.96 ± 6.87 grams) and in 2008 (mean = 50.22 ± 6.87 grams) ($U = 59.00$, $z = 2.30$, $P \leq 0.01$) and also the time it took them to reach it (mean 2007 = 31.55 ± 4.18 days; mean 2008 = 26.67 ± 4.18 days) ($U = 69.50$, $z = 1.97$, $P \leq 0.01$). This reflects the generally better weather conditions experienced in 2008, which enabled survival of smaller nestlings and quicker nestling development.

There was no association between asymptotic weight and parasite load in either year (2007, $r_s = -0.36$, $n = 7$, $P = 0.41$; 2008, $r_s = -0.98$, $n = 38$, $P = 0.55$). Using pooled data for 2007 and 2008 there was also no significant association between parasite load and either asymptotic weight (overall mean = 49.80 ± 4.93 g; $r_s = 0.19$, d.f. = 30, $P = 0.29$), or the number of days required to reach asymptotic weight (overall mean = 25.58 ± 4.94 days; $r_s = -0.07$, d.f. = 30, $P = 0.70$). At the asymptote mass nestlings in 2007 had larger left wing lengths (mean = 126.72 ± 10.23 mm) than in 2008 (mean = 113.93 ± 10.22 mm), and this difference was almost significant ($U = 85.50$, $z = 1.47$, $P = 0.07$). There was, however, no significant correlation between parasite abundance and wing length over the two years (overall mean = 116.34 ± 15.73 mm; $r_s = -0.11$, d.f. = 30, $P = 0.54$), or between parasitism and primary feather length (overall mean = 82.83 ± 18.87 mm; $r_s = -0.08$, d.f. = 30, $P = 0.64$) in 2008.

There were no significant differences in mean mass between fledglings in 2007 (mean = 37.60 ± 16.43 g) and 2008 (mean 40.40 ± 4.05 g; $U = 146.00$, $z = -0.39$, $P = 0.34$), but a significant difference in their wing lengths (mean 2007 = 116.98 ± 4.61 mm; mean 2008 = 157.97 ± 5.11 mm; $U = 37.00$, $z = 2.99$, $P \leq 0.01$). The mean primary feather length in 2008 was 123.79 ± 5.31 mm).

Figure 1: Parasitic abundance at nests with different brood sizes for 35 nests from 2007 (black bars) and 38 nests from 2008 (white bars). Error bars indicate the level of SD.

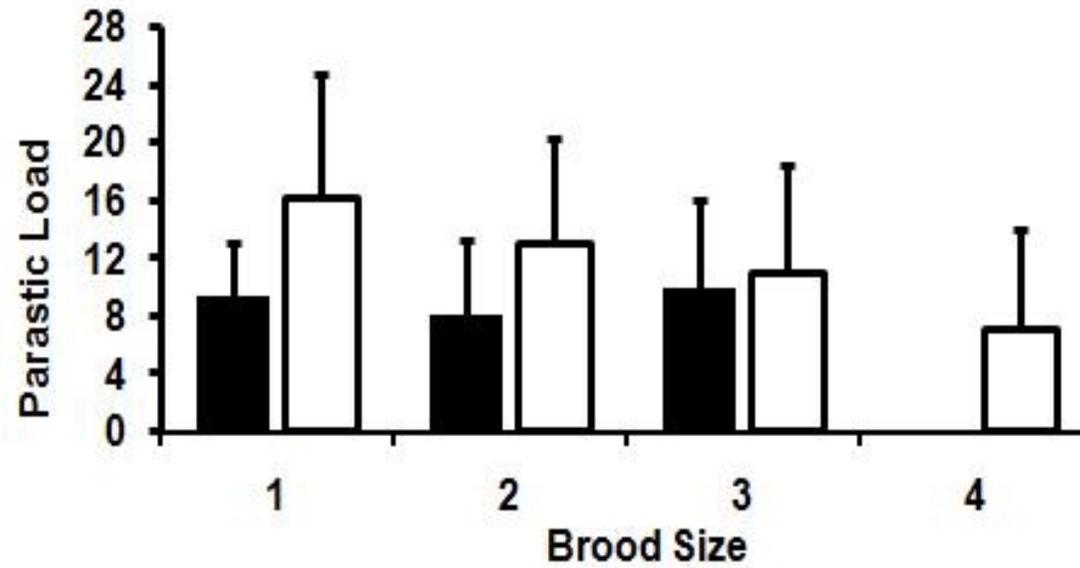
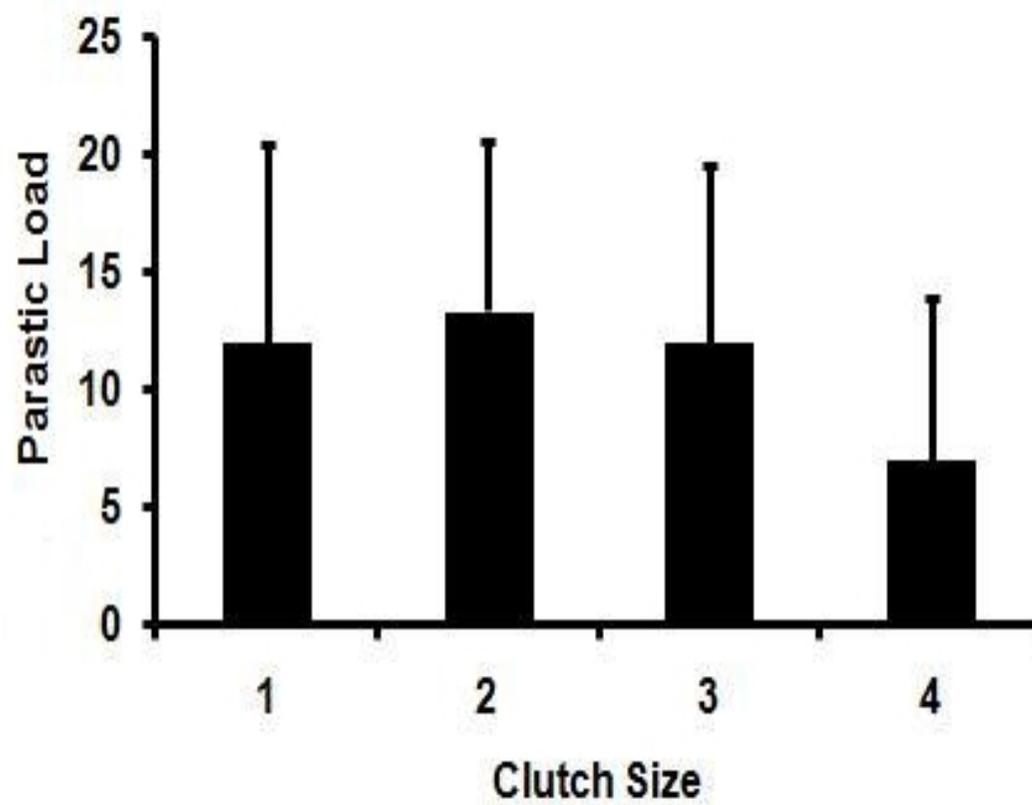


Figure 2: Parasitic load at nests with different clutch sizes. Data for 38 nests from 2008. SD indicated by error bars.



Fledging Mass: There was no notable correlation between fledging mass and parasite abundance in either 2007 or 2008 (2007, $r_s = 0.22$, d.f. = 6, $P = 0.63$; 2008, $r_s = -0.005$, d.f. = 37, $P = 0.97$). There were also no significant associations between parasitism and left wing size in 2008 ($r_s = -0.121$, d.f. = 37, $P = 0.471$), or longest left primary length (2008, $r_s = 0.038$, d.f. = 37, $P = 0.822$). A significant effect on left wing size was seen in 2007 ($r_s = 0.85$, d.f. = 6, $P < 0.01$), but this was probably because of the small sample size. Using pooled data for both 2007 and 2008 there was likewise no noticeable association between parasite load and either fledgling weight ($r_s = 0.03$, d.f. = 30, $P = 0.86$), left wing size ($r_s = -0.04$, d.f. = 30, $P = 0.80$), or longest left primary length ($r_s = -0.01$, d.f. = 24, $P = 0.96$).

There was a significant difference in the age at which fledging occurred in 2007 (mean = 31.66 ± 3.94 days) and in 2008 (mean = 40.01 ± 2.57 days; $U = 202.50$, $z = -2.16$, $P \leq 0.01$). Poor weather probably initiated earlier nestling fledging in 2007. The age taken to reach fledging was not significantly correlated with parasite abundance ($r_s = 0.02$, d.f. = 30, $P = 0.91$).

Fledging success: There was a significant difference in the per nest number of fledglings between 2007 (mean = 0.21 ± 0.48) and 2008 (mean = 1.00 ± 0.84) ($U = 1038.00$, $z = -4.11$, $P \leq 0.01$), and in the number of nestlings which died per nest in 2007 (mean = 1.94 ± 0.84) and 2008 (mean = 1.34 ± 0.91 ; $U = 420.00$, $z = 2.70$, $P \leq 0.01$), which given the high level of nestling mortality in 2007 is not surprising.

There were no notable correlations between either parasitism and the number of fledglings per nest (overall mean = 0.62 ± 0.79 ; $r_s = 0.11$, d.f. = 71, $P = 0.34$), or parasite abundance and the number of nestlings dying before fledging per nest (overall mean = 1.63 ± 0.92 ; $r_s = 0.03$, d.f. = 71, $P = 0.73$). The glm analyses revealed that there was no statistically significant interaction between variables on parasite ranking ($R^2 = 0.18$, d.f. = 70, $F = 0.84$, $P = 0.47$). Year was the variable that most strongly influenced parasite rank ($\beta = 2.30$, $SE = \pm 1.69$, $P = 0.17$), followed by brood size ($\beta = 0.80$, $S.E. = \pm 1.05$, $P = 0.44$).

7.6: DISCUSSION

As in other studies examining this host-parasite system, no convincing association between parasite load and the breeding success of the host swifts was found. This is surprising given the considerable level of resources this parasite appears to extract from hosts and the constraints that swifts face in their reproduction. Swift breeding has to be completed within an extremely short time period and given the vagaries of European summers, with the changeable weather conditions and fluctuating aerial insect abundances, parasite load would be thought to be an important factor influencing breeding success in this species. That no effects on clutch size were found is perhaps not unexpected as adult parasites emerge from diapause once clutch size is already established. Parasitism could, therefore, only influence clutch size if swifts could anticipate parasite loads before incubation begins. Parasites could influence brood size if they disrupted adult behaviour during incubation; however, such disturbance has not been reported and, therefore, is unlikely (Lack 1956).

That Common Swift nestlings exhibit flexibility in development rates in response to detrimental environmental conditions is well documented (Weitnauer 1947, Lack and Lack 1951, Lack 1956). Increased parasitism might, therefore, be thought to be a prime candidate leading to an extension of the nestling period. However, we found no connection between parasite load and the time required for nestlings to reach asymptotic weight or the time required to reach fledging. Nestling mass is an important predictor of fitness (Magrath 1991). Therefore, any detrimental effect of parasitism on asymptotic or fledging weight is likely to have substantial future fitness costs. No relationship between parasitism and either asymptotic or final fledgling size was found. It might be expected that no influence of parasitism upon traits of pertinence to fledgling flight ability, such as final fledgling weight and size, would be found.

Swifts are aerial specialists, spending the majority of their lives airborne. The physiological demands of flight impose strict constraints on body design. Fledging swifts have to be perfectly capable of flight immediately on leaving the nest. It has been shown that nestling fledging is dependent on specific wing loadings being reached, and that nestlings do not fledge until this is reached (Martins 1997). Any fledgling deviating from such constraints will have low survival chances. Effects of parasitism upon fledgling size should, therefore, be avoided at all costs. It may be more advantageous

for such costs to be deferred onto traits with later lifetime consequences in order to maximize immediate survival chances.

The population abundance of *C. pallida* that we recorded was considerably greater than that reported by Lee and Clayton (1995) and by Tompkins *et al.* (1996). Lee and Clayton (1995), in their examination of *C. pallida* population abundances, found a nest parasite prevalence of 67%, and a mean parasitic intensity, of 1.0 ± 0.2 larvae per nest (range 0-5), and a mean pupae number per nest of 1.7 ± 0.4 (range 0-9). Tompkins *et al.* (1996) experimentally manipulated parasite abundances to create nests with enhanced parasite loads, and these had mean per nest parasite loads (based on the maximum number of adults seen) of 7.39 ± 0.87 . Lee and Clayton 1995, and Tompkins *et al.* (1996) proposed that the vertical nature of Louse Fly transmission may account for lack of virulence observed. The development of reduced virulence is expected where host and parasite reproductive success is linked (Poulin 2007).

The high level of host specificity exhibited by species within the *Crataerina* genus upon their respective hosts indicates that such co-adaptation may have occurred in these host-parasite systems. However, although vertical transmission between adult and nestling swifts is common, the extent of horizontal or phoretic transfer between nests and unrelated hosts and the implications this would have on parasite virulence remain unknown.

Studies on the Alpine Swift *Apus melba* Linnaeus and its related parasite, *Crataerina melbae* Rondani, have found detrimental effects upon such subtler host traits than those here studied, including growth rates (Bize *et al.* 2003a), nestling behaviour (Bize *et al.* 2003b), and parental lifetime reproductive success (Bize *et al.* 2004). Conversely, a study on a more obvious host life-history trait, host condition, found no correlation with Louse Fly abundance (Tella *et al.* 1995). This may indicate that costs of such parasitism are indeed deferred upon more subtle traits. Likewise studies of other aerial insectivores have found parasitic effects upon a myriad of host traits, with, for example, parasitism being found to effect immune system investments and trade-offs in the Barn Swallow *Hirundo rustica* (Møller *et al.* 2001). Studies of these and other life-history traits in the Common Swift may be a promising avenue of further research. Another potential avenue of research is an examination of the effects different sexes of *C. pallida* have on

hosts. As observed in chapter 3, where differences in parasite population ratios were observed, chapters 5 where differences in host selection by male and female *C. pallida* were observed, and in chapter 6 where mating clusters were discovered, there may be differing costs of parasitism by the different sexes. A closer examination of sexual differences and their influence of parasitic effect may be pertinent.

Also in the studies of *C. pallida* populations undertaken in chapter 3 it was found that previous attempts to quantify parasite load may have been inaccurate. A correct quantification of parasite load is essential when attempting to elucidate parasital effects. The figures for parasite abundance seen in chapter 3 are more likely to reflect true parasite abundances levels. Further studies into parasite effects should consider the conclusions made in chapter 3. As mentioned in chapter 3 parasite pressure should be established over as wide a number of dates as possible and not simply over a small number of population counts.

A limitation of the present study was its purely observational nature. Although host-parasite systems are often studied in such a fashion, such studies do not provide conclusive evidence of parasitic effects. Experimental studies where parasitic abundance is artificially manipulated are required to reach more rigorous conclusions. Such an experimental study would be a logical next step in our research.

7.7: CHAPTER SUMMARY

This investigation examined whether there was an association between *C. pallida* abundance and various parameters of *A. apus* breeding success. The results were that; There was no association between parasite abundance and clutch size; adult swifts in more heavily parasitized nests did not lay fewer eggs.

- However, nests with higher parasitic abundances had smaller brood sizes, suggesting that parents experiencing higher parasitism may hatch out fewer offspring.
- There was no relationship between parasite abundance and either nestling mass at asymptoty, nestling mass at fledging, wing length at asymptoty or fledging, or in the time taken to reach fledging mass. This indicates that parasitism does not influence nestling development.
- There was no association between parasitism and the number of fledglings per

nest or in nestling mortality. This indicates that parasitism does not influence nestling mortality.

The implication of these results are that *C. pallida* has no obvious large influence on host reproductive success. Parasitic costs may be being expressed upon subtler traits than those examined and thus are not evident here. The lack of association between *C. pallida* abundance and host reproductive traits suggests that *C. pallida* is not parasitic in nature. This conclusion is contrary to expectations, and does not support the dissertation hypothesis. Given the considerable amount of resources this species removes the expected costs to *A. apus* of experiencing *C. pallida* infestation would be expected to be considerable and clearly evident.

This investigation complements the only other observational study of *C. pallida* parasitism, which likewise found no relationship between parasitic abundance and host breeding success (Lee and Clayton 1995). However, its main limitation is its purely observational nature. Mere correlation of two features famously does not necessarily imply causation. Therefore, an obvious line of further inquiry is more detailed empirical study involving experimental manipulation of parasitic abundances. Also of interest would be examination of more detailed host life-history traits upon which parasitic costs may be more evident. Obvious traits of examination, given their importance to swift success and the time-constrained nature of swift breeding, are traits indicative of nestling growth and development.

7.8: CHAPTER REFERENCES

BIZE, P., ROULIN, A., BERSIER, L.F., PFLUGER, D. and RICHNER, H. (2003a). Parasitism and developmental plasticity in Alpine Swift nestlings. *Journal of Animal Ecology*, **72**, 633-639.

BIZE, P., ROULIN, A. and RICHNER, H. (2003b). Adoption as an offspring strategy to reduce ectoparasite exposure. *Proceedings of the Royal Society London .B.*, **270**, S114-S116.

BIZE, P., ROULIN, A., TELLA, J., BERSIER, L.F. and RICHNER, H. (2004). Additive effects of ectoparasites over reproductive attempts in the long-lived Alpine Swift. *Journal of Animal Ecology*, **73**, 1080-1088.

BROWN, C.R. and BROWN, M.B. (1986). Ectoparasitism as a cost of coloniality in

- Cliff Swallows (*Hirundo Pyrrhonota*). *Ecology*, **67**, 1206-1218.
- CHRISTE, P., RICHNER, H. and OPPLIGER, A. (1996). Begging, food provisioning, and nestling competition in Great Tit broods infested with ectoparasites. *Behavioural Ecology*, **7**, 127-131.
- LACK, D. and LACK, E. (1951). The breeding biology of the swift. *A. apus*. *Ibis*, **93**, 501-546.
- LACK, D. (1956). *Swifts in a tower*. Methuen publishing, London.
- LEE, P.L.M. and CLAYTON, D.H. (1995). Population biology of swift (*Apus apus*) ectoparasites in relation to host reproductive success. *Ecological Entomology*, **20**, 43-50.
- MAGRATH, R.D. (1991). Nestling weight and juvenile survival in the Blackbird, *Turdus merula*. *Journal of Animal Ecology*, **60**, 335-351.
- MARTINS, T.L.F. (1997). Fledging in the Common Swift: weight-watching with a difference. *Animal Behaviour*, **54**, 99-108.
- MERINO, S. and POTTI, J. (1995). Mites and blowflies decrease growth and survival in nestling pied flycatchers. *Oikos*, **73**, 95-103.
- MØLLER, A.P. (1991). Ectoparasite loads affect optimal clutch size in swallows. *Functional Ecology*, **5**, 351-359.
- MØLLER, A.P., MERINO, S., BROWN, C.R. and ROBERTSON, R.J. (2001). Immune defense and host sociality: a comparative study of swallows and martins. *American Naturalist*, **158**, 136-145.
- MØLLER, A.P. (2005). Parasites, predators and the duration of developmental periods. *Oikos*, **111**, 291-301.
- MOSS, W.W. and CAMIN, J.H. (1970). Nest parasitism, productivity and clutch size in Purple Martins. *Science*, **168**, 1000-1003.
- KEMPER, H. (1951). Beobachtungen an *Crataerina pallida* Latr. Und *Melophagus ovinus* L. (Diptera, Pupipara). *Zeitschrift Fuer Hygiene.(Zool.)*, **39**, 225-259.
- POULIN, R. (2007). *Evolutionary ecology of parasites*. Princeton University Press, Princeton, NJ.
- RICHNER, H., OPPLIGER, A. and CHRISTE, P. (1993). Effect of an ectoparasite on reproduction in Great Tits. *Journal of Animal Ecology*, **62**, 703-710.
- SVENSSON, L. (1992). *Identification Guide to European Passerines*. British Trust for Ornithology, Thetford.
- TELLA, J.L., GORTAZAR, C., GAJON, A. and OSACAR, J.J. (1995). Apparent lack of effects of a high Louse-fly infestation (Diptera, Hippoboscidae) on adult colonial

Alpine Swifts. *Ardea*, **83**, 435-439.

TOMPKINS, D.M., JONES, T. and CLAYTON, D.H. (1996). Effect of vertically transmitted ectoparasites on the reproductive success of swifts (*Apus apus*). *Functional Ecology*, **10**, 733-740.

WALKER, M.D. (2009). Daily fluctuations in the numbers of the Louse Fly *Crataerina pallida* (Latreille 1812) (Dip.: Hippoboscidae) seen at Common Swift *Apus apus* nests. *Entomologists record*, **121**, 157-158.

WEITNAUER, E. (1947). Am Neste des Mauerseglers, *A. apus apus* (L.). *Der Ornithologische Beobachter*, **44**, 133-182.

**CHAPTER EIGHT:
ECTOPARASITE LOAD DOES NOT REDUCE
REPRODUCTIVE SUCCESS OF
COMMON SWIFTS, *APUS APUS***

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ECTOPARASITE LOAD DOES NOT REDUCE REPRODUCTIVE SUCCESS OF COMMON SWIFTS, *APUS APUS*

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8.1: CHAPTER AIMS

This chapter aims to demonstrate empirically that increased *C. pallida* infestation results in a lowering of *A. apus* reproductive success, namely through the sub-optimal expression of traits associated with *A. apus* reproduction and growth. The specific objectives of this chapter are to:

- Experimentally manipulate *C. pallida* population abundances to create broods and hosts experiencing artificially high and low levels of *C. pallida* abundance.
- Assess whether there are differences between experimental treatments in the following host reproductive traits:
 - Clutch and brood sizes
 - Nestling development
 - Nestling and fledging number per brood.

Especially emphasis will be placed on traits related to *A. apus* growth and development as it may be that parasite costs are especially likely to be expressed upon these. Differences in the length of developmental period, rates of growth, and various indices of development such as the *k*-growth factor, will be sought between experimental treatments. These traits have either not been studied in previous investigations examining *C. pallida* parasitism, or have only been briefly considered. Differences in these traits between experimental treatments would successfully demonstrate that increased *C. pallida* abundance causes clear costs to hosts, and thus support the dissertation hypothesis that *C. pallida* is parasitic.

Such experimental study is necessary as simply demonstrating linkage between two variables as was attempted in Chapter 7, does not necessarily indicate a causative effect of one factor upon the other. To clearly demonstrate such an effect, experimental manipulation of the variable thought to be of influence is required.

8.2: CHAPTER ABSTRACT

Previous studies have failed to ascertain negative effects of Louse Fly *Crataerina pallida* parasitism on Common Swifts *Apus apus*. Abundances of *C. pallida* were experimentally manipulated to create broods experiencing either enhanced or reduced levels of parasitism and then host life-history traits were examined. No significant differences were observed in clutch and brood size, rate of growth, asymptotic and fledging mass and size, or the number of fledglings per nest. Reductions in parasite virulence may have evolved due to the dependence of successful *C. pallida* transmission on host reproductive success.

8.3: INTRODUCTION

By definition, parasitism results in costs to the host (Price 1980). However, previous studies of parasitism by the Louse Fly *Crataerina pallida* on the Common Swift *Apus apus* have found no negative effects (Hutson 1981, Lee and Clayton 1995, Tompkins *et al.* 1996, Walker and Rotherham 2010a). The costs of parasitism are expected to be high as *C. pallida* is an obligate haematophagous nest ectoparasite occurring at high population densities (Walker and Rotherham 2010b). Adults emerge from overwintering pupae each spring. Feeding occurs approximately every five days. Larvae develop internally before deposition as fourth in-star larvae, which pupate immediately (Walker and Rotherham 2010b).

The lack of recorded parasite virulence exhibited by *C. pallida* is surprising as studies of a closely related host-parasite system of Alpine Swifts *A. melba* have shown clear detrimental effects on hosts as a result of parasitism (Bize *et al.* 2003, 2004a, 2004b, 2005). However, the numbers of *C. pallida* seen in previous studies of Common Swifts may not reflect natural abundances. This is because the nests at the colony examined by Lee and Clayton (1995) and Tompkins *et al.* (1996) were cleaned annually. This is likely to have led to a reduction in parasite abundance, as has been shown to occur in other studies (Møller 1989), and reduced effects of parasitism as a consequence.

In this study, the availability of a colonial nesting site with natural parasite abundances offered the opportunity to re-examine this host-parasite system and the level of host resilience to parasitism. Abundances of *C. pallida* were manipulated between nests to create broods with either increased or reduced parasite loads. Life-history traits associated with reproductive success were compared between experimental treatments. Traits investigated included clutch size, brood size, growth rate, and nestling size and mass at asymptoty and fledging. Swift nestling development is especially likely to be influenced through parasitism as development is strongly time constrained and occurs quickly (illustrated by photographs 1 to 4). These photographs show nestling size at ages 2 days, 10 days, 20 days and 30 days. They illustrate the rapid development of nestling size in the short period of time comprising nestling development.

Differences in these life-history traits would be indicative of an effect on host fitness as expected by host-parasite theory. Failure to find such costs would provide support for Lee and Clayton (1995), Tompkins *et al.* (1996), and Walker and Rotherham (2010) (chapter 7), who concluded that a reduction in parasite virulence had occurred due to the close synchrony of *C. pallida* and host life-cycles. Where parasite fitness becomes linked with the reproductive success and fitness of hosts, the evolution of reduced parasite virulence is expected. Lee and Clayton (1995) postulated that the vertical nature of parasite transmission, occurring solely between parent and offspring and meaning parasite dispersal is dependent on host reproductive success, accounted for parasite avirulence.

8.4: METHODS

Study site: The Common Swift is a migratory insectivore returning to Europe in April to breed. Common Swifts were examined at a colonial nesting site beneath a concrete roadway bridge spanning the Bigge reservoir, north of Olpe, North Rhine Westphalia, Germany (51° 04' 00" N, 07° 81' 00" E). The site is similar in nature to traditional cliff vaults used by swifts for nesting, and the artificial substrate provides numerous nooks and crannies for pupal deposition by the parasite. Nests lie exposed upon the floor of enclosed internal concrete walkways beneath the bridge and are typically situated close to each entry hole. Nests are typically widely spaced (mean \pm SD = 5.3 \pm 4.8 metres).

Photographs illustrating development of *A. apus*:

Photograph 1: Nestling of approximately 2 to 3 days of age.



Photograph 2: Nestling development at approximately 10 days. Note the beginning of feather development at this age.



Photograph 3: Nestling of approximately 20 days of age. At this stage young are fully feathered but still somewhat dumpy and squat in appearance.



Photograph 4: Nestling of approximately 30 days of age. Development is effectively complete at this age, although lengthening of wings continues until time of fledging.



Experimental manipulations: *C. pallida* pupae and adults were transferred between nests to create broods experiencing either increased or reduced parasitism. The aim was to create bimodal population distributions, with nests encountering either little parasitism or approximately double that experienced in the previous year. Nests were randomly assigned to either ‘reduced’ or ‘enhanced’ treatments. Reduced regime nests were paired with a partner nest in the enhanced regime that had the same brood size and a similar parasite load in the previous year (2008). All parasites present within reduced-load nests were transferred to their parasite-increased partner nests. This resulted in parasite-reduced nests with no or little parasitism, or parasite-enhanced nests with levels of parasitism approximately double that seen previously. A similar method was used by Bize *et al.* (2004a).

Pupae were transferred between nests on 30th April 2009, before the arrival of adult swifts. On hatching of nestlings, nests were checked every five days and, when present, parasites were transferred from parasite-reduced nests to their enhanced partners. In practice, the initial transfer of pupae proved highly effective and few subsequent transfers of adult parasites were necessary.

Measurement of host life-history parameters: Nests were visited daily once nestlings hatched. Clutch size was determined from the presence of unhatched eggs, and brood size was taken as the maximum number of nestlings that hatched at each nest. Nestling mass was determined daily using electronic scales (Ohaus, Scout Pro, accuracy 0.01 g) between 07:00 and 13:00 hours. Maximum left wing length (closed), the length of the longest left outermost primary feather (PX), overall body length, and head length and width were measured daily following the methods outlined by Svensson (1992). Left wing length was measured from carpal joint to the tip of the longest primary. Measurements were taken with electronic measuring callipers (Lux-Tools, accuracy 0.01 mm). The parasitic load was calculated following the method outlined by Lee and Clayton (1995), using the maximum number of adult parasites observed at each nest during nest visits.

Data analysis: Data analysis was conducted using Excel and SPSS 14. Mean values per brood were calculated to avoid pseudo-replication. All means are presented + 1SD. Standard growth curves of nestling mass against age were produced for all nestlings

which subsequently fledged and for each parasite regime and described as brood means. The following indices of nestling growth were calculated:

- The point of growth inflection (slowing of growth rate).
- Linear growth rate at this point (k), assuming a logistic growth curve (Ricklefs 1967, 1968).
- Asymptotic and fledging measures of size and mass.
- Length of time taken to grow from 10% to 90% of asymptotic mass (t_{10-90}) (Ricklefs 1967).

Asymptotic measures were those attained by nestlings at maximum mass prior to fledging. Swifts undergo weight regression prior to fledging with the asymptotic mass being reached approximately five days before nestlings leave the nest. Before k can be calculated it is necessary to know the general pattern of nestling development. Swift nestling growth was best fitted by the logistic model (57 of 64 nestlings). Using the tables provided by Ricklefs (1967), the appropriate growth conversion rate and k were determined from the gradient of best fit for the logistic growth curve for each nestling. k was estimated for each nestling and means for each brood and then for each treatment level were calculated following Ricklefs (1967). The mean k -growth parameter for broods with increased and reduced parasitism could then be calculated and compared.

Nestling mass and size were compared between experimental treatment on the day asymptotic mass was reached and at fledging. Fledging was deemed to have been successful once a nestling left the nest following weight regression, and the attainment of a minimum age of 30 days. Nestling mass and size on the day prior to disappearance was used for comparisons at fledging. Fledging age was considered as the date nestlings were first absent. A total of 45 nestlings fledged successfully from the colony in 2009; 20 from broods facing enhanced parasitism (mean brood size = 1.00 ± 0.97), and 25 from broods facing reduced parasitism (mean = 1.39 ± 1.19).

8.5: RESULTS

The transfer of *C. pallida* pupae and adults produced significant differences in parasite loads between the parasite-increased and parasite-reduced treatments (Figure 1; mean parasite-increased = 9.94 ± 6.26 ; mean parasite-reduced = 2.14 ± 2.24 individuals; Mann Whitney $U = 186.5$, $z = -3.54$, $P \leq 0.01$). The increased parasite loads produced here are greater in magnitude than natural levels observed in 2007 and 2008 at this site (Walker and Rotherham 2010a), by Lee and Clayton (1995) (mean \pm SD = 1.00 ± 0.2) or those produced artificially by Tompkins *et al.* (1996) (mean \pm SD = 7.39 ± 0.87).

Ninety-five eggs were laid by 38 adult pairs (mean per brood \pm SD = 2.5 ± 0.69). Mean clutch size did not differ significantly between treatments (enhanced mean: \pm SD = 2.55 ± 0.69 , $n = 20$ nests, reduced mean \pm SD = 2.44 ± 0.70 eggs, $n = 18$ nests: $t = 0.5854$, d.f. = 35, $P = 0.56$) (Figure 2). Likewise, for brood size (mean enhanced \pm SD = 1.95 ± 1.28 , $n = 20$ broods; Mean reduced \pm SD = 1.94 ± 1.21 , $n = 18$ broods: $t = 0.0137$, d.f.= 36, $P = 0.99$) (Figure 3).

No significant effect of parasitism was seen between nestlings on hatching (parasite enhanced mean mass \pm SD = 3.22 ± 0.49 grams; parasite reduced mean \pm SD = 3.10 ± 0.40 grams; $t = -1.58$, d.f. = 39, $P = 0.12$; mean wing size enhanced \pm SD = 7.89 ± 1.27 mm; reduced = 7.85 ± 1.13 mm; $t = -0.41$, d.f. = 39, $P = 0.29$).

No effect of the parasite load treatment was found on any nestling size, mass or growth measure, except mean daily mass increase which was significantly greater in broods with increased parasite loads (Table 1). Standard growth curves for all nestlings, and comparing nestlings from enhanced and reduced parasitized broods are shown for nestling mass (Figure 4), left wing length (Figure 5) and longest left primary length (Figure 6).

Table 1. Mean nestling parameters at different stages of development, given for 12 broods (25 nestlings) experiencing increased parasitism and 11 broods (20 nestlings) experiencing reduced parasitism. Special emphasis is placed upon indices of nestling growth and development. This table illustrates the wide range and number of traits examined.

Stage	Parameter	Increased levels of parasite abundance	Reduced levels of parasite abundance	Significance test
Pre-/Post Hatching	Clutch Size	2.55 (0.69)	2.44 (0.70)	$t = 0.59$, d.f. = 35, $P = 0.56$
	Brood Size	1.95 (1.28)	1.94 (1.21)	$t = 0.01$, d.f. = 36, $P = 0.99$
	Hatching mass (g)	3.22 (0.49)	3.10 (0.40)	$t = 1.58$, d.f. = 39, $P = 0.12$
	Hatching wing length (mm)	7.89 (1.27)	7.85 (1.13)	$t = 0.41$, d.f. = 39, $P = 0.29$
Asymptoty	Mass (g)	50.59 (4.29)	49.21 (4.23)	$t = 0.94$, d.f. = 43, $P = 0.35$
	Wing length (mm)	108.44 (19.80)	105.35 (18.40)	$t = 0.54$, d.f. = 43, $P = 0.59$

Outermost primary length (mm)	73.72 (18.09)	72.60 (18.09)	$t = 0.19, \text{d.f.} = 43, P = 0.85$
Tarsus length (mm)	14.14 (1.16)	13.87 (1.11)	$t = 0.79, \text{d.f.} = 43, P = 0.43$
Head length (mm)	36.94 (3.25)	37.32 (4.83)	$t = 0.30, \text{d.f.} = 43, P = 0.76$
Head breadth (mm)	29.46 (2.09)	28.43 (2.75)	$t = 1.40, \text{d.f.} = 43, P = 0.17$
Body length (mm)	143.80 (12.45)	140.61 (13.47)	$t = 0.81, \text{d.f.} = 43, P = 0.42$
Fledging			
Mass (grams)	38.84 (5.99)	37.98 (7.18)	$t = 0.43, \text{d.f.} = 43, P = 0.67$
Wing length (mm)	148.31 (13.15)	144.53 (13.85)	$t = 0.93, \text{d.f.} = 43, P = 0.36$
Outermost primary length (mm)	113.41 (13.07)	110.53 (13.77)	$t = 0.72, \text{d.f.} = 43, P = 0.48$
Tarsus length (mm)	14.19 (0.50)	14.13 (0.60)	$t = 0.62, \text{d.f.} = 43, P = 0.53$
Head breadth (mm)	30.53 (1.63)	30.62 (1.47)	$t = 0.21, \text{d.f.} = 43, P = 0.84$

	Head length (mm)	38.33 (3.13)	38.32 (2.60)	$t = 0.01$, d.f. = 43, $P = 0.99$
	Body length (mm)	161.95 (8.30)	158.81 (10.20)	$t = 1.11$, d.f. = 43, $P = 0.27$
Nestling growth	K-growth parameter	0.26 (0.04)	0.25 (0.04)	$t = 0.33$, d.f. = 42, $P = 0.74$
	t (10-90) (days)	9.69 (1.64)	9.55 (1.28)	$t = 0.30$, d.f. = 43, $P = 0.76$
	Point of inflection (days)	12.78 (2.93)	11.98 (1.63)	$t = 1.15$, d.f. = 41, $P = 0.26$
	Mean daily mass increase (g)	1.07 (0.33)	0.85 (0.31)	$t = 2.29$, d.f. = 43, $P = 0.02$

Figure 1. The population distribution (parasites per nest) of adult Louse Flies between broods with experimentally increased (open bars) and reduced (filled bars) levels of parasitism.

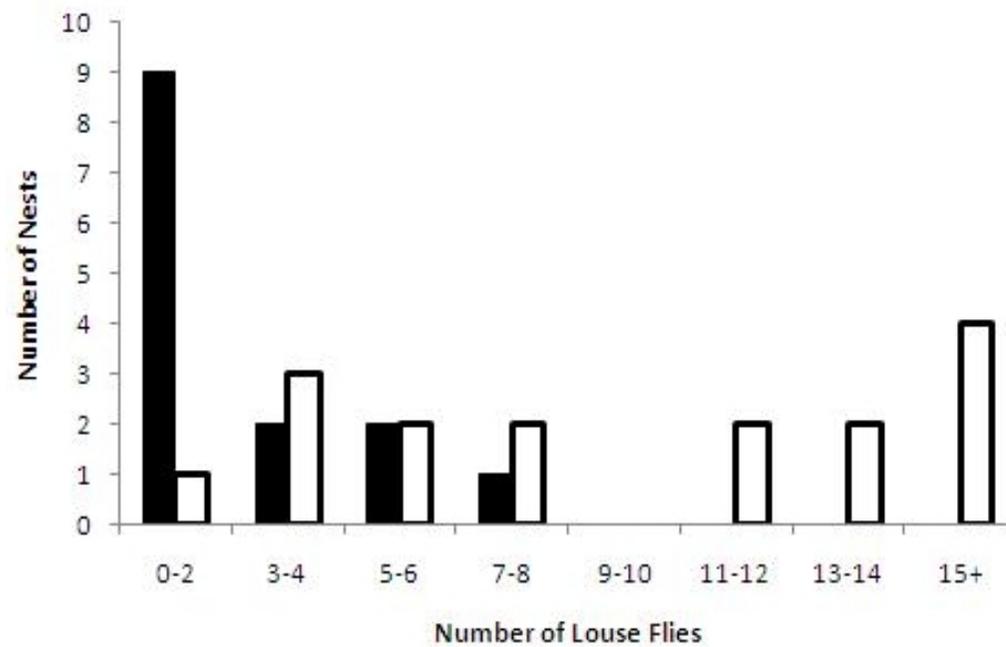


Figure 2: The number of clutches of different sizes laid by adults at nests experiencing enhanced and reduced *C. pallida* parasite loads. $n = 38$. Nests where parasite abundances were enhanced are represented by black bars ($n = 20$), those with reduced parasite loads ($n = 18$) by white bars.

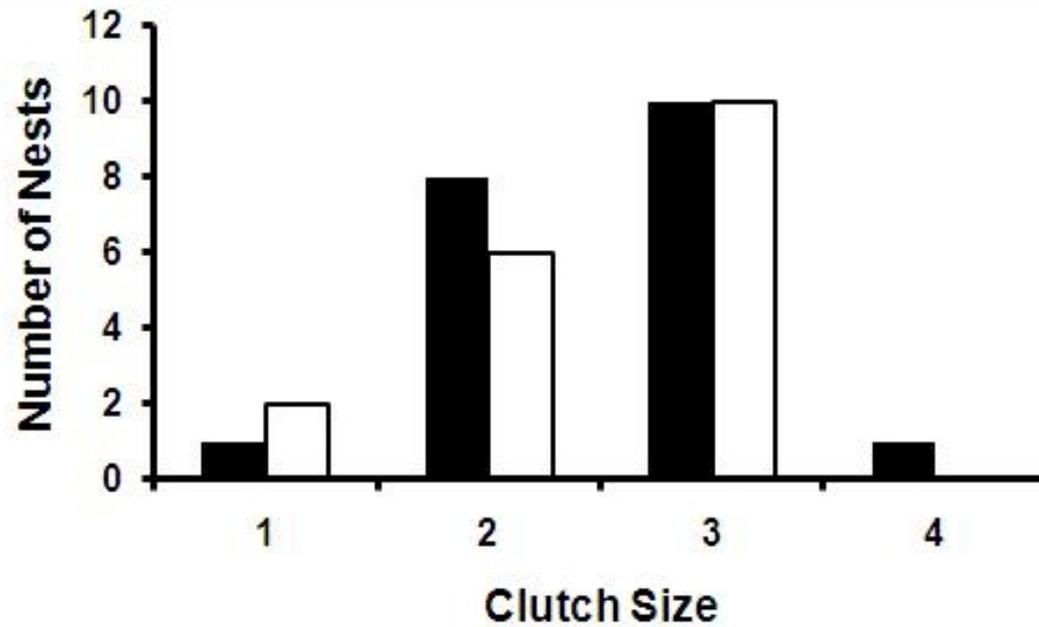


Figure 3: The number of broods of different sizes at nests with either enhanced or reduced *C. pallida* parasite abundances. Black bars represent broods where parasite abundances were enhanced ($n = 20$), white bars where abundances were reduced ($n = 18$).

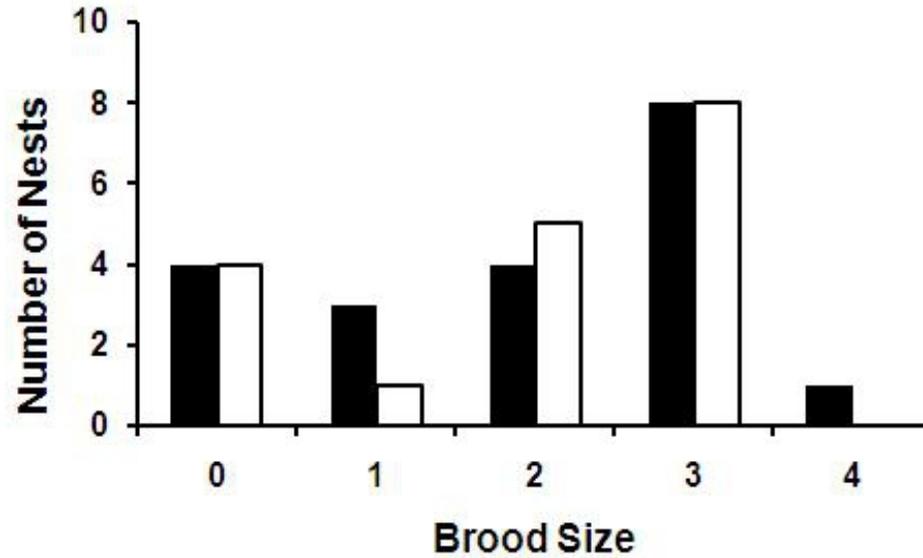
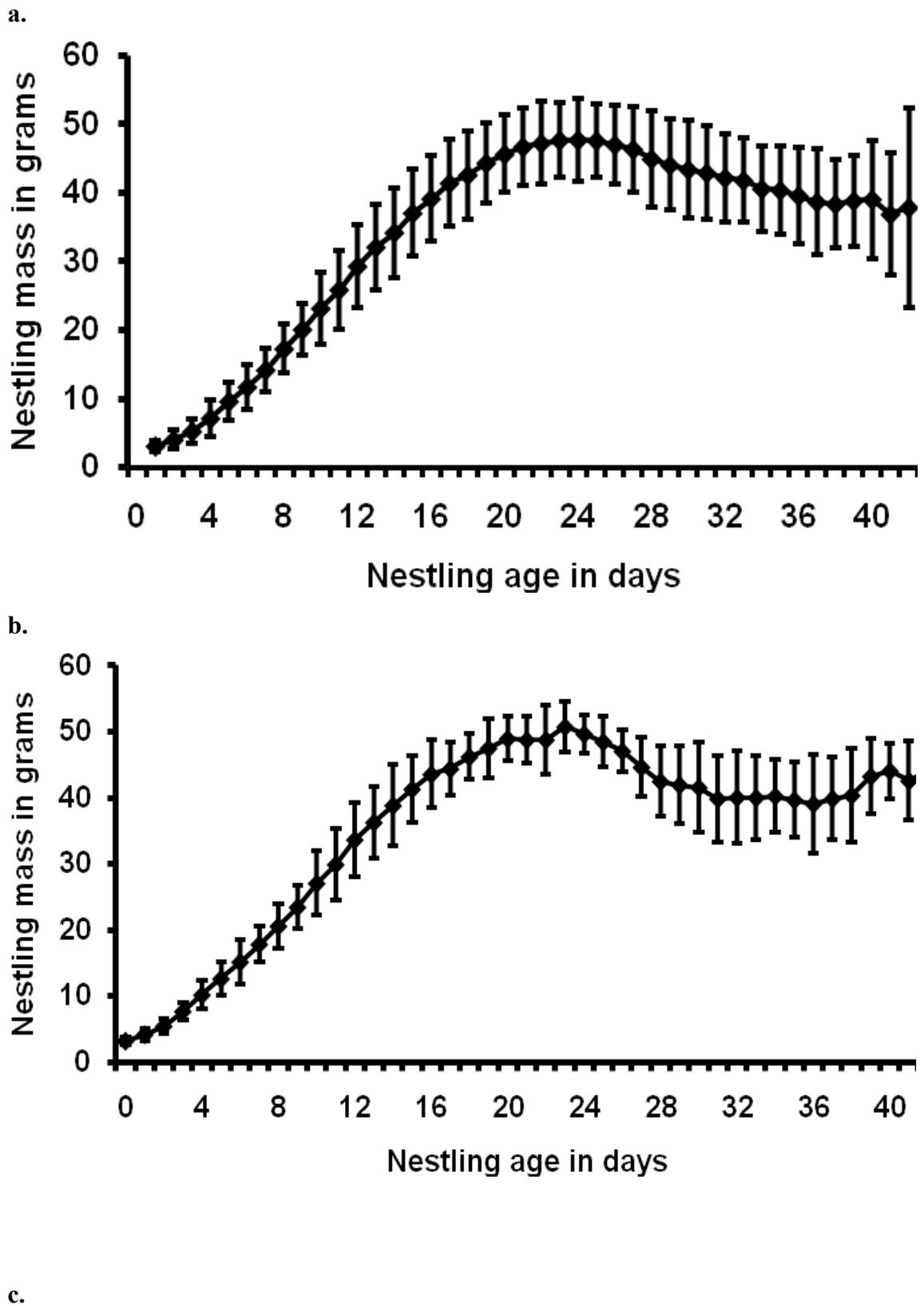


Figure 4: Growth curves showing development in nestling mass over time using data from (a) all 45 nestlings which fledged in 2009, (b) for 25 nestlings experiencing enhanced levels of parasitism, and (c) 20 nestlings experiencing reduced levels of parasitism. Error bars indicate levels of standard deviation.



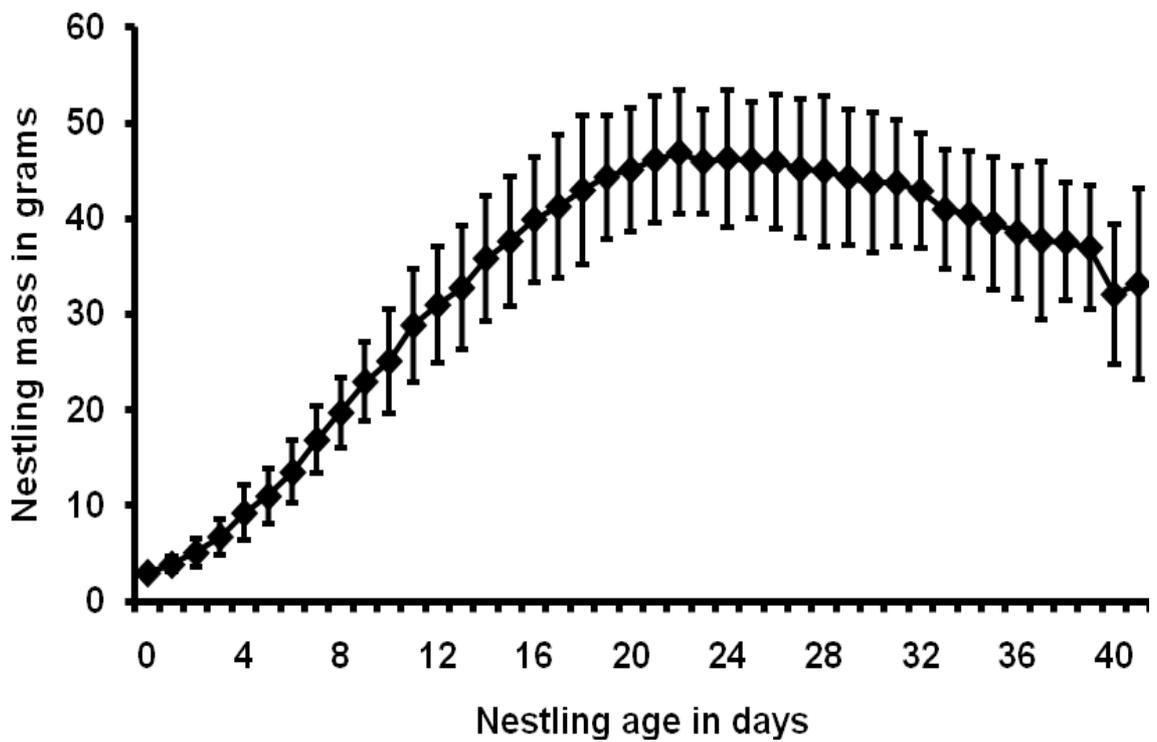
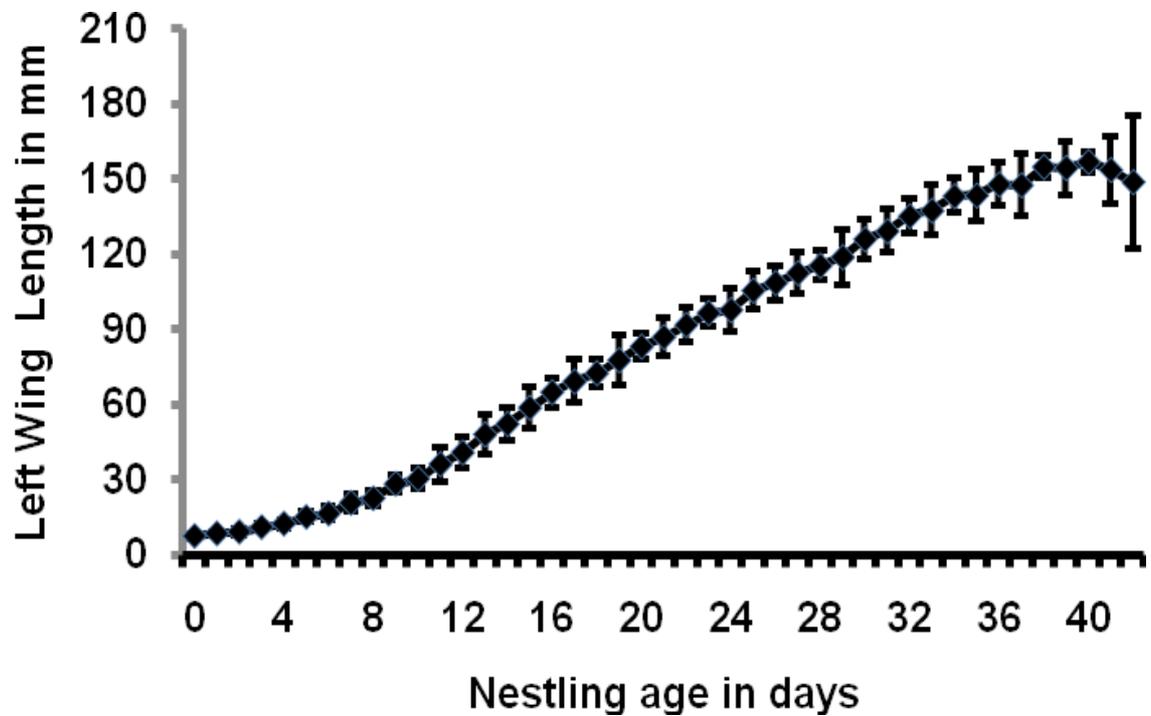
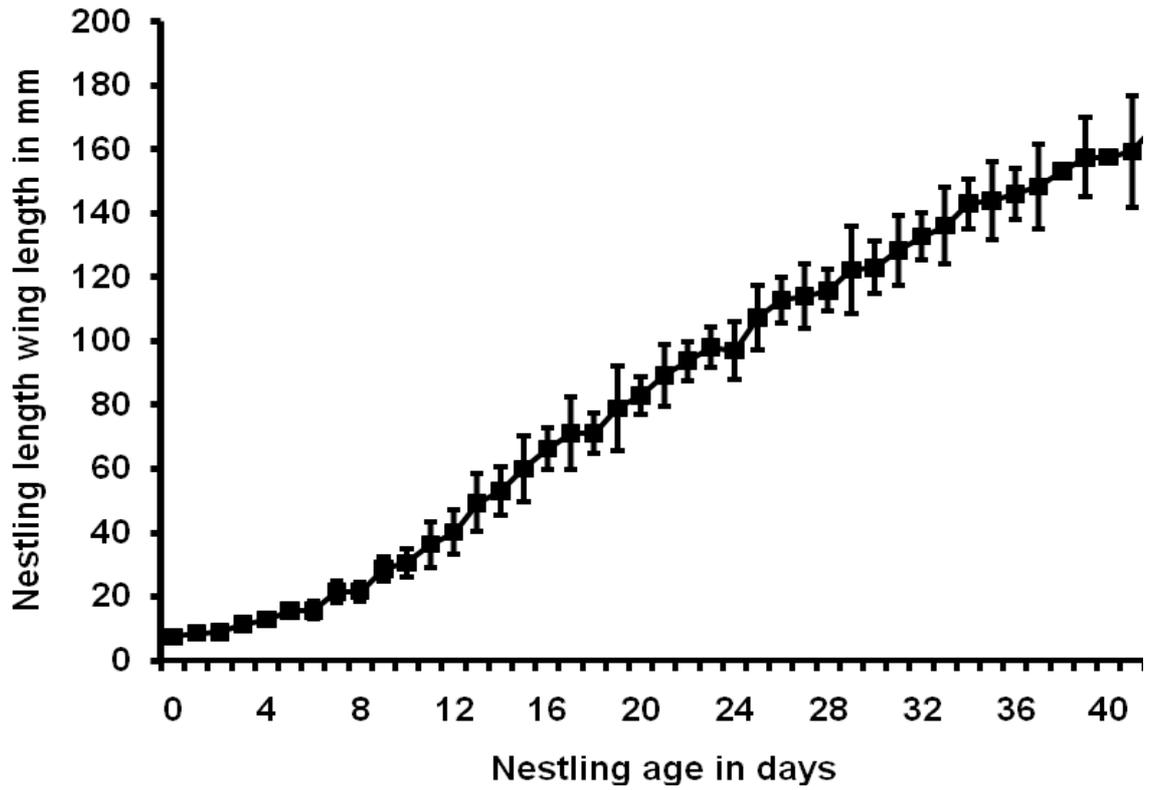


Figure 5: The mean left wing lengths for (a) all 45 nestlings which subsequently fledged, (b) those 25 nestlings from broods facing enhanced levels of *C. pallida* parasitism, (c) those 20 nestlings from broods facing reduced levels of *C. pallida* parasitism. SD indicated by error bars.

a.



b.



c.

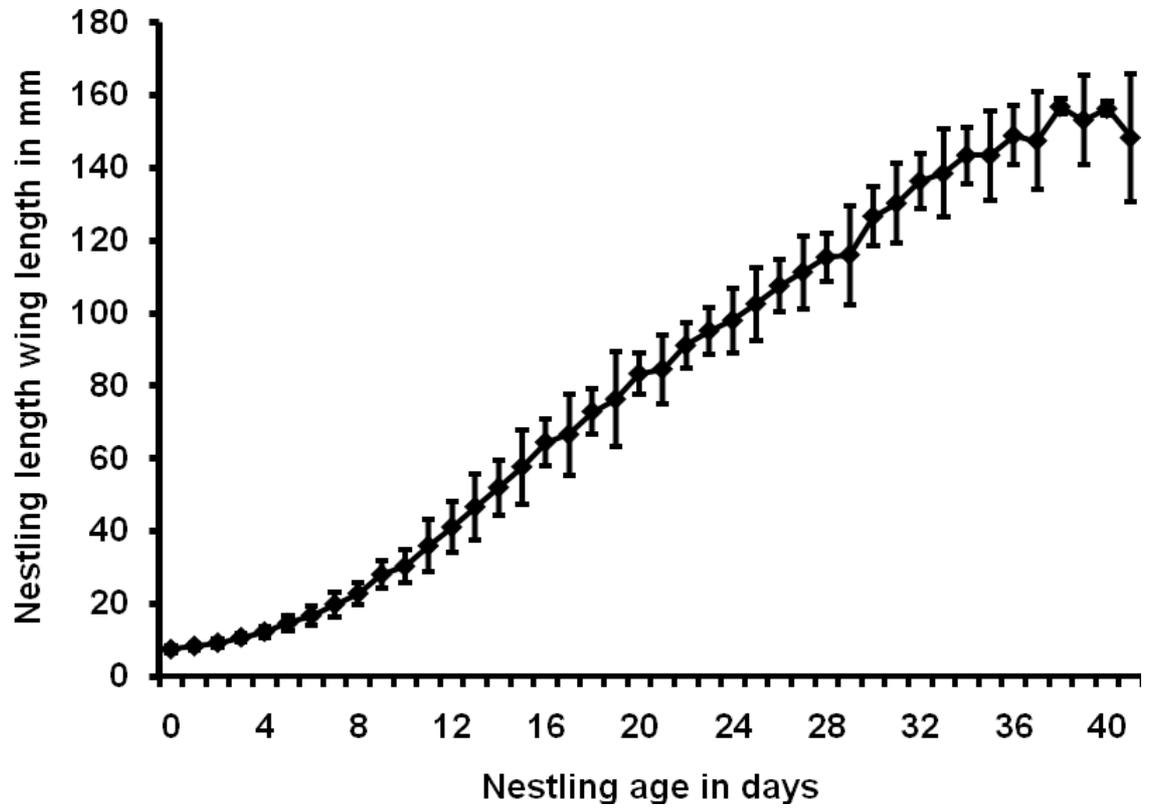
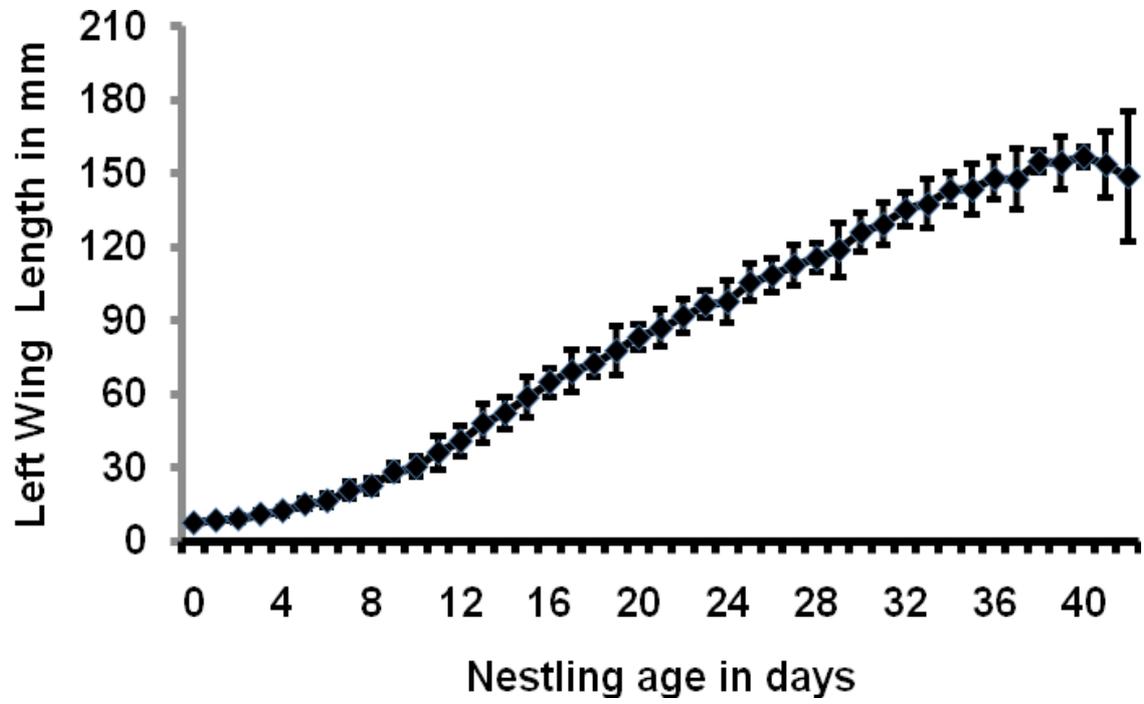
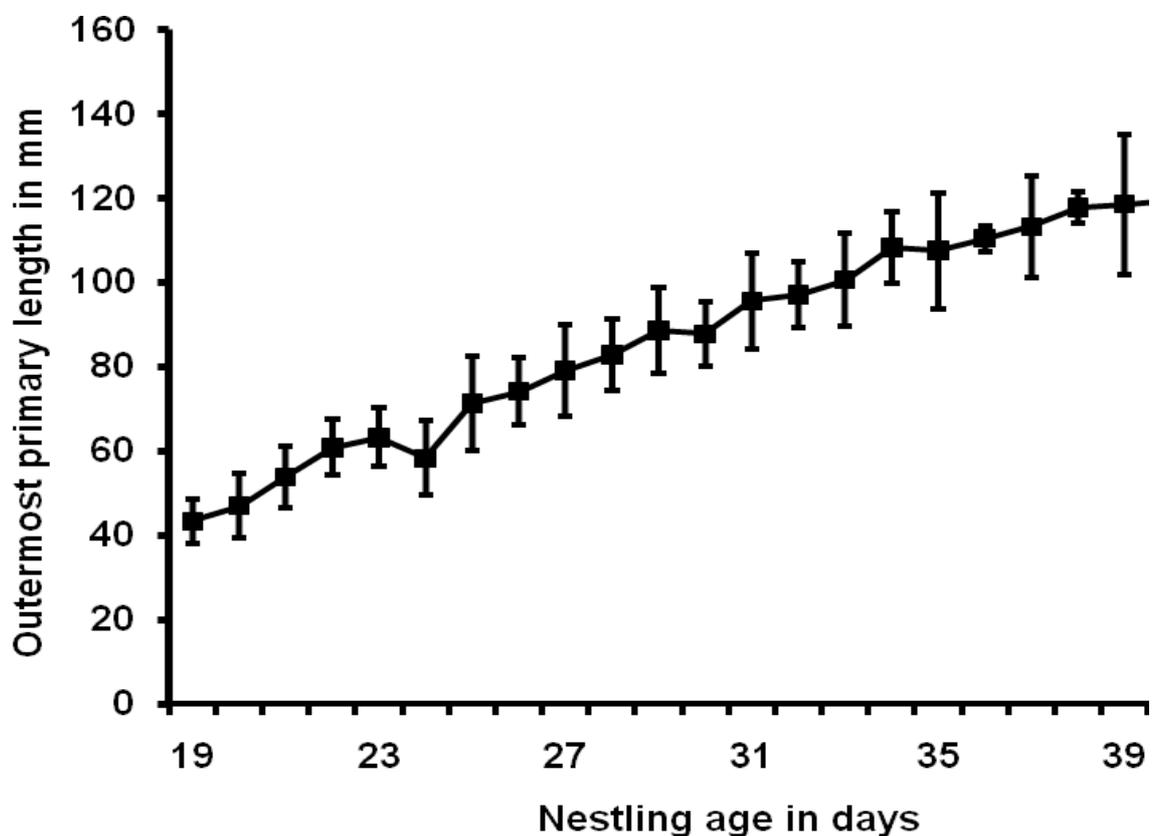


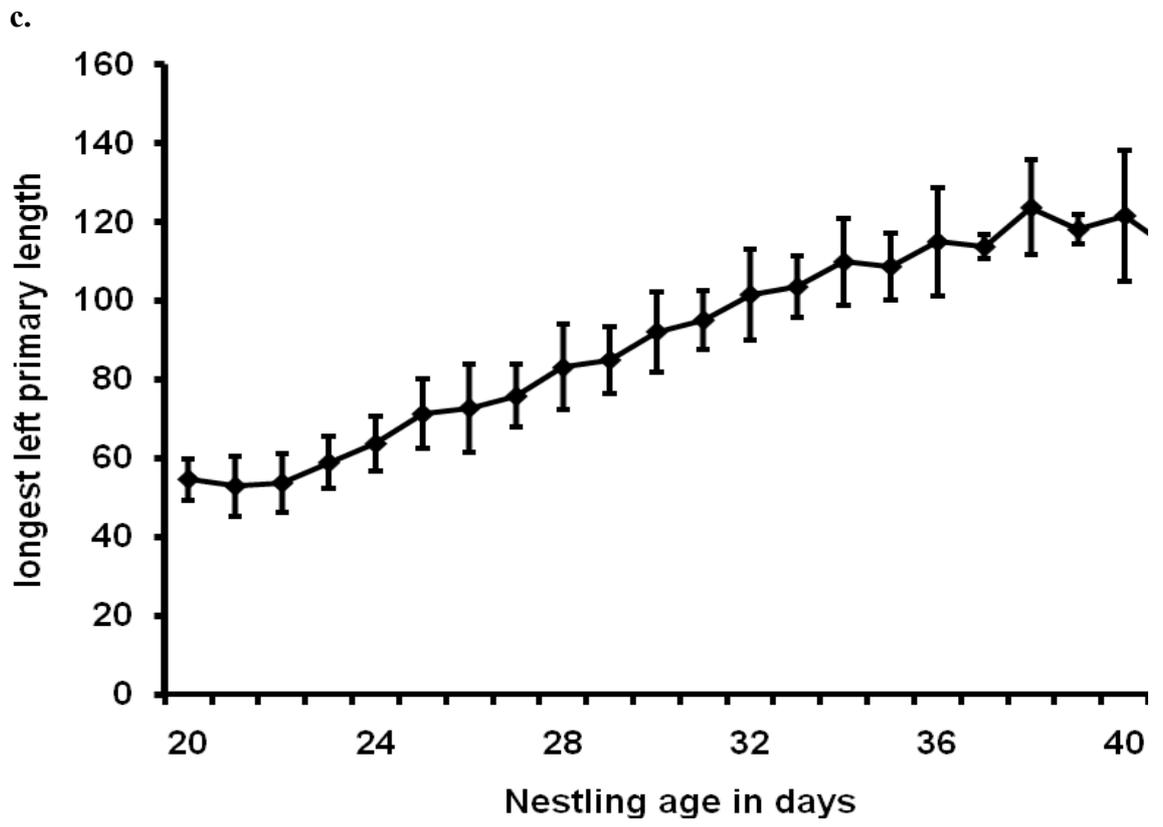
Figure 6: The mean length of the longest left primary feather for (a) all 45 nestlings which subsequently fledged, (b) those 25 nestlings experiencing enhanced levels of parasitism, (c) those 20 nestlings facing reduced levels of parasitism. SD indicated through error bars.

a.



b.





8.6: DISCUSSION

No reduction in any measure of reproductive performance was found in broods experiencing experimentally increased parasitism, when compared with those experiencing reduced parasitism. Although contrary to expectation, these results confirm findings of other studies of this host-parasite system (Hutson 1981, Lee and Clayton 1995, Tompkins *et al.* 1996, Walker and Rotherham 2010b). The results are surprising as the parasite abundance observed at this site is greater than those seen in previous studies and thus parasite pressure might have been expected to lead to clear detrimental effects.

These results contrast sharply with investigations of closely related host-parasite relationships in Alpine Swifts (Bize *et al.* 2003, Bize *et al.* 2004b, Bize *et al.* 2005). Why detrimental effects should be so apparent within the one system and not the other is unclear, but may be related to differences in parasite movement between nests and parasitic abundances. For example, Bize *et al.* (2004a) had parasite abundances at reduced parasite nests of 7 ± 1 adults per nestling, and 17 ± 1 per nestling at enhanced nests and observed horizontal movement of parasites between nests.

Lee and Clayton (1995) postulated that reduced parasite virulence had evolved due to parasite fitness becoming related to host success. The obligatory nature of the relationship, monoxenous diet, and predominately vertical transmission exhibited by *C. pallida* parasites indicate that this may have occurred. For example, there may be selection pressure to reduce impacts on nestling survival and fledging success, as nestling swifts must be capable of sustained flight immediately on fledging. Alternatively the costs of parasitism may be being expressed upon other traits not examined. Alpine Swifts are able facultatively to modulate development in response to poor weather conditions and compensate later during development and such compensatory growth may also occur in response to parasitism (Bize *et al.* 2004a).

Power to detect effects may have been limited in this study as sample sizes were small, as has also been the case in previous studies (Lee and Clayton 1995, Tompkins *et al.* 1996). However, because larger swift colonies with easy access are rare, opportunities to obtain larger samples may be few.

In conclusion, no costs of parasitism by Louse Flies on the reproductive success of Common Swifts were found. Further studies should investigate whether parasitic biological traits or deferment of costs influences parasitic virulence.

8.7: CHAPTER SUMMARY

The results of the investigation composing this chapter are:

- Manipulation of adult insects abundances resulted in the successful creation of broods experiencing either experimentally high or low levels of infestation.
- No difference in the expression of a variety of host life-history traits of pertinence to reproductive success, and in particular to nestling growth and development, were seen between empirical regimes.

These results show that *A. apus* facing higher levels of *C. pallida* infestation do not demonstrate lower reproductive success, and this indicates that *C. pallida* has no virulent effect upon those traits examined which were indicative of host reproductive success. This is contrary to expectations and does not support the dissertation hypothesis that *C. pallida* is parasitic.

This conclusion is justified because the host life-history traits considered, are known to be of prime importance in determining individual lifetime fitness. Therefore effects of parasitism would be thought to be readily ascertainable if they occurred. This would be expected to be especially the case for this study species, as Common Swift must be capable of full flight upon fledging as it becomes immediately independent and is totally dependent upon an aerial diet.

These results extend the existing knowledge of *C. pallida* parasitism considerably. It confirms results of others studies. It extends the research on post-natal growth begun by Weitnauer (1947) and Lack and Lack (1951). The inter-relationship between factors influencing nestling growth are complex and such additional data helps elucidate general pattern influencing swift post natal development. Many aspects of nestling growth, and the calculation of several growth parameters here used, was performed for the first time for this species in this study.

8.8: CHAPTER REFERENCES

- BIZE, P., ROULIN, A., BERSIER, L.F., PFLUGER, D. and RICHNER, H. (2003). Parasitism and developmental plasticity in Alpine Swift nestlings. *Journal of Animal Ecology*, **72**, 633-639.
- BIZE, P., ROULIN, A. and RICHNER, H. (2004a). Parasitism, developmental plasticity and bilateral asymmetry of wing feathers in Alpine Swift (*Apus melba*) nestlings. *Oikos*, **106**, 317-323.
- BIZE, P., ROULIN, A., TELLA, J., BERSIER, L.F. and RICHNER, H. (2004b). Additive effects of ectoparasites over reproductive attempts in the long-lived Alpine Swift. *Journal of Animal Ecology*, **73**, 1080-1088.
- BIZE, P., ROULIN, A., TELLA, J. and RICHNER, H. (2005). Female-biased mortality in experimentally parasitized Alpine Swift (*Apus melba*) nestlings. *Functional Ecology*, **19**, 405-413.
- HUTSON, A.M. (1981). The population of the Louse Fly, *Crataerina pallida* (Diptera, Hippoboscidae) on the European Swift, *Apus apus* (Aves, Apodidae). *Journal of Zoology, London*, **194**, 305-316.
- LACK, D. and LACK, E. (1951). The breeding biology of the swift. *A. apus*. *Ibis*, **93**, 501-546.
- LEE, P.L.M. and CLAYTON, D.H. (1995). Population biology of swift (*Apus apus*) ectoparasites in relation to host reproductive success. *Ecological Entomology*, **20**, 43-50.
- MØLLER, A.P. (1989). Parasites, predators and nest boxes: Facts and artefacts in nest box studies of birds. *Oikos*, **56**, 421-423.
- PRICE, P.W. (1980). *Evolutionary biology of parasites*. Princeton: Princeton University Press.
- RICKLEFS, R.E. (1967). A graphical method of fitting equations to growth curves. *Ecology*, **48**, 978-983.
- RICKLEFS, R.E. (1968). Patterns of growth in birds. *Ibis*, **110**, 419-451.
- SVENSSON, L. (1992). *Identification guide to European Passerines*. British Trust Ornithology/ Privately published.
- TOMPKINS, D.M., JONES, T. and CLAYTON, D.H. (1996). Effect of vertically transmitted ectoparasites on the reproductive success of Swifts (*Apus apus*). *Functional Ecology*, **10**, 733-740.
- WALKER, M.D. and ROTHERHAM I.D. (2010a). Characteristics of *Crataerina pallida* (Diptera: Hippoboscidae) populations; a nest ectoparasite of the common swift

(Aves: Apodidae). *Experimental Parasitology*, **126**, 451-455.

WALKER, M.D. and ROTHERHAM, I.D. (2010b). The breeding success of Common Swifts *Apus apus* is not correlated with the abundance of their Louse Fly *Crataerina pallida* parasites. *Bird Study*, **57**, 504-508.

WEITNAUER, E. (1947). Am Neste des Mauerseglers, *A. apus apus* (L.). *Der Ornithologische Beobachter*, **44**, 133-182.

**CHAPTER NINE:
PARENTAL INVESTMENT IN RESPONSE TO
PARASITISM**

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PARENTAL INVESTMENT IN RESPONSE TO PARASITISM

The following investigation has been accepted for publication by the ornithological journal *Bird Study*;

- WALKER, M.D. and ROTHERHAM, I.D. (2011). No evidence of increased parental investment in response to parasitism by Common Swifts. *Bird Study*. (In press.)

9.1: CHAPTER AIMS

The aim of this chapter is to determine if parent swifts increase their levels of parental investment to nestlings experiencing greater *C.pallida* parasitic abundances. The specific objective is to:

- To test the parental compensation hypothesis.

The reason for this objective is that parent birds may be bearing the costs nestlings are expected to experience as a result of the resource removal from *C. pallida*. This may thus account for the previously observed apparent lack of detriment to hosts as a result of such parasitism found in previous studies and earlier in this dissertation in chapters 7 and 8. The parental compensation hypothesis proposes that parent birds may mediate the costs their offspring face as a result of parasitism by increasing levels of parental investment (Moss and Camin 1970).

The method to be used will involve recording the length and rate of parental visits to broods with experimentally raised or lowered levels of *C.pallida* parasitism. According to the parental compensation hypothesis, parental visitation rates will be greater to those broods facing enhanced parasitism. This aspect of parasitism has not been studied within this host-parasite system.

9.2: CHAPTER ABSTRACT

Parasitism is known to cause substantial costs to avian nestling hosts in the form of increased mortality or decreased rates of development. The parental compensation hypothesis postulates that parent birds may attempt to mediate these costs by increasing

provisioning to more heavily parasitized nestlings thus accounting for the lack of parasital effect sometimes seen in host-parasite studies. Whether parental compensation occurs in Common Swifts was examined. Visitation rates and lengths to nestling experiencing either enhanced or reduced parasite pressures was examined. Common Swifts did not increase levels of parental care in response to increased levels of Louse Fly parasitism, as would have been expected according to the parental compensation hypothesis. The expected costs of parasitism may thus be being borne upon other traits or may not be present indicating that this parasite has become benevolent.

9.3: INTRODUCTION

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 and 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 and Richner 1997). However the empirical evidence for parental compensation is limited and originates almost entirely from nest box studies of tits (Tripet and 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 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 and Rotherham 2010a). *C. pallida* life-history traits were investigated earlier in this dissertation, and the features found, including the high levels of parasite abundance, high levels of host prevalence, and high level of parasite aggregation are highly indicative that this species should be particularly pugnacious. Therefore the impact of such parasitism would be expected to be great. Despite this no detrimental effect from such infestation has been observed upon hosts in a number of studies (Lee and Clayton 1995, Tompkins *et al.* 1996, Walker and Rotherham 2010b).

Parental compensation may account for the apparent lack of parasitic virulence observed in these studies and in chapters 7 and 8 of this dissertation. Swift life-history traits make the use of such a strategy particularly likely. Swift nestlings are altricial and require substantial levels of parental care. Photographs 1 and 2 show parent swifts provisioning nestlings. As reported in chapter 1, swift breeding is severely time constrained. Vagaries in weather and food abundance make nestling success particularly precarious (Lack and Lack 1951, Thomson *et al.* 1996). Any mechanism which 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 enhance overall fitness.

9.4: METHOD

The possibility of parental compensation in response to parasitism was investigated by studying 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 at a colony within a highway bridge spanning the Bigge reservoir at Olpe, Germany (51° 04' 00" N, 07° 81' 00" E).

Nests were randomly allocated into one of two experimental treatment groups as described in chapter 6. 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 the 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, 6 with elevated and 5 with reduced levels of *C. pallida* parasitism. The average brood size at all these nests was 2.72 ± 0.46 , the average brood size at parasitized nests being 3 ± 0.00 , and at reduced parasitized nests 3.2 ± 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 (E.L.V. Elektronik AG, Leer). The number of adult *C. pallida* parasites at study nests was ascertained on a daily basis as described in Walker and Rotherham (2010a). Accurate surveying of parasite populations was possible as parasites are closely associated with nests; have a relatively large size (of approximately one centimetre 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 levels of parasitic pressure was calculated following Lee and Clayton (1995) and Tompkins *et al.* (1996).

Recordings were made on alternate days, with a total of 18 days spanning a total of 32 days of the swift breeding season. Recording was conducted over two sessions running from 8:00 to 12:00 and from 13:00 to 15:00 daily. A total of 2,226 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 to 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 were due to other factors such as differences in parasitism rather than through differences in the times of day or weather experienced by each nest.

9.5: RESULTS

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 (see figure 1 in chapter 6). The maximum number of *C. pallida* seen per nest on any one occasion during the breeding season may provide a reliable index of parasitic pressure (Lee and Clayton 1995). The maximum parasitic load seen at those nests studied with enhanced levels of parasitism (mean = 10.17 ± 5.10) was significantly higher than that seen at parasite reduced nests (mean = 3 ± 2.53) ($U = 3.05$, $z = 2.01$, $P \leq 0.05$). Additionally the mean number of *C. pallida* seen per nest over the entire season was calculated and this was also significantly higher at parasitized (mean = 3.41 ± 1.27) than non parasitized nests (mean = 0.21 ± 0.23) ($U = 0$, $z = 2.65$, $P \leq 0.05$). In comparison the mean parasite load at non manipulated nests was 3.72 ± 2.65 at 47 nests in 2007 , and 4.21 ± 3.09 at 37 nests in 2008 (Walker and 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 (Figure 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 (Figure 2). This difference was, unlike that seen for mean hourly visitation rate, statistically significant ($U = 3$, $z = 2.1$, $P \leq 0.05$). 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 in feeding young at reduced parasitized nests, than at nests with enhanced parasitism, where it was 26.82%. Nestling care composed 9.56% of parental time at reduced and 15.64% at enhanced nests.

Figure 1: The mean hourly parental visitation rate at nests with enhanced and reduced levels of parasitic abundance. Parasite enhanced nests in black, parasite reduced nests in white. Error bars indicate standard deviation.

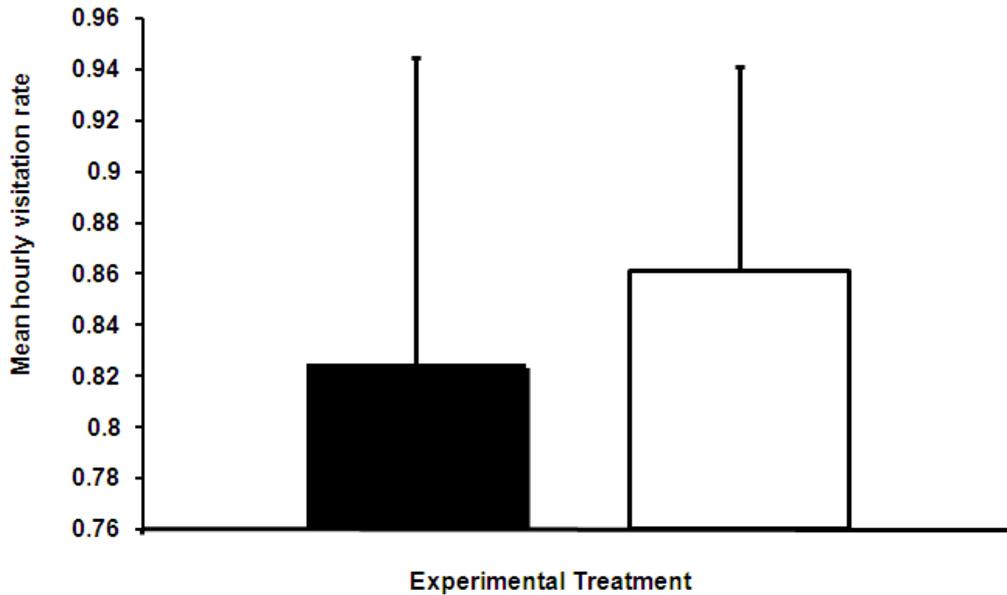
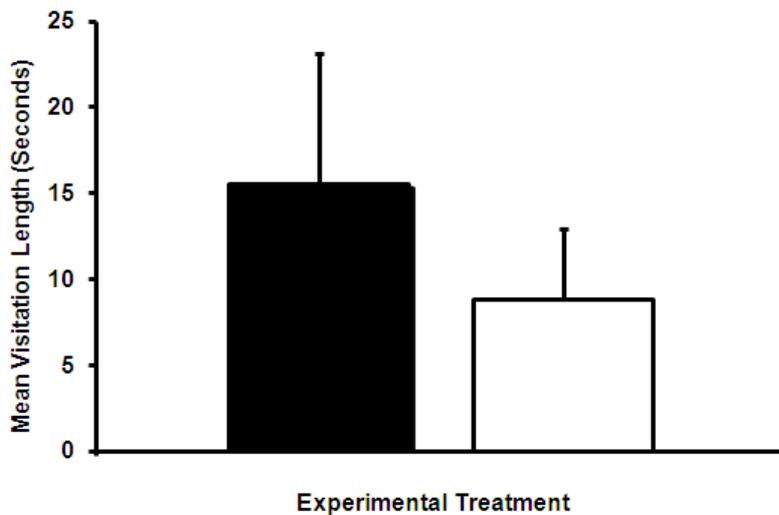


Figure 2: The mean visitation length by parents at nests with enhanced and reduced abundances of *C. pallida* parasites. Parasite enhanced nests in black, parasite reduced nests in white. Error bars indicate standard deviation.



9.6: DISCUSSION

In summary, no convincing evidence of differences in the level of parental provisioning between nests experiencing different levels of parasitism were 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 made 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 upon a closely related host-parasite system between the Alpine Swift *Apus melba*, and its associated Louse Fly species has found evidence of detrimental effects (e.g. 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 and Camin (1970). Although no negative effect of bird fleas *Ceratophyllus gallinae* were found on nestling Blue Tits *Parus caeruleus*, parents were found to increase their rates of provisioning where they were present (Tripet and 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 (Banbura *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 is difficult.

This investigation is limited in that only a small number of nests could be examined. Additional nests could not be studied due 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. However, 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 however extremely useful in that parental compensation was not readily apparent thus indicating that parental compensation may not be occurring. It also raises awareness of this hypothesis, maybe prompting investigation of these themes by others. Hopefully, more comprehensive study of parental care at this site in further years will result in larger samples being obtained.

The study illustrates the wide range of host traits that can be influenced through parasitism and of the pernicious influence parasites may have. The clearly parasitic nature of *C. pallida* observed in chapter 2 and the features of *C. pallida* population structure which are parasitic in nature seen in chapter 3 should lead to clear costs to hosts. These costs may be borne by various host life-history traits such as 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 conjunction with poor weather periods and thus lead to the identification of clear parasitic costs during adverse conditions. Even in host-parasitic systems where the effects of parasitism are not apparent, their absence should not be assumed before all ways in which they may be being borne are explored.

Photograph 1: An adult swift feeding a nestling at the nest. Photographs courtesy of Erich Kaiser, Frankfurt, 2010.



Photograph 2: The transfer of food from parent to nestling. The nestlings here are approximately 12 days old.



9.7: CHAPTER SUMMARY

There were no differences in the rate of parental visitation to offspring facing either experimentally enhanced or reduced levels of *C. pallida* parasitism. Neither was there a notable difference in the length of feeding visits. Thus it can be concluded that adult swifts do not increase levels of parental care in response to higher levels of parasitism.

The results do not support the tenets of parental compensation hypothesis that parents bear the costs of their offspring's parasitism through increased parental care. The provision of extra or additional care to parasitized offspring would be a significant additional cost to breeding swifts and a notable disadvantage of parasitism. It appears that the costs of *C. pallida* parasitism to nestlings are therefore not being deferred or masked through increased care by parents.

The number and length of parental feeding bouts made to offspring is a reliable indicator of levels of parental care. That no increase in the number or length of such visits was apparent in the face of increased parasitism indicates that other variables are of more importance in influencing parental investment. Weather and insect abundance may be more important factors limiting the parental feeding.

This study, although restricted in extent, is useful, as previously only a limited number of experimental studies have tested this hypothesis. This aspect of swift life-history might have been thought especially likely to demonstrate such costs in this way, due to the dependence of nestling success on parental provisioning rates. This facets of parasitism had previously not been investigated in this study system.

9.8: CHAPTER REFERENCES

BAÑBURA, J., PERRET, P., BLONDEL, J., THOMAS, D.W., CARTAN-SON, M. and LAMBRECHTS, M.M. (2004). Effects of *Protocalliphora* parasites on nestling food composition in Corsican Blue Tits *Parus caeruleus*: consequences for nestling performance. *Acta Ornithologica*, **39**, 93-103.

BOUSLAMA, Z., LAMBRECHTS, M.M., ZIANE, N., DJENIDI, R.D. and CHABI, Y. (2002). The effect of nest ectoparasites on parental provisioning in a north-African population of the Blue Tit *Parus caeruleus*. *Ibis*, **144**, E73-E78.

BIZE, P., ROULIN, A., TELLA, J., BERSIER, L.F. and RICHNER, H. (2004). Additive

- effects of ectoparasites over reproductive attempts in the long-lived Alpine Swift. *Journal of Animal Ecology*, **73**, 1080-1088.
- COMBES, C. (2001). *Parasitism. The ecology and evolution of intimate interactions*. Chicago University Press, Chicago.
- HURTREZ-BOUSSÈS, S., RENAUD, F., BLONDEL, J., PERRET, P. and GALAN, M.J. (2000). Effects of ectoparasites of young on parents' behaviour in a Mediterranean population of blue tits. *Journal of Avian Biology*, **31**, 266-269.
- KEMPER, H. (1951). Beobachtungen an *Crataerina pallida* Latr. und *Melophagus ovinus* L. (Diptera, Pupipara). *Zeitschrift für Hygiene (Zoologie)*, **39**, 225-259.
- LACK, D. and LACK, E. (1951). The breeding biology of the swift, *Apus apus*. *Ibis*, **93**, 501-546.
- LEE, P.L.M. and CLAYTON, D.H. (1995). Population biology of swift (*Apus apus*) ectoparasites in relation to host reproductive success. *Ecological Entomology*, **20**, 43-50.
- MOSS, W.W. and CAMIN, J.H. (1970). Nest parasitism, productivity, and clutch size in purple martins. *Science*, **168**, 1000-1003.
- THOMSON, D.L., DOUGLAS-HOME, H., FURNESS, R.W. and MONAGHAN, P. (1996). Breeding success and survival in the common swift *Apus apus*: a long-term study on the effect of weather. *Journal of Zoology, London*, **239**, 29-38.
- TOMPKINS, D.M., JONES, T. and CLAYTON, D.H. (1996). Effect of vertically transmitted ectoparasites on the reproductive success of Swifts (*Apus apus*). *Functional Ecology*, **10**, 733-740.
- TRIPET, F. and RICHNER, H. (1997). Host responses to ectoparasites: Food compensation by parent blue tits. *Oikos*, **78**, 557-561.
- WALKER, M.D. and ROTHERHAM, I.D. (2010a). Characteristics of *Crataerina pallida* (Diptera: Hippoboscidae) populations; a nest ectoparasite of the Common Swift, *Apus apus* (Aves: Apodidae). *Experimental Parasitology*, **126**, 451-455.
- WALKER, M.D. and ROTHERHAM, I.D. (2010b). The breeding success of Common Swifts *Apus apus* is not correlated with the abundance of their Louse Fly *Crataerina pallida* parasites. *Bird Study*, **57**, 504-508.

**CHAPTER TEN:
DISSERTATION DISCUSSION:
IS THE LOUSE FLY *C. PALLIDA* PARASITIC?**

CHAPTER AIMS	10.1
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DISSERTATION DISCUSSION:

IS THE LOUSE FLY *C. PALLIDA* PARASITIC?

10.1: CHAPTER AIMS

A number of interesting discoveries were successfully made during the course of research into *C. pallida*. This chapter aims to summarize these and to conclude whether *C. pallida* successfully fulfils the criteria of Price's (1977) definition of a parasite. Is the Louse Fly a parasite? The specific objectives are:

- To summarize the results and discoveries about *C. pallida* life-history, especially those which may be influencing the effect it has upon its swift host.
- To assess whether there is any evidence that *C. pallida* influences *A. apus* fitness.

The following will be discussed:

- Explanations accounting for the life-history traits exhibited by *C. pallida* and how these could be influencing its virulence will be formulated.
- Limitations of the empirical investigations conducted both here and by others will be discussed. Ideas for improvement will be suggested.
- Further potentially productive avenues of research into *C. pallida* will be identified.
- Finally, a decision will be made as to whether the research question and investigation hypothesis around which the dissertation is structured have been answered or supported. Does *C. pallida* demonstrate parasitic traits? Does *C. pallida* influence host fitness? Is *C. pallida* parasitic according to Price's definition?

This discussion is necessary because the research presented throughout the course of the dissertation has become increasingly complex. An overview of what has been discovered and its implications is therefore needed to provide a clear summary of the results.

10.2: RESULTS OF EACH CHAPTER

The important results and discoveries of each investigation are stated. How these results complement existing knowledge and their possible implications are discussed. Limitations of previous research and possible methods of improvement are discussed. The overall findings of the dissertation are then summarized.

Chapter 2: The Common Swift Louse Fly

The literature review examining *C. pallida* life-history found that this species exhibits biological features clearly indicative that it is parasitic and has a parasitic life-style. Evidence that *C. pallida* removes considerable resources from its swift hosts was found. *C. pallida* demonstrates a high level of physical specialization towards a parasitic life-style. The relationship with *A. apus* is obligate. These are characteristic features typically exhibited by a species that is parasitic.

This was the first time such a review has been conducted on *C. pallida* and as such it is a significant contribution towards understanding this host-parasite system. Previously information about this parasite had been disparate in nature and published in a variety of languages. Research into *C. pallida* life-history was mostly of a substantial age. This hindered a good understanding of this host-parasite system.

Numerous physical and ecological adaptations indicating *C. pallida* has a parasitic life-style were identified. These included possession of physical features facilitating resource removal from hosts, adaptations aiding its retention on hosts, and the close synchrony of its life-cycle with that of swifts. The review identified many typically parasitic features of *C. pallida* population structure, for example the high but unexplained levels of parasite prevalence (Hutson 1981). There are conflicting reports as to the deleterious impact of *C. pallida* upon its hosts (for; Büttiker 1944, Hutson 1981; against: Lee and Clayton 1995, Tompkins *et al.* 1996). The paucity of knowledge about this Louse Fly and this particular host-parasite system meant that the scope of the review was limited, but suggested further investigation of *C. pallida* biology is necessary. This review supports the hypothesis that *C. pallida* is parasitic as it shows this species possesses the features indicative of having a parasitic mode of life and that it should therefore have a significant detrimental effect upon its host.

Chapter 3: Characteristics of *C. pallida* populations

The population structure of *C. pallida* was successfully investigated. It was discovered that *C. pallida* exhibits high levels of population aggregation, has high rates of prevalence upon hosts and exerts a high level of parasite pressure. An association of parasite abundance with nestling presence was established, with larger broods containing more *C. pallida* adults. Populations were discovered to decline throughout the swift breeding period. The sexual composition of populations was also discovered, with populations being found to be heavily female biased but changes in sexual composition were found to occur over time..

The levels of parasite prevalence and population aggregation observed were considerably higher than those reported for *C. pallida* by Lee and Clayton (1995) and by Tompkins *et al.* (1996), and by McClure (1984) and Tella and Jovani (2000) in other Hippoboscids. The strongly skewed sex ratio supports the observations of Hutson (1981) and Kemper (1951), however, the variations in population sexual composition over time were discovered here for the first time. This is the first time that the parasite load has been found to be associated with nestling presence and brood size.

Parasitic abundance was also found to be much higher than that seen by Lee and Clayton (1995) and Tompkins *et al.* (1996). Differences in parasite load depending on the method used in its calculation were found. Measures of parasite load based on daily mean *C. pallida* abundance were found to provide a more accurate way of measuring parasitic pressure.

These results have large implications for studies of *C. pallida* parasitic efficacy. The higher levels of parasite abundance, prevalence and aggregation, suggest that previous studies may have falsely gauged parasitic pressure and thus obtained an unrealistic impression of the effect *C. pallida* has on hosts. This may account for the lack of parasite virulence previously observed.

The population parameters of *C. pallida* are in accordance with those typically seen in parasitic species and thus suggest that *C. pallida* is likewise parasitic in nature. This further supports the overall hypothesis that *C. pallida* is parasitic.

Chapter 4: Inter-nest Dispersal

Marking of *C. pallida* adults led to the discovery that they move between host nests. This discovery was unexpected and is contrary to previous assumptions that such movements do not occur (e.g. Lee and Clayton 1995). Previous studies have assumed that *C. pallida* transfers itself exclusively between adult and offspring hosts (e.g. Lee and Clayton 1995, Tompkins *et al.* 1996). Bize *et al.* (2003) noted anecdotally the possible occurrence of parasite self-mediated inter-nest dispersal by *C. melbae*. This investigation was the first time that dispersal by adult *C. pallida* between *A. apus* nests had been studied. It is also only the second investigation examining parasitic transmission by any Hippoboscid parasite altogether. This was also the first time this method of marking parasites had been used and thus is an important development in the study of this and similar insects.

This discovery is of importance as the mode of dispersal influences parasitic virulence. Where transmission is mainly horizontal transmission high levels of virulence can develop as parasite fitness is not connected to that of hosts. Thus the discovery that *C. pallida* transmission is probably predominately horizontal in nature would lead to the supposition that *C. pallida* could develop high levels of virulence. Previously the assumed vertical nature of transmission was thought to favour and explain the reduced parasite virulence observed (Lee and Clayton 1995). This supports the dissertation hypothesis that this parasite should have a strong negative effect upon its host, and makes the lack of such costs found in previous studies even more puzzling.

Chapter 5: Host Selection

It was shown that *C. pallida* were found in greater abundances upon higher ranking than lower ranking nestlings. There was also the surprising and unexpected discovery that the ratio of females to males was greater on nestlings than at the nests. The findings support the idea that *C. pallida* exhibits active host selection, with higher ranking and thus potentially resource rich hosts being preferred over lower ranking possibly resource scarce but weaker hosts. Despite the possibly higher levels of immunological defence of higher ranking nestlings, these are probably preferred as hosts as they provide more resources for parasites than their smaller ranking siblings. The sexual differences in host selection are also potentially important. That proportionally more females than male are seen upon hosts indicates that females feed more frequently than males, probably

because of the higher nutritional demands that larval production entails. Thus female parasitism may have a greater impact upon hosts than male.

This is the first time parasite host selection has been investigated or demonstrated within this system. However, study of host selection by a related Hippoboscid parasite, *C. melbae*, has found greater parasite numbers on hosts intermediate in size (Bize *et al.* 2008).

These findings have important implications for the study of parasite virulence. Previous studies have failed to investigate the effect of parasitism upon different ranks of nestlings, instead examining parasitic effect on the entire brood and all the nestlings they contained. Earlier studies have failed to quantify or consider the sexual composition of nest parasite populations, thus potentially falsely gauging subsequent parasitic pressures upon hosts.

Chapter 6: Other aspects of *C. pallida* and *A. apus* biology

Other factors possibly influencing parasitic virulence, including short term population fluctuations, the presence of mate guarding, the timing of parasitic emergence, and host hetero-thermy, were studied in this chapter. It was discovered that nest populations of *C. pallida* can fluctuate considerably over relatively short spans of time, in some cases on a daily basis. Evidence for parasite mate guarding and male clustering due to mating competition was discovered. A close synchrony of parasitic emergence with host presence was established, with the emergence of adult *C. pallida* being found to be temperature mediated. Evidence that nestling host body temperature varies under environmental stress was found.

These results were contrary to expectations and in most cases had not been previously described. Parasite populations had been assumed to be relatively stable in nature (e.g. Hutson 1981, Lee and Clayton 1995, Tompkins *et al.* 1996). The presence of mate guarding and the formation of mating clusters has not been described previously. This is the first empirical study investigating how temperature influences parasite emergence, but its results do confirm the anecdotal reports made by Kemper (1951) and Lack (1956) that adult *C. pallida* emergence occurs on arrival of adult swifts and initiation of breeding at the nest sites. Nestling body temperature under environmental stresses have

not previously been investigated in swifts, although there are anecdotal reports of adult swifts being able to endure periods of cooling (Koskimies 1948, Lack 1956).

These discoveries may affect parasite virulence. The short term population fluctuations indicate that previous investigations of *C. pallida* efficacy may have falsely estimated parasitic abundances, as populations sizes were determined on only a limited number of occasions thus not providing a true representation of parasite numbers. As *C. pallida* transfer between nest and host in order to feed, the number of adults temporarily absent from the nest needs to be considered when estimating parasite load. The discovery of male mate guarding and male clustering may influence population structure and thus likewise influence parasitic loads and pressures. The synchrony of parasitic emergence with host presence indicates the close association and likely parasitic nature of *C. pallida*. The ability of nestlings to reduce temperatures and thus save energy, suggests a possible mechanism by which swifts may mediate costs due to parasitism.

Chapter 7: Swift breeding success and *C. pallida* abundance

No notable association between parasite abundance and host breeding success was found. This is unexpected given the specialized features of *C. pallida* biology previously discovered, which suggest that it should have a strong detrimental effect on hosts.

The results extend previous knowledge by presenting data from a previously unstudied swift colonial nesting site. The results confirm these earlier studies which likewise failed to find an association of parasitic abundance with parasitic effect (Hutson 1981, Lee and Clayton 1995). The results from this study may confirm the conclusion made by Lee and Clayton (1995) that this parasite has developed low levels of virulence. However, the lack of virulence observed may be the result of the specialized nature of Common Swift biology, meaning the transfer of parasitic costs onto traits with longer term fitness implications is favoured.

The apparent lack of correlation between parasitic abundance and host breeding success indicates that *C. pallida* does not have a particularly strong impact upon hosts or it may indicate that the expected detrimental effect of *C. pallida* is expressed upon traits other than those studied here.

Chapter 8: Ectoparasitic load

There were no significant differences in a range of nestling host traits between nestlings facing experimentally different levels of parasitism. This is a surprising finding and contrary to the assumptions of host-parasite theory. A novelty of the study was that it examined a number of host nestling traits which had previously not been studied for the effects of parasitism, such as those indicative of nestling development. These results imply that parasitism by *C. pallida* has no detrimental effect upon host reproductive success.

These results are in accordance with the only other experimental investigation of this system. (Tompkins *et al.* 1996). However, empirical studies looking at closely related parasites, such as *Crataerina melbae*, have found clear effects due to parasitism (Bize *et al.* 2003, Bize *et al.* 2004a, Bize *et al.* 2005). A limitation of this study is that although it considers previously unexplored host traits, it does not consider some of the traits examined in these studies. For example, Bize *et al.* (2004a) showed that *C. melbae* parasitism caused nestling compensatory growth, while Bize *et al.* (2004b) showed that such parasitism affected host lifespan. Also, it did not consider some of the findings on *C. pallida* biology elucidated earlier in this dissertation, such as the evidence of host selection, intra-nest differences in parasitism, or ephemeral population fluctuations. Further work should examine these and other host and parasite traits.

The main implication of these results is that there is apparently no clear detriment to hosts as a result of resource removal by *C. pallida*. This does not therefore support the dissertation hypothesis.

Chapter 9: Parental investment in response to parasitism

No difference in parental investment was observed between broods experiencing either enhanced or reduced parasitic abundances. This is unexpected as it has been proposed that parents may increase levels of support to offspring in order to offset the costs they face from parasitism. This is known as the parental compensation hypothesis (Moss and Camin 1970).

Other studies have found a connection between parental investment and parasitism (e.g. Tripet and Richner 1997, Bouslama *et al.* 2002, Bañbura *et al.* 2004). However, the

results of this investigation failed to support the parental compensation hypothesis and are thus further contrary to the dissertation hypothesis. However, the results are limited because only a very small number of broods could be studied and that the quality or exact quantity of food provided could not be determined. The study is useful in demonstrating the varied ways parasitic costs may be borne and in prompting others to conduct further study. This finding likewise illustrates that no clear costs of parasitism are apparent to the host; contrary to expectations and the dissertation hypothesis.

Summary of main findings:

The specific results of each chapter were discussed in detail above. However, a summary of those findings which are of especial importance or which were previously unstudied may be of interest in emphasising the novelty of research:

- *C. pallida* found to exhibit strong physical and behavioural specialization towards a parasitic life-style.
- Higher levels of parasite prevalence, population aggregation, and parasite abundance were found than has previously been the case.
- Decline in *C. pallida* population size observed and documented. Short term variations in *C. pallida* populations were documented for first time.
- Sexual composition on *C. pallida* populations documented; discovery of temporal variation in population sexual composition.
- Evidence for parasite host selection sought and found.
- Possibility of inter-nest dispersal, mating competition, host torpor, and linkage of parasite emergence with host presence, studied or documented for first time.
- Experimental study of *C.pallida* efficacy confirms previous study which found no detrimental effect on hosts due to parasitism. First quantification of a number of parameters associated with nestling development.
- First investigation of parasitic effect on parental investment in this system.

10.3: OVERALL CONCLUSION

From these specific findings, the following can be surmised:

- *C. pallida* was found to exhibit life-history traits and ecological features indicative that it is parasitic in nature and that it is involved in a host-parasitic relationship with *A. apus*. *C. pallida* possess morphological and population traits indicative of possessing a parasitic mode of life. *C. pallida* removes considerable amounts of resources from hosts. There is close synchrony of *C. pallida* and *A. apus* life-cycles. Therefore *C. pallida* is expected to be a particularly effective and pugnacious parasite and to thus have a considerable effects upon its hosts. (Evidenced by Section A)
- However, subsequent investigation failed to determine any detrimental impact upon *A. apus* as a result of being infested by *C. pallida*. Observational study failed to find an association of host success with *C. pallida* abundance. There was no difference between broods experiencing increased and reduced levels of *C. pallida* infestation in a number of *A. apus* life-history traits. Parents of broods with experimentally increased *C. pallida* abundances did not increase parental provisioning rates. (Evidenced by section B).

This is a definition of parasitism, provided by Price (1977), which was selected to provide a structure around which to frame research. A parasite is:

'an organism in or on another living organism obtaining from in part or all of its organic nutriment, commonly exhibiting some degree of adaptive structural modification, and causing some degree of real damage to its host.'

Strictly following this definition, to be classed as a parasite a species should remove resources from another, be specialized for such a life-style, and as a result of this resource removal cause some detrimental effect upon hosts. Under these criteria, and considering the evidence discovered in the course of these scientific inquiries, it can be concluded that:

- *C. pallida* does not fulfil this strict definition of parasitism; although it exhibits

considerable adaptation to obtaining resources from *A. apus*, and there being good evidence that it removes such resources, no discernible detriment to *A. apus* hosts could be established as a result of this interaction.

There are a number of implications of this conclusion. Firstly, as to whether the relationship between Common Swifts and Louse Flies should be termed parasitic. Secondly, an investigation into the true nature of the relationship between the swift and its host needs to be made.

10.4: CONTEXT OF CONCLUSION TO PREVIOUS RESEARCH

It is necessary to examine these results and associated conclusion in context with previous research. There is a strong body of evidence that avian parasites have negative effects upon hosts (reviewed by: Møller *et al.* 1990, Lehmann 1993, Møller 1997). Seminal volumes published within the previous decades have highlighted the growing understanding of host-parasite systems and the clear negative consequences of parasitism, especially to avian hosts (e.g. Loye and Zuk 1991, Clayton and Moore 1997, Poulin 2007).

However, there is no clear evidence regarding this specific relationship between *A. apus* and *C. pallida*. A number of authors state that *C. pallida* should have negative consequences upon *A. apus* fitness (Büttiker 1944, Weitnauer 1947, Lack and Lack 1951, Lack 1956, Bromhall 1980, Hutson 1981, Hutson 1984). Despite these anecdotal reports and observations, basic observational and empirical investigation has failed to demonstrate the presence of such detrimental effects on hosts:

- Hutson (1981) failed to demonstrate any association between *C. pallida* parasite load and the physical condition of adult swifts.
- No correlation between Common Swift breeding success and *C. pallida* nest population abundance was found (Lee and Clayton 1995).
- An experiment found no difference in host breeding success between broods (Tompkins *et al.* 1996).

Thus, the results and conclusion of the investigations conducted here confirm and substantiate these previous findings. This lack of clear detrimental effects is especially surprising as such costs are clearly evident in other closely related Hippoboscid host-

parasite systems:

- The physical condition of cardueline finches was found to be related Hippoboscid louse fly parasite, *Ornithoica turdi* abundance (Senar *et al.* 1994).
- Clear detrimental effects of parasitism caused by a roughly analogous species of Louse Fly to *C. pallida*, *C. melbae*, a parasite of the Alpine Swift *A. melba*, have been found (Bize *et al.* 2003, Bize *et al.* 2004a, Bize *et al.* 2004b).

Table 1: Examples of how some of the main findings and discoveries found during the course of investigations on *C. pallida* support and contradict the results of other studies of this and related host-parasitic systems. This table demonstrates the novelty of the research conducted and how its complements and contributes to existing knowledge. It also highlights areas not previously studied before this set of investigations.

Results	Supports work of..	Contradicts work of..
Parasitic adaptations of <i>C. pallida</i>	Kemper (1951), Hutson (1984)	-
Parasitic aggregation and prevalence	-	Greater than Lee and Clayton (1995), Tompkins <i>et al.</i> (1996)
Horizontal transmission	Report by Bize <i>et al.</i> (2004a) in <i>A. melba</i>	Lee and Clayton (1995)
Parasite abundances and parasite load	-	Higher than Lee and Clayton (1995)
Association of <i>C. pallida</i> abundance with host presence	First documentation	
Sexual nature of <i>C. pallida</i> populations and parasitism	Hutson (1981)	Temporal changes previously unstudied
Mating Competition		None. Previously unreported.

Host selection	Previously unstudied in this system	Roulin <i>et al.</i> (1998) in <i>A. melba</i>
Population stability/fluctuations	Previously unstudied in this system	
Parasite emergence	Anecdotes by Kemper (1951)	-
Effect of <i>C. pallida</i> on general host fitness	Hutson (1981), Lee and Clayton (1995), Tompkins <i>et al.</i> (1996), Tella <i>et al.</i> (1995)	Bize <i>et al.</i> (2003, 2004a, 2004b, 2005) in <i>A. melba</i>
Effect of <i>C. pallida</i> on nestling development	Tompkins <i>et al.</i> (1996)	Bize <i>et al.</i> (2004a) in <i>A. melba</i> .
Effect of <i>C. pallida</i> on parental provisioning	Previously unstudied in this system	

10.5: EXPLANATIONS FOR CONCLUSION

What has happened to the expected 'costs' of parasitism? Why are the expected costs of this relationship to *A. apus* either not apparent or not present? What factors are mediating or obscuring these costs?

Reduced Parasite Virulency: According to the tenets of host-parasitic theory reduced parasitic virulence will develop over evolutionary time and with increasing closeness and dependency between host and parasite (Anderson and May 1978). Where parasite reproductive success is dependant upon host success, those parasites having a reduced effect upon hosts will experience higher levels of fitness and be selected for. There are many examples of this occurring, notably the reduced virulence exhibited by H.I.V. recently.

Such a development of reduced parasitic virulence may have occurred between *C. pallida* and *A. apus*. There is good circumstantial evidence that this is the case. The obligate nature of the relationship, with *C. pallida* being totally dependent upon a single specific host, *A. apus*, is indicative that a linkage of *C. pallida* fitness with that of the hosts has occurred. The close synchrony of parasitic emergence with host arrival and corresponding convergence of swift and *C. pallida* breeding demonstrates the closeness of the relationship. *C. pallida* is unable to survive without its *A. apus* host. The lack of apparent costs to *A. apus* hosts indicates that the *C. pallida* is no longer parasitic and that the relationship between these two species has become commensal.

The costs of parasitism may become reduced either through reduced parasitic efficacy, though better host defence against parasitism, or a combination of both factors. Avian host-parasitic research has concentrated upon studying aspects of host defence and immunity, for example with the development and use of assays of host immunology and by considering the theoretic implications of trade-offs between host immunology and host condition (Poulin 2007). However, although parasites are expected to develop reduced efficacy, the ways this may occur has been relatively little studied. The host centred viewpoint of host-parasite research has resulted in factors causing such reduced parasite efficacy, such as modifications in parasite behaviour, life-history and ecology, being neglected.

Emphasis of parasite biology: This dissertation is therefore a useful counterweight and its emphasis on parasite biology is pertinent and novel. It suggests ways in which such reductions in parasite virulence influenced by parasite ecology and behaviour could have occurred. This can be exemplified through the discovery of temporal changes in *C. pallida* population sexual composition. The seemingly puzzlingly high female sex ratios exhibited by *C. pallida*, may not be puzzling at all, but a consequence of an evolved 'kamikaze' strategy of males which once mated can best increase their own fitness through mortality. This would thus reduce parasitic impact upon hosts and potentially reduce the risk of nestling mortality and associated adult swift nest desertion. Such nest desertion would lead to the cessation of breeding by female *C. pallida* inseminated by males.

Specialization of swift lifestyle: The development of reduced parasitic virulence may be especially likely within the *C. pallida* and *A. apus* relationship, due to the extreme biological constraints and specializations *A. apus* experiences and exhibits. *A. apus* reproductive success is extremely time constrained; with successful fledging of offspring being necessary within 100 days of commencement of adult breeding. The unpredictable nature of European summers and consequent vagaries in insect food abundance means that reproductive success is highly precarious. Thus an additional negative impact from parasitism may be of critical importance in determining host success and may have favoured a reduction in parasitic vulnerability by this host. Even a closely related species, the Alpine Swift, does not experience such heavy constraints, and thus hosts and parasites may not be under the same pressure to exhibit reduced virulence or susceptibility, accounting for why costs are present in this systems but not between *C. pallida* and *A. apus*.

A reduction in *C. pallida* populations?: *C. pallida* populations may not reach levels needed to have a substantial or even detectable effect upon the swift hosts. There may be a number of reasons for this. Selection for low *C. pallida* population abundances may have occurred. *C. pallida* may 'choose' not to occur at high population densities. Although such an argument may sound somewhat group selectionist, there are nevertheless ways in which this may be selected for. Individual *C. pallida* success is strongly related to the success of nestling hosts. Only with continued nestling survival can the *C. pallida* reproductive cycle be successfully completed. Therefore it is in each

individual *C. pallida* own interest to reduce the pressure it exerts upon hosts. This may occur in a number of ways. *C. pallida* is not fecund, producing only 7 or 8 offspring per annum, compared with other Diptera this is an extremely low rate of population renewal. This may developed in order to reduce nest population levels in order to have avoid detrimentally impacting the host. Likewise male *C. pallida* may emerge earlier than females and die sooner in order to reduce parasite population levels at the nest. Such self-induced mortality may be favoured if it ensures survival of males own offspring.

This idea of lowered populate size accords well with host-parasite theory. With increasing evolutionary closeness between parasite and host species, parasite virulency is expected to decrease. This can be either through increased host immunity or through reduced parasitic pathogenicity. It appears that lower *C. pallida* population abundance may indicate the increasing evolutionary closeness between parasite and host. This leads weight to the idea that relationship has become commensualistic.

However, there are other reasons why the parasite population seen may not reach levels detrimental to the host. At the Oxford nesting site studied nests are cleaned each year meaning that parasite populations do not reach higher levels. Study at this study site, as seen in chapter 3, found higher parasite populations at undisturbed nests. Other factors may be lowering *C. pallida* populations. Parasite pupal mortality may be high during harsh winters. The previous few winters have been particularly harsh. Also, how *C. pallida* interacts with other parasites and microparasites is unknown. Other parasites which swifts harbour may lead to a reduction in *C. pallida* population size or pathogenicity.

10.6: IMPLICATIONS OF CONCLUSION

The discoveries made have implications for further studies of this inter-specific relationship and for host-parasite research in general. The implications for the relationship between *C. pallida* and *A. apus* are:

- The association between *C. pallida* and *A. apus* may not be parasitic but instead commensal. Although the lack of costs may appear puzzling and counter-intuitive, it may in fact reflect what is expected to occur between host and parasite through evolutionary time.
- The relationship between *C. pallida* and *A. apus* may be an example of an inquiline relationship. Parasitism, as a discrete category of inter-specific relationship, can and has been subdivided into various more exact relationships more precisely defining the specific nature of costs and benefits. Inquilism is a type of parasitic relationship in which one species is obligate upon another but which causes no detriment to its host. Inquiline means 'lodger'. Such relationships have possibly developed from previous strictly parasitic relationships, in which reduced parasitic virulence developed either through selection of parasites with reduced virulence or through increases in host resistance.

The wider implications of this study include:

- The study demonstrates that host-parasitic systems can only be fully understood once a good knowledge of the biology and ecology of both participants in the relationship is known. Knowledge of host and parasite life-history is a prerequisite to the full understanding of host-parasitic system functioning.
- The effects of parasitism can only be deciphered once correct levels of parasitic pressure and load can be quantified. The correct quantification of this is only possible when parasite ecology and life-history is well known.
- Parasites will exhibit traits which enhance their own fitness. However, how parasites increase their own fitness has rarely been studied in comparison to that of hosts (e.g. Poulin and Combes 1999, Poulin 2007). An increasing emphasis

upon parasite fitness and a more parasite centred viewpoint may be equally productive in allowing understanding of host-parasitic relationships.

- The dissertation demonstrates the growing depth and breadth of general host-parasitic research. Initial research simply quantified whether parasitic effects were observable upon basic host life-history traits such as nestling survival (e.g. Møller *et al.* 1990). However, the effects of parasitism have been shown to be much more widespread and occur over a much wider range of host traits (e.g. Møller 1997).
- A strict categorization of inter-specific relationships may not be possible. Such relationships may be best seen as occurring upon a movable scale of increasing benefit and detriment to each partner, rather than as being part of discrete category. The classification of relationships as being symbiotic, mutualistic, or parasitic, is artificial and simplistic. Such categorization may be an unhelpful construct that does not reflect the complex realities of inter-specific relationships.

10.7: LIMITATIONS

There are a number of limitations to research into the *C. pallida* and *A. apus* relationship conducted both here and previously. Limitations to pre-existing research on this host-parasite system include:

- The scarcity of swift, *A. apus* nestling sites offering the possibility of study. This means that *C. pallida* parasitism has only been examined at a single nesting colony previously, that within the Oxford Biological Museum in Oxford. The limitations of this site has meant that in former studies only limited sample sizes could be obtained. In comparison the effect that the analogous insect, *C. melbae*, has upon its Alpine Swift hosts has been investigated at a number of sites.
- The previous studies investigating the efficacy of *C. pallida* considered only an extremely limited range of host traits: For example the study by Lee and Clayton (1995) considered only basic host life-history traits associated with host reproductive success. In addition this study was purely observational in nature

and thus could make no firm conclusions as to the effect *C. pallida* was having. This study did not consider a number of traits related to nestling growth or traits which affect longer term host fitness.

- The abundances of *C. pallida* reported in previous studies, such as that by Hutson (1981), may not reflect their true nature. The findings of the investigations into *C. pallida* life-history presented here, suggest that assessing *C. pallida* population abundance is more difficult than initially thought. An incorrect estimation of *C. pallida* abundance may lead to a false estimation of parasitic load, which in turn could lead to a consequent failure to find evidence that *C. pallida* has a detrimental effect upon its hosts.

This dissertation shares some of the limitations of these previous studies:

- Study sizes were likewise limited in extent and only a single site could be examined. This is best demonstrated through the parental provisioning study, in which less than a dozen nests could practically be examined due to financial and practicality constraints.
- Whether the correct level of parasitic pressure was determined remains likewise unknown. Although it was acknowledged that quantifying abundance is complex and factors possibly affecting it were studied, its exact quantification remained difficult. *C. pallida* life-history requires more study to allow a correct assessment of abundance and therefore parasitic pressure to be made.
- Although several previously unstudied host traits were examined, nevertheless only a limited number and range of parameters could be examined for parasitic costs. The main emphasis of the investigations presented here was upon traits important to nestling growth and development. This allowed a more thorough examination of this aspect of host biology than that conducted in previous studies, but meant that other traits were neglected. The range of traits upon which parasites could be having an effect is large, and it was necessary to concentrate upon those believed most likely to exhibit such costs. Time, financial and practical constraints limited the range of traits that it were possible to study. Examining the effects of parasitism on swift lifespan, is for example,

difficult due to the difficulty of tracking swifts throughout entire lifespans.

- Aspects of host biology such as host immunity, sibling competition, or host behaviour were not studied. This was done on purpose in order to concentrate instead on features of parasite biology which are typically neglected in host-parasite study. This concentration on the biology of the parasite is instead one of the key strengths of these investigations. More thorough examination of host biology may lead to the discovery of detrimental effects as a result of the *C. pallida* relationship.
- Only the effects of a single parasite; *C. pallida*, were considered. Actually swifts are host to a wide range of both ecto- and endoparasitic species. These include feather mites, nasal mites, and chewing lice (*Dennyus hirundinis* (L.) (Phthiraptera: Menoponidae). Swifts may also harbour microscopic parasitic organisms such as viruses and bacteria, for example avian malaria. The effect these other parasites have on *A. apus* is unknown and has yet to be studied. How such parasitism interacts with that of *C. pallida* remains likewise unknown.

10.8: AVENUES OF FURTHER STUDY:

These limitations and the results of the investigations conducted here suggest numerous avenues of potential further study:

- *Synchrony of C. pallida and A. apus lifecycles:* The mechanisms behind the close synchrony in *C. pallida* and *A. apus* life-cycles requires further study. For example the processes initiating *C. pallida* emergence are unclear. Do *C. pallida* pupae possess an internal clock allowing emergence at the correct period? Is such emergence mediated by weather condition, and if so which? Or is emergence initiated through detection of host presence through movement or olfactory senses?
- *Sexual differences in C. pallida parasitism:* Determining the difference in parasitic pressure exerted by female and male *C. pallida* would be pertinent. Female *C. pallida* remove larger quantities of blood from *A. apus* hosts, thus the costs they incur should be greater. Future studies should consider these differences and study their possible effects. Also examining whether *C. pallida* populations are affected, or indeed, suffer from parasitism should be examined. *C. pallida* has been reported to be prey to a parasitoid insect, pictured in Photograph 1, which may be influencing *C. pallida* population sizes.
- *C. pallida* emergence: Further investigation of *C. pallida* emergence is needed. Whether equal proportions of males and females emerge over the entire summer needs to be determined, and also whether there are differences at specific nests. In addition clarification as to whether males emerge earlier than females is needed. The lifespan of Louse Flies should be determined and also possible differences between males and females. Males may have lower lifespans due to the costs of male-male competition. Given the potential differences in parasite cost caused by males and females examination of such differences is most pertinent in determining parasite efficacy.
- *Establishment of host-parasite phylogenies:* The length and closeness of association of *C. pallida* with *A. apus* is unknown. Genetic analysis may reveal its extent and length. Phylogenetic study comparing and contrasting

evolutionary relationships between host and parasite for *A. apus* and other Apodidae species, along with their Hippoboscid hosts, may illustrate the link between host-parasite relationship closeness and parasitic virulence.

- *Immunological study of host resistance:* Biochemical or genetic assessment of swift host ability to resist parasitism would allow study of host biology contrasting with the parasite centred view presented here. The relationship of nestling rank, size, and resource availability with host resistance to parasitism and its corresponding effect on parasite fitness would be of interest. Study of the predisposition of hosts to parasitism would be pertinent. as parasitic abundance of populations is somewhat dependent of host ‘quality’ and fitness. This has been studied in Bize *et al.* (2008), in *A. melba*, but not in *A. apus*.
- *Intra-brood effects of parasitism:* The discovery of intra-brood differences in parasite host selection identified within this dissertation open up the possibility of intra-brood differences in the expression of parasitic costs occurring. This, and previous studies of this host-parasitic system, have considered the effects of parasitism only upon the entire nest system. Further work could investigate such within nest differences in parasitism and its consequences.
- *Study of relationship of parasitism with other environmental and social factors:* Multivariate analysis of the inter-relationship between parasitism and other factors such as weather, food abundance, and host competition is required. Whether parasitic effects can be determined under regimes where additional and cumulative environmental and social stresses are apparent may be pertinent.
- *The effect of other ecto- and endoparasites:* An investigation into the effects of cumulative parasitism by the numerous parasitic species to which Common Swifts play host may reveal true costs of such parasitism. It may be that *C. pallida* infestation may offer host benefits by leading to a reduction in other forms of parasitism. For example parasitism by *Protocalliphora* nest ectoparasites is low at swift nests and this may be the result of competition with *C. pallida* at the nest sites. As such parasitic Blow Fly lead to high host mortality, swifts may actually preferentially favour the relatively benign Louse

Fly. *C. pallida* may act as a vector of microscopic blood parasites (Baker 1967). This may influence the negative effect of *C. pallida* parasitism. The costs of *C. pallida* parasitism may vary depending on whether such phoretic transfer occurs and impose additional costs or even benefits to hosts. Such phoretic transfer of blood parasites may lead to benefits to hosts and thus mediate the costs of *C. pallida* parasitism. There are several examples where infection by one agent, offers resistance to attack from other pathogens e.g. infection by cowpox is classically known to offer resistance to smallpox.

- *Examination of host traits of lifetime fitness consequence:* Examination of host life-history traits not previously studied may elicit parasitic costs and demonstrate that the costs of parasitism are borne upon traits with longer term fitness implications than those studied here. The practical difficulties of studying such traits may however make such study impossible over the short time and with the limited number of study sites available.
- *Need for species specific explanations:* Rather than simply collecting evidence of the effect which parasitism has, such evidence must be explained in the species specific context in which it occurs. Simply documenting parasitic effects, without attempting to explain why they occur in the way they do is unproductive.

Photograph 1: *Dibrachys cavus* Walker, 1835, (Hymenoptera: Pteromalidae) is a chalcid wasp parasitoid of *C. pallida*, predated upon the pupae of *C. pallida*. However, it remains totally unstudied.



10.9: STATE OF DISSERTATION

Has the research question been answered? Is *C. pallida* parasitic?

The overriding research question initially proposed in the introduction and around which investigations were structured, was:

Does the Louse Fly, *Crataerina pallida*, fulfil the conditions defining a parasite species?

This investigation has shown that *C. pallida* possesses the attributes expected of a species engaged within a parasitic association. Many of its life-history traits, particularly the large quantities of blood it removes from hosts, indicates that it should be a particularly efficacious and pugnacious parasite. However, no evidence that there are negative effects to Common Swift hosts as a consequence of its association with *C. pallida* were found. Thus the answer to the research question is in the negative. An assumption contained within the standard definition of parasitism provided by Price (1977) is that as a result of such an inter-action there should be some negative effect upon hosts. The conclusion is that the relationship does not, strictly fulfil the definition of a host-parasitic relationship.

The discoveries and results contained within this dissertation suggest that *C. pallida* may have reduced its own virulence in order to maximise its own fitness. Thus the relationship between *C. pallida* and the *A. apus* Common Swift host has become inquiline in nature as predicted by host-parasitic theory.

State of hypothesis

The dissertation hypothesis, stated in the introduction, was:

The inter-specific relationship between the Louse Fly, *C. pallida*, and the Common Swift, *A. apus*, is parasitic in nature.

As the research question has been answered in the negative, with no evidence of a negative effect upon *A. apus* hosts, the following statement about the hypothesis can be made:

The hypothesis has not been supported or proved.

The dissertation has emphasized the highly specialized and inter-connected nature of swift host and parasite louse fly biology. Examinations of other host-parasite systems should likewise consider the species-specific contexts in which parasitism is occurring. The unique features of each specific host-parasitic association mean that a full understanding of the functioning of each system can be gained only by considering it in its own specific context. The expression of detrimental effects due to parasitism should not be expected or assumed to occur, but the reasons possibly mitigating them or accounting for an absence should be sought.

Table 2: Overview of research: This table provides an overview of the research contained within each chapter. It can be compared with the initial table summarizing research questions for each investigation within the introduction.

	Research Question	Method Used	Important Findings	Results relate to
	DOES <i>C. PALLIDA</i> EXHIBIT LIFE-HISTORY TRAITS INDICATIVE THAT IT IS PARASITIC?			
2	Does previous research show that <i>C. pallida</i> is parasitic?	Review of literature.	<i>C. pallida</i> has physical and population features typical for parasites. Good evidence of resource removal from hosts.	This is the first comprehensive review.
3	Does <i>C. pallida</i> exhibit population parameters indicative that it is parasitic?	Observational investigation of natural <i>C. pallida</i> populations.	<i>C. pallida</i> exhibits features typically seen in parasitic species e.g. high host specificity, high levels of population aggregation, high prevalence.	Confirms: Hutson (1981), Tella and Jovani (2000). Temporal changes in sex ratio studied for first time.
4	How does <i>C. pallida</i> disperse between nests?	Marking of <i>C. pallida</i> and subsequent observation of movement.	Discovery of inter-nest movement.	Contrary to: Lee and Clayton (1995), Tompkins <i>et al.</i> (1996).
5	Does <i>C. pallida</i> exhibit selection between hosts?	Observation of inter-brood parasite abundance	Parasites select nestlings of higher rank. Sexual differences in host selection occur.	Not previously studied.

6	What features does <i>C. pallida</i> exhibit that may influence its virulence?	Observation and study of <i>C. pallida</i> and swift hosts.	Discovery of short term fluctuations in nest populations. Observation of mating clusters and male mate competition for first time. Increased emergence under higher temperature regimes.	Not previously studied.
DOES <i>C. PALLIDA</i> HAVE AN IMPACT ON <i>A. APUS</i> FITNESS?				
7	Is <i>A. apus</i> reproductive success related to <i>C. pallida</i> abundance?	Correlation of <i>A. apus</i> success with <i>C. pallida</i> abundance.	No correlation of Louse Fly abundance with Common Swift traits studied.	Confirms: Lee and Clayton (1995), Tompkins <i>et al.</i> (1996). Contrary to: Bize <i>et al.</i> (2003, 2004a, 2005).
8	Do <i>A. apus</i> experiencing higher levels of infestation exhibit lower reproductive success?	Experimental manipulation of <i>C. pallida</i> abundances.	No difference between broods facing different levels of <i>C. pallida</i> infestation in clutch size, clutch size, nestling growth or nestling success.	Confirms: Tompkins <i>et al.</i> (1996). Contrary to: Bize <i>et al.</i> (2003, 2004b, 2005). Nestling development studied in detail for first time.
9	Do adult <i>A. apus</i> increase levels of parental provisioning to nestlings experiencing higher <i>C. pallida</i> infestation?	Recording of parental provisioning to broods with altered <i>C. pallida</i> abundances.	No differences in parental provisioning apparent between broods facing different levels of parasitism.	Previouly unstudied in this system. Contrary to Tripet and Richner (1997), Moss and Camin (1970).

TABLE 3: SUMMARY OF DISCUSSION: This table provides a summary of the discussion and whether the research question was answered and whether the dissertation hypothesis was supported.

Question	Answer
<i>What was the aim of the dissertation?</i>	To determine the true nature of the relationship between <i>C. pallida</i> and <i>A. apus</i> . Namely to determine whether it is a parasitic association.
<i>Why is this important?</i>	Previous studies had found no detrimental effect of <i>C. pallida</i> parasitism upon <i>A. apus</i> hosts, contrary to expectations.
<i>What is the broader scientific context?</i>	A detrimental effect of parasitism upon hosts is expected and such costs have been demonstrated in numerous study systems. Parasite biology is often neglected in host-parasite study.
<i>How did I attempt to achieve my aim?</i>	<i>C. pallida</i> biological traits, especially those with possible pertinence to the level of virulence it exhibits, were investigated. Detrimental effects caused by <i>C. pallida</i> upon <i>A. apus</i> hosts were sought.

<p><i>What observations were made?</i></p>	<p><i>C. pallida</i> possesses features indicative that it is parasitic. It demonstrates clear specializations towards a parasitic mode of life. It exhibits population parameters typical for parasites. However, no detrimental effect on swift hosts could be deciphered.</p>
<p><i>What conclusions were made?</i></p>	<p>The relationship can not strictly speaking be classed as 'parasitic', as there is no apparent detrimental effect to hosts. The close inter-relationship between <i>C. pallida</i> and <i>A. apus</i> may have resulted in a decrease in parasite virulence meaning the relationship is more commensal in nature. .</p>
<p><i>Was the research question answered?</i></p>	<p>Yes. Despite appearances, strictly speaking <i>C. pallida</i> does not fulfil the criteria defining a parasitic species.</p>
<p><i>Was the dissertation hypothesis supported?</i></p>	<p>The initial hypothesis was not supported. It was not successfully shown that <i>C. pallida</i> is parasitic.</p>

10.10: CHAPTER SUMMARY

The investigations conducted during the course of this dissertation demonstrate the closeness of the relationship between *C. pallida* and *A. apus*. *C. pallida* is clearly obligate and dependent upon its host. However, although the nature of *C. pallida* biology indicates that it is parasitic, and should therefore have a clear detrimental effect upon its hosts, no such effect is apparent. An apparently more commensal relationship has developed.

The answer to the dissertation research question asking whether there are negative effects to *A. apus* as a result of being engaged within this relationship is therefore in the negative. Thus the dissertation hypothesis stating that such an effect should be seen has not been supported.

An explanation for this lack of virulence, the development of reduced parasitic virulence, was presented and appears likely. Further research upon this host-parasite system could investigate whether this has occurred, or seek the expected costs of parasitism upon host traits not examined in the investigations contained within this dissertation.

10.11: DISCUSSION REFERENCES

ANDERSON, R.M., and MAY, R.M. (1978). Regulation and stability of host-parasite population interactions. 1. Regulatory processes. *The Journal of Animal Ecology*, **47**, 219-247.

BAÑBURA, J., PERRET, P., BLONDEL, J., THOMAS, D.W., CARTAN-SON, M. and LAMBRECHTS, M.M. (2004). Effects of *Protocalliphora* parasites on nestling food composition in Corsican Blue Tits *Parus caeruleus*: consequences for nestling performance. *Acta Ornithologica*, **39**, 93-103.

BAKER, J.R. 1967. A review of the role played by the Hippoboscidae (Diptera) as vectors of endoparasites. *The Journal of Parasitology*, **53**, 412-418.

BIZE, P., ROULIN, A., BERSIER, L.P., PFLUGER, D., and RICHNER, H. (2003). Parasitism and developmental plasticity in Alpine Swift nestlings. *Journal of Animal Ecology*, **72**, 633-639.

- BIZE, P., JEANNERET, C., KLOPFENSTEIN, A. and ROULIN A. (2008). What makes a host profitable? parasites balance host nutritive resources against immunity. *American Naturalist*, **171**, 107-118.
- BIZE, P., A. ROULIN and RICHNER, H. (2004a). Parasitism, developmental plasticity and bilateral asymmetry of wing feathers in Alpine Swift (*Apus melba*) nestlings. *Oikos*, **106**, 317-323.
- BIZE, P., ROULIN, A., BERSIER, L.F. and RICHNER, H. (2004b). Additive effects of ectoparasites over the reproductive attempts in the long-lived Alpine Swifts. *Journal of Animal Ecology*, **73**, 1080-1088.
- BIZE, P., ROULIN, A., TELLA, J.L. and RICHNER, H. (2005). Female-biased mortality in experimentally parasitized Alpine Swift *Apus melba* nestlings. *Functional Ecology*, **19**, 405-413.
- BOUSLAMA, Z., LAMBRECHTS, M.M., ZIANE, N., DJENIDI, R.D. and CHABI, Y. (2002). The effect of nest ectoparasites on parental provisioning in a north-African population of the Blue Tit *Parus caeruleus*. *Ibis*, **144**, E73-E78.
- BROMHALL, D. (1980). *Devil birds. The life of the swift*. Hutchinson, London, U.K.
- BÜTTIKER W. (1944). Die Parasiten und Nestgäste des Mauerseglers (*Micropus apus* L.). *Der Ornithologische Beobachter*, **41**, 25-35.
- CLAYTON, D.H. and MOORE, J. (1997). *Host-parasite evolution: General principles and avian models*. Oxford University Press, New York.
- HUTSON, A. M. (1981). The population of the Louse Fly, *C. pallida* (Diptera, Hippoboscidae) on the European Swift, *A. apus* (Aves, Apodidae). *Journal of Zoology, London*, **194**, 305-316.
- HUTSON, A.M. (1984). *Keds, flat-flies and bat-flies (Hippoboscidae and Nycteribiidae)*. Handbooks for the identification of the British Insects. Volume 10 Part 7. Royal Entomological Society, London, U.K.
- KEMPER, H. (1951). Beobachtungen an *C. pallida* Latr. und *Melophagus ovinus* L. (Diptera, Pupipara). *Zeitschrift für Hygiene (Zoologie)*, **39**, 225-259.
- KOSKIMIES, J. (1948). On temperature regulation and metabolism in the Swift *micropus a. apus* L., during fasting. *Experientia*, **4**, 274-276.

- LACK, D. and LACK, E. (1951). The breeding biology of the swift, *A. apus*. *Ibis*, **93**, 501-546.
- LACK, D. (1956). *Swifts in a tower*. Methuen publishing, London, U.K.
- LEE, P.L.M. and CLAYTON, D.H. (1995). Population biology of swift (*A. apus*) ectoparasites in relation to host reproductive success. *Ecological Entomology*, **20**, 43-50.
- LEHMANN, T. (1993). Ectoparasites: direct impact on host fitness. *Parasitology Today*, **9**, 8-13.
- LOYE, J.E. and ZUK, M. (1991). *Bird-parasite interactions: Ecology, evolution and behaviour*. Oxford University Press, Oxford, U.K.
- MCCLURE, H.E. (1984). The occurrence of Hippoboscidae flies on some species of birds in southern California. *Journal of Field Ornithology*, **55**(2), 230-240.
- MØLLER, A.P., ALLANDER, R. and DUFVA, R. (1990). *Fitness effects of parasites on passerine birds: a review*. In: BLONDEL, J., GOSLER, A., LEBRETON, J.D. and MCCLEARY, R.H. (eds.). *Population biology of passerine birds: an integrated approach*. Springer-Verlag, Berlin, Germany.
- MØLLER, A.P. (1990). Fluctuating asymmetry in male sexual ornaments may reliably reveal male quality. *Animal Behaviour*, **40**, 1185-1187.
- MØLLER, A.P. (1997). Parasitism and the evolution of host life-history. In: CLAYTON, D.H. and MOORE, J. (eds.). *Host-parasite evolution: general principles and avian models*. Oxford University Press, Oxford, U.K.
- MOSS, W.W. and CAMIN, J.H. (1970). Nest parasitism, productivity, and clutch size in purple martins. *Science*, **168**, 1000-1003.
- POULIN, R. and COMBES, C. (1999). The concept of virulence: interpretations and implications. *Parasitology Today*, **15**, 474-475.
- POULIN, R. (2007). *Evolutionary Ecology of Parasites; from individuals to communities*. Chapman and Hall Publishers, London, U.K.
- PRICE, P.W. (1977). General concepts on the evolutionary biology of parasites. *Evolution*, **31**, 405-420.
- SENAR, J.C., COPETE, J.L., DOMENECH, J. and VON WALTER, G. (1994). Prevalence of louse flies Diptera: Hippoboscidae parasitizing a cardueline finch and its effects on body condition. *Ardea*, **82**, 157-160.
- TELLA, J.L., GORTÁZAR, C., GAJÓN, A. and OSÁCAR, J.J. (1995). Apparent lack of

effects of a high louse fly infestation (Diptera, Hippoboscidae) on adult colonial Alpine Swifts. *Ardea*, **83**, 435-439.

TELLA, J.L. and JOVANI, R. (2000). Sources of variability in aggregation and sex ratios of *Crataerina melbae* (Diptera: Hippoboscidae) among adult colonial alpine swifts. *Journal of Parasitology*, **86**, 933-938.

TOMPKINS, D.M., JONES, T. and CLAYTON, D.H. (1996). Effect of vertically transmitted ectoparasites on the reproductive success of Swifts (*A. apus*). *Functional Ecology*, **10**, 733-740.

TRIPET, F. and RICHNER, H. (1997). Host Responses to ectoparasites: Food compensation by parent blue tits. *Oikos*, **78**, 557-561.

WEITNAUER, E. 1947. Am Neste des Mauerseglers, *A. apus apus* (L.). *Der Ornithologische Beobachter*, **44**, 133-182.

APPENDICES

CANDIDATE STATEMENT	I
WORD COUNT	II
ARTICLE LIST	III
AUTHOR CV	IV

APPENDIX I:

CANDIDATE STATEMENT

As an article based dissertation the contribution of each author of published work must be stated.

- The lead author of all article either published or accepted for publication is myself, Mark David Walker. All work contained within these articles was conducted solely by myself. All investigation planning and design, financing, result collection, data analyses, and article drafting and writing, was conducted solely by myself. I received advice on various aspects of parasite and swift biology which is acknowledged below.

- The co-author for a number of articles is Professor Ian Rotherham of Sheffield Hallam University. Professor Rotherham acted as my doctoral supervisor during the course of my doctoral studies, providing me with support and assistance from the autumn of 2009. He commented on drafts of several of the articles subsequently published.

- The article; Walker, M., Rozman, J. and Witte, K. 2009. Brutkolonie des Mauerseglers (*A. apus*) in einer Autobrücke; was written solely by myself and introduces the study site. J, Rozman and K. Witte corrected the German contained within an early draft of this article.

APPENDIX II: WORD COUNT

CHAPTER	TITLE	WORD COUNT
CHAPTER 1	General introduction	6573
CHAPTER 2	The Common Swift Louse Fly	6147
CHAPTER 3	Characteristics of <i>C. pallida</i> populations	4419
CHAPTER 4	Inter-nest dispersal	2193
CHAPTER 5	Host selection by the Louse Fly	5026
CHAPTER 6	Other aspects of <i>C. pallida</i> biology	4092
CHAPTER 7	Louse Fly abundance	3511
CHAPTER 8	Ectoparasite load and host reproduction	3359
CHAPTER 9	Parental investment	2774
CHAPTER 10	Discussion	7413

Dissertation Abstract: 297 (limit 300)

Word count of articles: 31,521

Introduction and discussion word count: 13,986

TOTAL WORD COUNT: 39,507 (limit 40,000)

APPENDIX III:

ARTICLES PUBLISHED OR ACCEPTED FOR PUBLICATION

PUBLISHED

WALKER, M.D. and ROTHERHAM, I.D. (2010). Characteristics of *Crataerina pallida* (Diptera: Hippoboscidae) populations; a nest ectoparasite of the Common Swift, *Apus apus* (Aves: Apodidae). *Experimental Parasitology*, **126**, 451-455.

WALKER, M.D. and ROTHERHAM, I.D. (2010). The breeding success of Common Swifts *Apus apus* is not correlated with the abundance of their Louse Fly *Crataerina pallida* parasites. *Bird Study*, **57**, 504-508.

WALKER, M.D. and ROTHERHAM, I.D. (2010). The Common Swift Louse Fly, *Crataerina pallida*: An ideal species for studying hostparasite interactions. *Journal of Insect Science*, **10**, 193.

WALKER, M.D. and ROTHERHAM, I.D. (2010). Temperature affects emergence of *Crataerina pallida* (Diptera: Hippoboscidae). *Journal of Medical Entomology*, **47**, 1235-1237.

WALKER, M.D. (2009). (Latreille 1812) (Dip.: Hippoboscidae) Daily fluctuations seen in the number of Louse Fly, *Crataerina pallida*, seen at Common Swift *A. apus* nests. *The Entomologists' Record*, **121**, 157-158.

WALKER, M., ROZMAN, J. and WITTE, K. (2009). Brutkolonie des Mauerseglers (*A. apus*) in einer Autobrücke.(A breeding colony of the Common Swift in a highway bridge). *Vogelwarte*, **47**, 41-43.

AWAITING PUBLICATION

WALKER, M.D. and ROTHERHAM, I.D. 'Cool dudes.' torpor in Common Swifts. Accepted for publication by *British Birds*.

WALKER, M.D. and ROTHERHAM, I.D. No evidence of increased parental investment in response to parasitism by Common Swifts. Accepted for publication by *Bird Study*.

WALKER, M.D. and ROTHERHAM, I.D. Effect of an ectoparasitic Hippoboscid Louse Fly, *Crataerina pallida*, upon the breeding success of Common Swifts *Apus apus*. Accepted for publication by *Ibis* journal of ornithology.

WALKER, M.D. And ROTHERHAM, I.D. Previously unreported mate guarding and 'clustering' by a nest ectoparasite (Diptera, Hippoboscidae). Accepted for publication by *Dipterist's Digest*.

APPENDIX IV:
AUTHOR CURRICULUM VITAE

Mark David Walker

10 The Ridgeway, Coal Aston, Sheffield, S18 3BY

Employment History

- 2004-2009 **Lecturing assistant**
Siegen University, Germany.
- 2002-2003 **Biology Researcher: Tick-borne Diseases in Wild Mice**
Centro de Ecologia Alpina, Trento, South Tyrol, Italy.
- 2000-2002 **Biology Researcher: Behaviour of Alpine Chamois.**
University of Bern, Switzerland.

Voluntary Work Experience

- June-Dec 2003 **Hallam Environmental Consultancy, Sheffield.**
Six months voluntary position.
- June-July 2002 **Bat Conservation in Berlin**
Old nuclear bunkers were converted into bat hibernating quarters.
- April-June 2002 **Sea Turtle Conservation Work, Greece**
Monitoring of nesting by sea turtles.

Education

- Currently **Doctoral Study:** Under Prof. I. Rotherham, Sheffield Hallam
University, U.K.
- 1999-2000 **MSc Biodiversity and Conservation,** University of Leeds, U.K.

1996-1999 **BSc (Hons) Biological Sciences 2:1**, University of Leeds, U.K.

Languages Fluent in German. French to an intermediate/conversational level.

Non Swift Related Publications

WALKER, M., GRÖGER, M., MOSLER, B. and SCHLÜTER, K. (2008). A bright spark: open teaching of science using Faraday's lectures on candles. *Journal of Chemical Education*, **85(1)**, 59-63.

KREMER, A., WALKER, M. and SCHLÜTER, K. (2007). Food for Thought: Teaching about taste in an inquiry way. *Teaching Science*, **53(3)**, 30-31.

KREMER, A. WALKER, M. and SCHLÜTER, K. (2007). Learning to teach inquiry. A course in inquiry-based science for future primary school teachers. *Bioscene: Journal of College Biology Teaching*, **2**, 1-3.

WALKER, M., KREMER, A. and SCHLÜTER, K. (2007). The Dirty Water Challenge. *Science and Children*, **44(9)**, 26-29.