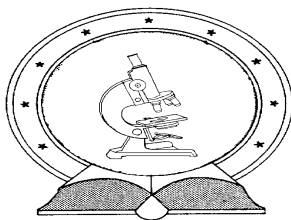


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**Parasitism and parental assistance: Factors affecting early development
in nestling house sparrows (*Passer domesticus*)**

**Parazitizmus és szülői gondoskodás: a korai fejlődést befolyásoló
tényezők háziveréb-fiókákban (*Passer domesticus*)**

Egyetemi doktori (PhD) értekezés

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A doktori értekezés betétlapja

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háziveréb-fiókákban (*Passer domesticus*)**

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1.1 INTRODUCTION

In altricial birds, early stages of development is an important and critical period, with extremely rapid growth and high energetic demands (Case 1978). Many features of the environment, both biotic and abiotic impinge on the developing offspring in various stages of early development (Norris & Evans 2000, Tschirren & Richner 2006, Taborsky 2006, Monaghan 2008), with significant consequences on condition, survival, physiology, behaviour and reproductive performance in adulthood (Lindström 1999; Metcalfe & Monaghan 2001; Qvarnström & Price 2001; Strasser & Schwabl 2004, Gustafsson et al. 1995, Desai & Hales 1997, de Kogel 1997, Birkhead et al. 1999).

Parental performance is one of the most important among these features. Altricial bird offspring rely on one or both parents for early nutrition (Clutton-Brock 1991). Therefore, parental nutrition effort is crucial in offspring survival and quality. In biparental caring birds, parental provisioning effort depends on many variables. Besides individual quality, actual health status or condition, the interplay between the caring parents (by adjusting the parental efforts to the mate's effort or quality; Houston & Davies 1985, Burley 1986, Saino & Møller 1995, Dearborn 2001, Houston et al. 2005, Harrison et al. 2009) can strongly influence the level of parental provisioning behaviour. In short-lived species, male sexual ornaments might serve as a cue for females that honestly indicates male parenting ability.

However, male sexual displays might signal also other (e.g. genetic) benefits, females mated with more/less ornamented males might therefore adjust their own parental effort to the reproductive value of their actual partner (Burley 1986). So thus, early development of the nestlings is influenced also by the outcome of these parental decisions. Numerous male secondary sexual traits have been examined for their putative utility as reliable indicators of male parental competence (e.g. Mountjoy & Lemon 1997, Linville et al. 1998, Buchanan & Catchpole 2000, Candolin 2000), but whether or not bird ornaments are a signal for direct benefits to prospective partners in sexual selection is controversial.

Even in case of beneficial environment and superior parental investment,

the presence of parasites during offspring development can ruin a good start in life. Nest-dwelling arthropod ectoparasites are adapted to feed on early life stages of developing birds, they might have radical consequences on both short and long-term fitness, given that nestlings are exposed to them in a sensitive period of energy demanding fast growth and development (Møller et al. 1990, Loye & Zuk 1991 and Clayton & Moore 1997, Proctor & Owens 2000). These ectoparasites may have a number of detrimental effects on nestlings, (e.g. loss of nutrients, tissue damage, immune reactions, or transmission of micropathogens) often impairing nestling growth and development and resulting offspring in poor condition at fledging (Allander 1998, Clayton & Tompkins 1995, Fitze et al. 2004, Fitze et al. 2004, Brown, Brown & Rannala 1995, Gebhardt-Henrich & Richner 1998, Simon et al. 2004).

The impact of nest-dwelling ectoparasites on nestling quality, however, may vary considerably due to variation in environmental factors, offspring quality, and individual parasite load. Within-brood distribution (and with this, parasite infestation of a given chick in a brood) is usually explained either by the parasites' preference for certain kinds of host characteristics, or by individual differences in offspring's susceptibility to parasites (Møller 1990, Lochmiller 1996, Christe et al. 1998, Roulin et al. 2003, Simon et al. 2003). Beside these factors, avoidance of certain nestling by the parasites can give an alternative approach to understand within-brood variance in ectoparasite infection. Identification and abandonment of mature nestlings that are ready to fledge could be adaptive for the parasites, allowing them to stay in the nest and continue reproduction.

1.2 AIMS OF THIS STUDY

In this thesis, based on observational results of field studies, I attempted to highlight important aspects of rearing conditions experienced during early development of house sparrows, focusing on two biotic factors - parasitism and parental assistance - that are amongst the most important ones that development of altricial nestling is influenced by.

First, (in 4.1) I focus on ectoparasitism, and investigate whether natural levels of nest mite parasitism have any short-term consequences on developing house sparrow nestlings, focusing mainly on body condition and haematological responses. I hypothesised that if parasitic mites impose any health impact on their avian hosts, different levels of infection should be revealed in some blood health indices, such as the relative number of immunologically active leukocytes or reduced haematocrit level (anaemia). Additionally, I also investigated the effects of nest mites on condition, growth and fledging success of nestling sparrows.

Moreover, (in 4.2) I attempt to reveal factors and mechanisms that shape intranest distribution of macronyssid fowl mites on house sparrow nestlings, shortly before their fledging. My main purpose was to determine whether within-brood distribution of nest mites indicates preference towards specific nestling characteristics. For example, if mites prefer large or susceptible nestlings as proposed by the hypotheses described above, their numbers should increase with nestling body size or decrease with the intensity of the host's immune response. Furthermore, by scoring the mites' feeding status, I investigated whether large or susceptible nestlings provide superior feeding conditions for parasites, which could explain the preference for such hosts. As an alternative explanation, I also tested whether the distribution patterns of mites suggest adaptive host-abandonment by the parasites, which is characterised by the lower mite load on older or more developed nestlings.

Second, (in 4.3) I focus on parental performance, and study whether aspects of parental quality of house sparrows males is related to their secondary sexual trait, addressing two specific questions: (i) Does parental investment of male sparrows (measured as nestling provisioning and risk-taking) vary with the size of their badge? (ii) Is there any relationship between the mothers' parental effort and the size of their mate's ornament? If yes, do females benefit from these differences in form of high quality offspring or reduced parental effort?

2. BACKGROUND

2.1 EARLY DEVELOPMENT, GROWTH AND CONDITION IN ALTRICIAL BIRDS

Early development is the period from conception to developmental maturity (Henry & Ulijaszek 1996). In altricial birds, early stages of somatic growth and development constitute an important and critical period, with high energetic demands. Growth rates of altricial birds typically are extremely rapid early in life, with most small passerines attaining full adult mass within 10 to 20 days after hatching. (Case 1978). In many passerines, for example, extremely rapid growth and development transforms tiny, ectothermic, naked and helpless hatchlings into adult-sized, endothermic, fully feathered fledglings in just two weeks. Developmental trajectories during this period can strongly influence the likelihood of nestlings' survival (Hochachka & Smith 1991, Starck & Ricklefs 1998, Metcalfe & Monaghan 2001). In many species there is strong selection on rapid growth in order to fledge as early as possible, reducing the length of the dependent period, which can influence exposure to predation and the level of parental care (Lack 1968, Bosque & Bosque 1995, Winkler & Allen 1996; Monrós, Belda & Barba 2002). On the other hand, longer developmental periods can be associated with greater physiological development, greater flight ability, and better fledging condition, all of which can increase survival rates (Tinbergen & Boerlijst 1990, Hochachka & Smith 1991, Ricklefs 1984, 1992, Lindén et al. 1992).

Nestlings face a trade-off of investing resources in somatic growth or body maintenance and/or reproduction (Stearns 1992). Under most conditions, allocating resources to growth reduces resource stores, so high growth rates should correspond to reduced body reserves. Excess body reserves, however, can provide a buffer against starvation during periods of adverse rearing conditions, and as many studies of birds have shown, body condition is a good predictor of fledgling survival (Perrins 1964, Hochachka & Smith 1991, Lindén et al. 1992, Adriaensen et al. 1998). The optimal solution to this allocation trade-off depends on the selection pressures imposed by the various environmental components during

development. In altricial birds, many features of the environment, both biotic and abiotic impinge on the developing offspring in various stages of early development (Norris & Evans 2000, Tschirren & Richner 2006, Taborsky 2006, Monaghan 2008), with significant consequences on condition, survival, physiology, behaviour and reproductive performance in adulthood (Lindström 1999; Metcalfe & Monaghan 2001; Qvarnström & Price 2001; Strasser & Schwabl 2004, Gustafsson et al. 1995, Desai & Hales 1997, de Kogel 1997, Birkhead et al. 1999).

2.1a Body condition and its measurement

Body condition is referred usually as the energetic (or nutritional state) of an animal, characterized with the relative size of energy reserves such as fat and protein, compared with structural components of the body (Blem 1990, Krebs & Singleton 1993, Brown 1996, Schulte-Hostedde et al. 2001). Condition is thought to be an indicator of an animal's health and quality (Peig & Green 2010). In birds, exact information about body condition can be important in a wide range of studies in ecology, evolution and behaviour (Lindström 1999). It is important to separate effects of structural size of the body from the size of the energy reserves, since both aspects can be expected to have major consequences for survival and fitness (Green 2001). However, most authors are not explicit about what they mean by condition. In many cases, body condition is used *sensu lato*, as a synonym for “good quality” animals in a good nutritional state. In the majority of papers, body condition is used *sensu stricto* (as an assessment of mobilizable energy reserves), but sometimes, other variables of growth, such as body mass or skeletal size are used as a surrogate of body condition. Many studies have shown that *sensu stricto* body condition is a good predictor of post-fledgling survival and expected reproductive success (Perrins 1964, Hochachka & Smith 1991, Thompson & Flux 1991, Lindén et al. 1992, Adriaensen et al. 1998). This was, however, also the case when other body condition predictors were measured (body size; Richner 1989, 1992, Lindén et al. 1992, Merilä and Svensson 1997, Verhulst et al. 1997, Haywood & Perrins 1992, Lindström 1999, Gebhardt-Henrich and Richner 1998 or simple body mass;

Tinbergen & Boerlijst 1990, Magrath 1991, Naef-Daenzer et al. 2001, Pettifor et al. 2001, Monrós et al. 2002, Brotons & Broggi 2003).

In living animals, measuring real body condition (that is, the proportion of body mass made up of energy stores) is possible only by using destructive procedures (Weatherhead & Brown 1996, Ardia 2005). However, numerous methods have been introduced to assess body condition in a non-destructive way: either by using a simple visually estimated scale of fat reserves (mostly at ringing of adult birds), or simply using the body mass or skeletal size as the predictor of condition (e.g. Naef-Daenzer et al. 2001, Monrós et al. 2002). To get more sophisticated measurements, several statistical procedures were introduced that attempt to separate aspects of body mass that are due to structural size from aspects that reflect real energy reserves (that is, to remove the effect of body size from body mass). The majority of these methods rely on relating body mass and some linear measure of body size (body size indicator, BSI) to calculate a condition index (CI) (Green 2001, Stevenson & Woods 2006). Initially, simple ratios between body mass and linear body size measures have been used (Blem 1990, Brown 1996, Møller 1987, Chastel et al. 1995, Brinkhof 1997). Later, it has become fashionable to use residual body masses (RBM; Brown 1996) that are computed as the residuals of a Type I regression (or ordinary least squares linear regression, OLS) of one or more BSI (mainly skeletal measures but sometimes also feather length) against body mass, suggesting that RBM provides the cleanest way to separate the effects of condition from the effects of body size (Reist 1985, Krebs & Singleton 1993, Brown 1996, Green 2001). Positive residuals are assumed to represent excess mass relative to body size and therefore more physiological stores.

To increase the accuracy of body condition measurements, some authors suggest to use the first principal component of a principal component analysis (PCA) of multiple structural size measures (Kirk & Gosler 1994, Blanco et al. 1997) instead of using single structural traits as BSI or the “scaled mass index” instead of OLS residuals (Peig & Green 2009).

2.1b Factors affecting early development and condition in altricial birds: rearing environment, parental performance and parasites

Postnatal growth rates in altricial birds may show considerable variation not only among species, but also among populations of the same species (O'Connor 1978, Ricklefs 1984), mostly due to adaptations to variable environments, such as habitat quality (Tremblay et al. 2003), aridity (Tieleman et al. 2004), and latitude (Ricklefs 1976, Wikelski et al. 2003), predictability of food supply (e.g. insect availability), nest predation risk, or length of the breeding season. (Ricklefs 1984, Remes & Martin 2002, Lack 1968, Bosque & Bosque 1995, Halupka 1998, Kunz & Ekman 2000).

Among climatic factors, temperature is particularly important, since body metabolism and hence condition can be sensitive to thermal microclimatic environment of the nest during development (Chaplin et al. 2002, Dawson et al. 2005). Altricial nestlings are faced with an energy allocation trade-off between growth and thermoregulation. In particular, after young begin to thermoregulate on their own and are no longer brooded by parents, they need to allocate their available resources to both tissue growth and maintenance activities such sustaining elevated body temperature (Schew & Ricklefs 1998). Warm nest environments may reduce costs of maintaining homeothermy and so promote faster growth, which, in turn, results in greater lipid stores (Ardia 2005), enhanced survival while in the nest, and larger and heavier offspring at fledging (Dawson et al. 2005).

Besides abiotic factors, chick development in altricial birds is largely influenced by parental performance, both in the pre-hatching (e.g. parental attendance of eggs during incubation: Gorman & Nager 2004; incubation temperature: Reid et al. 2000) and post-hatching (nutrition) period. Offspring of virtually all birds (and many other taxa) rely on one or both parents for early nutrition (Clutton-Brock 1991). In altricial birds, access to food in the post-hatching period may be controlled entirely by parents, typically delivered as single-item prey (insect) loads by one or both parents. Therefore, parental nutrition effort

is crucial in offspring survival and quality. Parental provisioning effort, however, depends on many variables. For iteroparous organisms, decisions about how much effort can be allocated in the current breeding attempt depends on the individual's current state and its future expectations. Parents in poor condition or subjected to stresses (e.g. due to pathogen attacks, intense predation risk, or adverse social environment) may reduce their current effort to avoid risking survival and future reproductive attempts, giving rise to poorly provisioned, low-quality offspring (Chastel et al. 1995, Moreno et al. 1997). In case of biparental care, decisions about parental effort is a result of a complex interplay between the caring parents (Houston & Davies 1985, Houston et al. 2005). An individual usually decreases but sometimes increases its own effort in response to the mate's effort or quality, as a compensation for the mate's reduced effort (e.g., Saino & Møller 1995, Burley 1986, Dearborn 2001, Harrison et al. 2009).

Many studies on birds have demonstrated that nestling growth rates vary with food availability (e.g. Nilsson & Gårdmark 2001, Keller & van Noordwijk 1994, Tremblay et al. 2003) and quality (e.g. Johnston 1993, Romano et al. 2006). Quality of parental provisioning (measured in form of feeding frequency, or size and quality of delivered prey items) has been repeatedly found as highly related to both short- and long-time survival, growth, condition and reproductive success of offsprings (Lack 1954, 1968, Martin 1987, Maccoll & Hatchwell 2004, Schwagmeyer & Mock 2008). Similarly, a series of experimental manipulations of food quantity (Searcy et al. 2004) or quality (e.g. protein content) have been reported to have profound effects on nestlings (Martin 1987, Kunz & Ekman 2000, Dawson & Bidwell 2005). Development of altricial birds depends not only on protein mass delivered by feeding parents but also on availability of critical dietary nutrients. Antioxidants, dietary carotenoids, vitamins and other biologically active molecules that can not be synthesized *de novo* by nestlings, have great importance during the nestling phase (Royle et al. 2003, Blount et al. 2002). A part of these limiting resources can be delivered to offspring via maternal effects (see below), but during the period of fast growth in the nest, these can only be achieved by

parental provision. If they are available in limited amounts to nestlings, this limitation may affect growth, development or immune defence against nest parasites (Tschirren et al. 2003, O'Brien & Dawson 2008).

Intranest competition for food is another important biotic environmental component that affects offspring development. Numerous studies have shown that experimentally enlarged brood sizes (by reducing the amount of food provided per nestling and hence enhancing intensity of sibling competition) resulted in lower condition (Tinbergen & Boerlijst 1990, Birkhead et al. 1999, Brinkhof et al. 1999, Naguib et al. 2004) survival (Dijkstra et al. 1990, de Kogel 1997) and recruitment rates after migration (e.g. Gustafsson & Sutherland 1988). Outcome of this competition can partly be influenced by both maternal effects and behavioural adaptations.

An organism's phenotype can be influenced not just by its own current environment, but also by influences that result from current or past environmental effects on its reproducing parent(s) that are transmitted to the developing offspring. These are generally referred to as maternal effects (Mousseau & Fox 1998). One of the most fundamental maternal effects concerns variation in propagule size and quality (Bernardo 1996). In birds, females have the ability to invest directly in their offspring by the size and content of their eggs (Rossiter 1996, Schwabl 1993, Janzen et al. 1998, Lovern & Wade 2001). This maternal investment can have a profound effect not only on the growth and development of offspring, but also on individual fitness in adulthood (Clark & Galef 1995, Lindström 1999). Egg size itself may constitute a maternal effect for the offspring (Rossiter 1996). In a wide range of bird species, egg size is positively correlated with hatchling size, nestling growth and survival (Williams 1994) due to larger amounts of energy reserves deposited in a larger yolk sac (Birkhead & Nettleship 1982). Furthermore, not only nutrients, but bioactive components like androgens (testosterone, dihydrotestosterone, and androstenedione) antioxidants (carotenoids, vitamin E) and antibodies are also available to embryos from the yolk of avian eggs (Schwabl 1993, Gil et al. 1999, Groothuis & Schwabl 2002, Royle et al. 1999, Royle et al.

2001, Blount et al. 2002, Buechler et al. 2002). Differential deposition of these biologically active molecules via egg to the developing offspring have been identified as adaptive mechanisms that influence offspring adaptations to changing environments (Mousseau & Fox, 1998), showing that mothers can actively shape offspring performance in an adaptive way. Carotenoids deposited in egg yolk, for example, affect immunocompetence of nestling birds (Saino et al. 2003), and may provide protection against parasites (O'Brien & Dawson 2008, but see Berthouly et al. 2007) and oxidative tissue damage during hatching (Surai & Speake 1998). Maternally derived immunoglobulins may enhance growth, survival and fertility of the offspring (Heeb et al. 1998, Buechler et al. 2002). Similarly, positive post-hatching effects of maternal yolk androgens have been found in several songbird species, with enhanced nestling growth (Schwabl 1996, Navara et al. 2005, Eising et al. 2001), hatching muscle development (Lipar & Ketterson 2000) begging behaviour and social dominance among siblings (Schwabl 1993, Eising & Groothuis 2003, Schwabl & Lipar 2002). Besides their beneficial effects, high androgen deposition in eggs may be limited by physiological requirements in both mother (eg. in form of reduced fecundity; Rutkowska et al 2005) and nestling (eg. in form of reduced growth and survival; Sockman & Schwabl 2000).

Even in case of beneficial environment and superior parental investment, the presence of parasites during offspring development can ruin a good start in life. Nest-dwelling ectoparasites are specially adapted to feed on vertebrate offspring (Proctor & Owens 2000). Since nestlings are exposed to them in the early period of energy demanding fast growth, (and with immature immunity; Christe et al. 1998), they can have radical consequences on both short and long-term fitness. Several nest-dwelling ectoparasitic taxa have been shown to have particularly detrimental effects on nestlings, causing poor early growth that leads to reduced condition, survival, fitness (Brown, et al. 1995, Gebhardt-Henrich & Richner 1998, Simon et al. 2003, Fitze et al. 2004) or even death (Badyaev et al. 2006). Nestling condition may be adversely affected by ectoparasites either directly by the loss of nutrients due to parasite feeding activities (Simon et al. 2003) or indirectly, by causing

increased investment in immune function in their hosts (Sheldon & Verhulst 1996, Lindström et al. 2004). If developing nestlings face a trade-off between investment in immune response and other metabolic processes, reduced allocation to growth could result in poor quality nestlings (Soler et al. 2003, Bize et al. 2003). Arrested growth, however, can be compensated for with plasticity in developmental programs, using delayed maturity or compensatory growth (Metcalf & Monaghan 2001, see later).

Of course, parents may also attempt to compensate for parasitism by increasing feeding rates (Perrin et al. 1996, Tripet & Richner 1997, Tripet et al. 2002) or by using parasite-repellent herbs in the nest (Clark & Masson 1985, Wimberger 1984, Petit et al. 2002, Gwinner & Berger 2005), and by adjusting the composition of food in the presence of nest ectoparasites by increasing the intake of limiting nutrients (e.g. carotenoids or other antioxidants that have essential role in immune defense against the parasites; Banbura et al. 2004, O'Brien & Dawson 2008). Such limiting nutrients can also be transferred to offspring via maternal effects (see above).

2.1c Immediate and long-term consequences of early development: growth, condition, survival and fitness

Since young birds in post-hatching and post-fledging period are particularly sensitive to perturbations, any stress (heavy parasite burden, extreme weather or food shortage) experienced during the period of rapid growth, together with a poor ability to handle them, may have serious consequences on an individual's phenotype while in the nest, at the time of fledging and later in adulthood. The earlier an individual's development is disturbed, the stronger are the effects (Henry & Uliaszek 1996).

During the nestling period, serious stress factors often cause retarded growth, and hence smaller size or poor condition (Boag 1987, Richner 1989, De Kogel & Prijs 1996, Lindström 1999). Note that small adult body size - as predicted by theory - could be even beneficial in many ways (Blackenhorn 2000),

empirical evidence is, however, yet lacking. Plasticity in developmental programs may help stressed individuals to escape the immediate severe consequences, and hence to catch up in size to reach the level of non-stressed individuals. Developmental plasticity as a response to food shortage (caused by either poor parental care or by short-term fluctuations in food supply within a season), low temperatures or heavy parasite infection is well documented (Wrege & Emlen 1991, Schew & Ricklefs 1998, Metcalfe & Monaghan 2001, Bize et al. 2005). Two compensatory strategies can be used to face poor growing conditions. First, after a period with harsh conditions, individuals may grow at a steeper rate if condition improves (called compensatory growth, reviewed by Hector & Nakagawa 2012). Second, if the length of the maturation is not fixed, individuals may prolong the period of growth and hence delaying fledging time (delayed maturation hypothesis). The two mechanisms can work in concert: nestling may simultaneously alter their growth rate and extend the growth period in response to poor rearing conditions. While these compensatory responses confer a net benefit, they may carry significant costs for nestlings and their parents. Delayed maturation increases the risk of mortality prior to breeding (Metcalfe & Monaghan 2001), and compensatory growth has been shown to correlate negatively with survival rates, adult longevity, reproductive output and social dominance (Dmitriew & Rowe 2007, Birkhead et al. 1999, Auer et al. 2010, Royle et al. 2005).

In short-lived birds, rate of recruitment to the reproducing population can be very low, mainly due to the high mortality during the post-fledging period and migration. In great tits, for example, only 5–30% of the juveniles fledged recruit into the local breeding populations (Perrins 1986, Tinbergen & Boerlijst 1990, Verboven & Visser 1998). Besides hatching date in the season (Perrins 1965, Harris et al. 1992, Olsson 1997, but see Nisbet 1996, Monrós et al. 2002), body condition and body size at fledging has been proposed as the most reliable predictor of post-fledgling survival (Gebhardt-Henrich & Richner 1998, Gustafsson & Sutherland 1988, Tinbergen & Boerlijst 1990, Magrath 1991, Lindén et al. 1992, Adriaensen et al. 1998, Naef-Daenzer et al. 2001, Monrós et al. 2002, but see Stienen &

Brenninkmeijer 2002, Brown & Roth 2004) and recruitment (Brotons & Broggi 2003). Fledging condition may reflect the capacity to resist food shortages (Perrins 1965), or the ability to compete with other fledglings (Both et al. 1999). Furthermore, in migratory birds, early conditions might influence the amount of energy reserves, that affects survival during the energetically demanding migration. In migratory blue tits (*Parus caeruleus*), nestling body condition (and hatching dates) were good predictors of the amount of fat reserves during autumn migration (Merilä & Svensson 1997).

Once survived until reproduction, birds face new challenges that are also affected by early development. Poor body condition at fledging forecasts reduced fecundity (Haywood & Perrins 1992, Gustafsson & Sutherland 1988), competitive ability (Royle et al. 2005), and sexual attractiveness (de Kogel & Prijs 1996) in adulthood. Haywood & Perrins (1992) showed that the clutch-size control mechanism of captive zebra finch and free-living great tit females is influenced permanently by conditions prevailing during ontogeny, so thus body weight after fledging was positively correlated with subsequent clutch size.

It has been repeatedly suggested that – besides the genetic background – the development of male secondary sexual signals (either acoustic or visual) are highly dependent on condition. Only individuals that experience good levels of nutrition can afford to invest adequately in both sexual signal development and development of the overall phenotypic quality (as proposed in theories of honest indicator mechanisms, Andersson 1994). Good condition is important during the time of sexual maturation when sexual signals are developing, but also early rearing conditions may be crucial in later expression of sexual signals.

In several songbird species, song repertoire was found to be negatively affected by suboptimal early nutritional conditions (reed warbler, *Melospiza* sparrows: Nowicki et al. 2000, 2002, bengalese finches: Soma et al. 2006, but see Gil et al. 2006 on zebra finches). As a proximate mechanism, Nowicki et al. (1998) proposed that brain structures associated with song learning and production (the caudal nucleus of the ventral hyperstriatum, the robust nucleus of the archistriatum,

or the lateral magnocellular nucleus of the anterior neostriatum) develop rapidly during the first few weeks after hatching, and hence are highly vulnerable to nutritional stress, due to the fierce trade-off between investing in the development of brain structures and many other aspects of growth (nutritional stress hypothesis).

In visual signals, both melanin- and carotenoid pigment-based ornaments have been found to be condition-dependent (Olson & Owens 1998; von Schantz et al. 1999; Blount et al. 2003; Galván & Alonso-Alvarez 2008). Besides genetic constraints, condition-dependent physiological mechanisms of pigment absorption, transport, storage, metabolism and deposition may affect colour intensity (Brush 1978, Frischknecht 1993, Hill & Montgomerie 1994, Bortolotti et al. 1996, Thompson et al. 1997, Vágási et al. 2012). Since environmental circumstances during early developmental states can highly influence body condition, colour expression may be also determined early in nestling life. Nutritional conditions during early growth (in form of protein intake and carotenoid availability, both provided by parental feeding during the nestling and post-fledged period) was found to influence the expression of male secondary sexual ornaments in adult life (e.g. wattle size and coloration in ring-necked pheasant: Ohlsson et al. 2002; plumage coloration in great tits: Tschirren et al. 2003, Fitze et al. 2003; yellow coloration in male blue tits: Peters et al. 2007, grey colouration in Eurasian kestrels: Fargallo et al. 2007). Condition-dependence was also demonstrated for structural colours. In blue tit nestlings, not only carotenoid-based traits, but also the chroma (spectral purity) of UV/blue tail feathers was positively associated with nestling condition (Johnsen et al. 2003).

Focusing on another measure of male quality, Verhulst et al. (1997) showed that the body condition of great tits, during early development, correlated positively with the quality of the breeding habitat that the birds later occupied.

2.2 EARLY DEVELOPMENT AND PARASITES

2.2a Impact of ectoparasites on nestling birds

By definition, parasites reduce the fitness of their hosts (Price 1980). Nest-dwelling arthropod ectoparasites that are adapted to feed on early life stages of developing birds (e.g. various genera of fleas, blowflies, chewing lice, bugs and mites), might have radical consequences on both short and long-term fitness, given that nestlings are exposed to them in a sensitive period of energy demanding fast growth and development (Møller et al. 1990, Loye & Zuk 1991 and Clayton & Moore 1997, Proctor & Owens 2000). Nest-based ectoparasites may have a number of detrimental effects on nestlings, including loss of nutrients and metabolites due to blood consumption, tissue damage, immune reactions, irritation or transmission of microbial or viral infections. As a result, they often impair nestling growth and development, resulting offspring in poor condition at fledging (Allander 1998, Clayton & Tompkins 1995, Fitze et al. 2004, Fitze et al. 2004, Brown, Brown & Rannala 1995, Gebhardt-Henrich & Richner 1998, Simon et al. 2004).

The impact of ectoparasites on nestling quality, however, may vary considerably due to variation in environmental factors such as climate, food abundance, parasite abundance, virulence and their interactions (Merino & Potti 1996, Lope et al. 1993). Furthermore, there may be differences between host populations with respect to their ability to defend themselves against ectoparasites. Hen fleas were, for instance, shown to have large impacts on great tit host by Richner et al. (1993), whereas in other studies no such effects (Eeva et al. 1994) or ambiguous results were found (Allander 1998, Dufva & Allander 1996). Good nutritional status (e.g. in experiments with additional dietary protein or carotenoids) can alleviate some of the otherwise detrimental effects of ectoparasites (Merino & Potti 1998, O'Brien & Dawson 2008).

To avoid nest-based parasites or to reduce their detrimental effects, bird hosts evolved various physiological defence mechanisms and behavioural strategies. For example, parents may select nest-sites with low loads of ectoparasites (Brown & Brown 1991), desert heavily infested nests (Richner et al. 1993, Oppliger et

al.1994, Christe et al. 1994, Merilä & Allander 1995), remove infected nest material (Pacejka et al. 1998), alter the start of reproduction (Møller 1993; Oppliger et al. 1994), alter clutch size (Richner & Heeb 1995, Richner & Tripet 1999, Martin et al. 2001) or increase feeding effort (Møller 1993, Christe et al. 1996, Tripet & Richner 1997).

In altricial birds, an increase in food provisioning may compensate for the impact of parasitism presumably by providing additional resources to fight off parasites (Perrin et al. 1996, Tripet & Richner 1997, Tripet et al. 2002). There is evidence that parents not only increase feeding rates, but also alter the composition of food provisioned in the presence of ectoparasites (Banbura et al. 2004, O'Brien & Russell 2008). This suggests that parents may be attempting to increase the parasitised nestling's intake of limiting nutrients (e.g. carotenoids or other antioxidants).

Environmental conditions, (e.g. the availability of food, climate, parasite abundance and virulence) however, can significantly modify the outcome of the parents' increased effort. In some cases, even hard working parents cannot fully redeem the negative effect of parasites (Hurtrez-Boussés et al. 1998). In other cases, even high loads of ectoparasites had no effect on parental feeding rates, or nestling begging intensity (Thomas & Shutler 2001, Morrison & Johnson 2002), which maybe due to selection on ectoparasites to avoid killing their hosts.

Besides the elevated level of food provisioning, parents might also allocate more time to nest sanitation in order to protect the nestlings (and the incubating adults) from harmful ectoparasites (Christe et al. 1996, Hurtrez-Boussés & Renaud 2000, Tripet et al. 2002), or incorporate plant materials with aromatic secondary compounds that may repel ectoparasites (and other pathogens) or mask the chemical cues that ectoparasites use to find their targets (Clark & Masson 1985, Wimberger 1984, Petit et al. 2002, Gwinner & Berger 2005).

Most of these behavioural adaptations are however time consuming for the breeding parents and compete directly with time devoted to other activities (e.g. foraging, courtship and mating behaviour etc.) and hence may reduce their future

reproductive success (Christe et al. 1996, Richner & Tripet 1999). To lower some of these fitness costs, brooding females could allocate more time to preening and nest sanitation at night at the expense of sleeping (Christe et al. 1996), or decrease the duration of food provisioning and nest sanitation events (Tripet et al. 2002).

Besides post-hatching parental responses such as increased parental care or nest sanitation, parents may reduce the effect of parasites and increase their reproductive success via pre-hatching mechanisms as well. Such a strategy is to increase the magnitude of hatching asynchrony. This results in the production of chicks that differ in competitiveness for parental food and the maturation of their immune system (called the 'tasty chick hypothesis' by Christe et al. 1998). Consequently, junior chicks would have less well developed immune system and hence can serve as a sink for the prevailing nest-based ectoparasites while larger senior chicks would enjoy reduced parasite loads, allowing the parents to produce more high quality offspring and achieve a higher fitness return as compared to the situation of synchronous broods with evenly distributed ectoparasites. Given that life cycle of most nest-dwelling ectoparasites is adjusted to nestling development, they are mostly low in numbers in the early nestling phase (Proctor and Owens 2000). So thus, first-hatched nestling (the only target parasites can feed on until their nestmates are hatched) might escape serious health damages; a further benefit of asynchronous hatching.

This adaptation was found in some bird-ectoparasite systems (Christe et al. 1998, Roulin et al. 2003), but not in others, suggesting the importance of specific aspects of the life history and ecological requirements of the various ectoparasite and host species (Roulin et al. 2003).

Other important pre-hatching parental mechanisms that might reduce the impact of ectoparasites are parasite-induced maternal effects, which have been observed in birds and mammals (e.g. Rose & Orlans 1981, Graczyk et al. 1994). The transfer of maternal antibodies (immunoglobulins) or hormones at egg laying might be beneficial for the offspring in various forms. In great tits, as a pre-hatching maternal response to hen flea parasitism, transfer of maternal yolk

testosterone via the egg enhanced the development and phenotypic quality of nestling birds (Tschirren et al. 2005), while maternal immunoglobulins (IgG) enhanced survival and fertility of the offspring (Heeb et al. 1998, Buechler et al. 2002) and reduced the survival of fleas (Walker et al. 2003, Gallizzi & Richner 2008). Additionally, great tits mothers exposed to fleas produced eggs with larger IgG-concentration, and their nestlings grew faster than nestlings of unexposed females (Buechler et al. 2002).

As another adaptation, developmental plasticity allows hosts' nestling to compensate for the effect of parasitism on their phenotype by adjusting their growth to the poor conditions caused by ectoparasites (by prolonging the period of growth, or showing accelerated growth if parasite load decreases (Bize et al. 2003, Metcalfe & Monaghan 2001, Bize et al 2005). Moreover, developmental plasticity enables parasited nestling to escape heavily parasitised nests sooner, by allocating more energy in feather development instead of body growth, as it was found in bank swallows (*Riparia riparia*) infested with ticks (Szép & Møller 1999).

Among the huge number of studies on various bird-ectoparasite systems, only a minor part focuses not on the bird host but the parasites itself. These are mainly involved in parasite life history (e.g. Heeb et al. 1996, Harper et al. 1992), parasite population structure and dynamics (Heeb et al. 2000, Pulin & Morand 1997, Pacejka et al. 1996, Tripet & Richner 1999a, Tripet & Richner 1999b, Garvin et al. 2004), their role as vectors of micropathogens (e.g. Moro et al. 2009, 2009b) or the effects of the host's physiological responses on their fitness (e.g. immune responses; Møller 2000, Harrington et al. 2009, Owen et al. 2009 or maternal effects; Walker et al. 2003, Badyaev et al. 2006, Gallizzi & Richner 2008).

2.2b Within-brood distribution of nest-dwelling ectoparasites

Within-brood distribution of nest-dwelling ectoparasitic arthropods among nestling in nests of altricial birds is usually explained by the parasites' preferences for certain kinds of host characteristics. First, some studies suggest that ectoparasites prefer the best quality (oldest and biggest) chicks within the brood, which may be

advantageous because parasites can find better food resources or more protection in the more developed feathers against host defense on larger host individuals than on smaller ones (Kethley & Johnston 1975, Clayton 1991, Darolová et al. 1997, Dawson & Bortolotti 1997). Note, however, that irrespectively from parasite preference, body size may affect ectoparasite abundance simply because larger hosts offer larger patches for parasites to inhabit than smaller nestlings (Kuris et al. 1980, Rózsa 1997a, 1997b, Groutler & Poulin 1998). Second, within-brood variation in parasite infestation may be explained by individual differences in offspring's susceptibility to parasites (Møller 1990, Lochmiller 1996, Christe et al. 1998, Roulin et al. 2003, Simon et al. 2003). Immune functions are costly to produce and maintain; thus, individuals in better condition can raise a more successful defense against parasites than individuals in poor condition (Lochmiller 1996, Saino et al. 1997, Brinkhof et al. 1999, Hoi-Leitner et al. 2001). Moreover, since nestlings need time to develop an effective immune system, older (and larger) chicks regularly show a better immunocompetence than younger ones in the brood (Ros et al. 1997, Apanius 1998). Consequently, nestling with low immunological quality (which are often the youngest and smallest ones) could be targets of parasite preference (Christe et al. 1998, Roulin et al. 2003, Simon et al. 2003).

An alternative approach to understand within-brood variance in ectoparasite infection could be to focus on the avoidance, rather than the preference of certain nestling by the parasites. Most macronyssid nest mites, for example, feed primarily on unfledged young birds (Clark & Yunker 1956, Proctor & Owens 2000, Webb & Bennett 2002). Their reproduction is largely adjusted to the development of chicks, and they can reach great abundances in short time in the brood (Mullen & O'Connor 2001). The entire developmental cycle occurs fully in the nest: non-feeding forms inhabit the nest material but also feeding protonymphs and adults spend a part of their time off their host, living and breeding in the nest material, and emerging only periodically to feed on the nestlings (Clark & Yunker 1956).

For such parasites, their removal from the nest could be detrimental because of the loss of breeding habitat, including mating partners, optimal climatic conditions

for offspring development, and potential food resources provided by the unfledged chicks from the current or subsequent breeding attempts. Dwelling or feeding on hosts just prior fledging can therefore be risky because it increases the chance of the undesirable removal from the nest. Thus, the ability to recognize that nestlings are ready to fledge, along with the abandonment of mature nestling before they leave the nest can be adaptive, allowing the parasite to stay in the nest and continue reproduction. This behavioural response of ectoparasites and its effects on within-brood parasite distributions has received little attention so far, and similar mechanisms have only been investigated in commensalist feather mites of passerine birds (Jovani & Serrano 2001, Pap et al. 2005)

2.2c Haematophagous macronyssid mites

Mite species of the family *Macronyssidae* are parasitic arthropods of birds and mammals (Clark & Yunker 1956, Proctor & Owens 2000, Webb & Bennett 2002). In birds, they feed primarily on unfledged nestlings (and sometimes on adults) of many wild bird species, but they can also be found on domesticated poultry as well. Haematophagous mites typically have a life cycle of 5-12 days, including larval, nymphal and adult stages (Fig.1). Blood meals are needed for moult of juvenile mites and for reproduction of adults. Adult females lay their eggs after their first blood meal on (or nearby) the host. In optimal conditions, these eggs normally hatch within 1-3 days, liberating six-legged larvae. These larvae do not feed, and moult in few hours to become protonymphs which have biting mouth parts and require blood meals. In 1-2 days, they moult again and become non-feeding deutonymphs. This stage develop into adults after a third moult within 3-4 days. Under favourable conditions the adults reproduce rapidly. Their complete life cycle from egg to egg-laying female can ideally take place in 5-7 days, but usually takes longer, depending on temperature and humidity. Therefore, although female mites lay only a few (2-9) eggs, mite numbers can rise rapidly and large populations can be built up in the nests within several generations through the breeding season, reaching great abundances in short time in the brood (Proctor and Owens 2000,

Webb & Bennett 2002). Typically, nestlings in most bird species spend at least 2-3 weeks in the nest before fledging (for example, house sparrow chicks leave their nest within 13-16 days after hatching; Summer-Smith 1963). Within this period, nest mites can raise potentially two or three generations enormously multiplying their numbers.

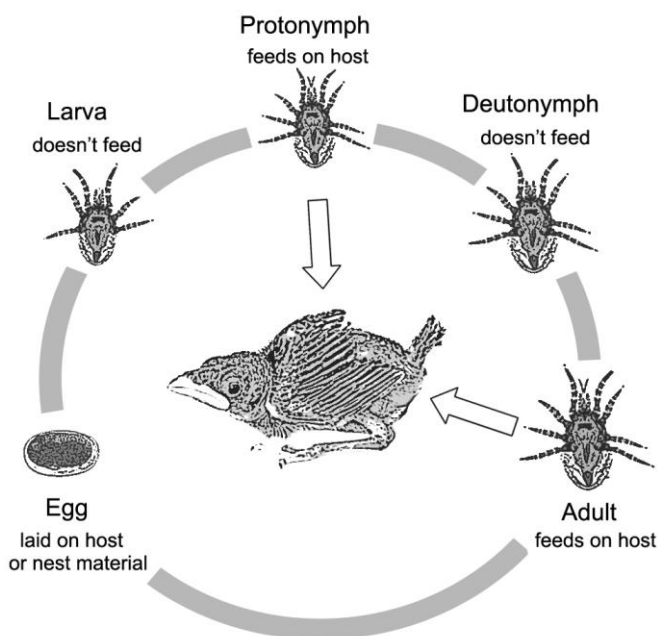


Figure 1. Life cycle of nest-dwelling macronyssid mites

Dermanyssus and *Ornithonyssus* mites, two genera in the *Macronyssidae* family, are well studied, mostly owing to their economic impact on domesticated birds. Fowl mites, such as *Dermanyssus gallinae* (chicken mite; De Geer 1778) *Ornithonyssus sylviarum* (northern fowl mite; Canestrini & Fanzago 1877) and *Ornithonyssus bursa* (tropical fowl mite; Berlese 1888) are well known ectoparasites feeding on the blood of many bird species and also as common pests of poultry and cage birds. The tropical rat mite (*Ornithonyssus bacoti*; Hirst 1931) is associated with a wide variety of mammals all over the world. Nest mites of the genus *Pellonyssus* are however much less studied despite the fact that they have been found in many wild birds. Some species are host specific; *P. gorgasi* (Yunker

& Radovsky 1966) is not known from any host but *Trochilidae* hummingbirds (Trochilidae; Radovsky 1998), while *P. reedi* (Zumpt & Patterson 1952) is described from various bird species (e.g. Clark & Yunker 1956, Baker et al. 1976, Stoehr et al. 2000).

Macronyssid mites belonging to different species are morphologically very similar in appearance, yet have different life cycle and ecological requirements. for instance, in *Ornithonyssus sylviarum*, adult mites spend virtually their entire life on the host bird, whereas the other life stages (and some of the adults) are found mainly in the nest material. Eggs are also laid on the host (Combs & Lancaster 1965). They cannot survive for longer than two weeks away from a bird host without a blood meal (Mullens et al. 2000). Life stages of *O. bursa*, however, predominantly inhabit the nests of their hosts with intermittent feeding forays made by the protonymphs and adults on the hosts themselves. Eggs may be found of the feathers as well as in the nest material. This species also cannot survive for longer than 10 days away from a bird host (Mullen & O'connor 2002). *Dermanyssus* mites spend much of its time off the host bird, hiding during the day and feeding at night. Eggs are also laid on nest material or debris near the host individuals. These arthropods can survive for extended periods off a host, starving up to 9 months without a meal of blood (Kirkwood, 1963, Phillis 1972). *Pellonyssus* mites are also less attached to their hosts. Non-feeding forms (larval and deuteronymph stages) inhabit mostly the nest material, but also feeding stages (protonymphs and adults) spend a part of their time off their host, living and breeding in the nest material, and emerging only periodically to feed on the nestlings (Clark & Yunker, 1956).

Bird mites are fairly mobile arthropods. When nestlings fledged from the nest, or die, many mites (often many thousands) are left behind in the absence of a suitable host, they might disperse from the nest into and throughout the dwelling searching for new hosts (Mullens et al. 2001). Because of their short life cycle and fast reproduction, bird mites can reach great abundances in the nest in short time, sometimes causing severe effects on the nestling hosts via blood consumption, tissue damage, irritation and microparasite transmission (Arrends et al. 1984, Moro

et al. 2009, 2009b). Heavy infestations can cause death by blood loss or exsanguination even in large birds (Arrends et al. 1984). *Dermanyssus* and *Ornithonyssus* mites has been reported to cause economic damage on poultry farms by causing anaemia and lower egg production (e.g. Arrends et al. 1984, Mullen & O'Connor 2000). Similarly, nestling of almost all wild bird species may be parasitized by thousands of macronyssid nest mites (Proctor and Owens 2000). High levels of mite parasitism may affect the hosts' reproductive success in many ways: slowed nestling development with reduced body weight and size at fledging (Møller 1990, 1990b, 1993, Berggren 2005, Morrison & Johnson 2002, Clayton & Tompkins 1995, Stoehr et al. 2000, Weddle 2000), anaemia (Morrison & Johnson 2002, Potti et al. 1999, Stoehr et al. 2000), increased chick mortality (Clayton & Tompkins 1995, Stoehr et al. 2000, Badyaev et al. 2006), increased inter-clutch intervals (Møller 1990b, 1991, 2002) or lower resource allocation to future reproduction because of elevated parental costs (Møller 1987, Møller 1993), were reported in various bird hosts. On the other hand, several studies found no unambiguous relationships between mite loads and hosts' reproductive success (e.g. Rendell & Verbeek 1996, Pacejka et al. 1998). Besides fitness effect studies, there are only few papers investigating the hosts' physiological and behavioural adaptations to the mite parasitism (Møller 2000, Badyaev et al. 2006, Owen 2009, Harrington et al. 2009).

2.3 EARLY DEVELOPMENT AND PARENTAL CARE

3.1a Sexual signals and female choice in birds

Sexual selection models usually predict directional selection for ornamental traits because of intra- as well as inter-sexual selection. Female preference for mates with elaborated ornaments has often been explained on the basis that exaggerated secondary sexual traits might reflect individual quality.

The '*direct benefit hypothesis*' predicts that male ornaments will reflect tangible benefits that females will acquire as a result of their preference. Examples of direct fitness benefits include resources (e.g. nest sites, territories, nuptial gifts, male parental care) or avoidance of infectious diseases (Heywood 1989; Hoelzer 1989; Kirkpatrick & Ryan 1991; Andersson 1994). Alternatively, when no direct benefits are at hand, females might choose their mates by assessing their genetic quality. The '*good genes hypothesis*' predicts that the sexual ornaments of males will reflect favourable genes that can be passed onto their offspring: either genes for increased viability (Williams 1966), parasite resistance (Hamilton & Zuk 1982), or genes for increased attractiveness (Fisher 1915, 1930).

Both direct benefit and good genes models predict a positive relationship between the reproductive success of a male and the size of his sexual ornaments (including being preferred by females; reviewed in Jennions & Petrie 1997, 2000).

Honesty and cost of signals

The evolution of signals used in animal communication is often explained by the honesty of the information content of these traits. In this way, honesty has become to be one of the main issues in signaling theory, suggesting that advertising traits must be costly to their bearer; thus, only individuals of high phenotypic quality can exhibit maximal expression of these traits. The '*handicap principle*', first proposed by Zahavi (1975), states that communication is essentially honest, and this honesty is maintained by the cost of the signal. This ensures that the investment in producing the signal is acceptable to an honest signaler but prohibitive to a cheater. Otherwise low quality individuals would be able to cheat by producing showy

signals and consequently destabilize the signalling system. Therefore, expression of secondary sexual signals (used both in male-male competition for mates and attractiveness to females) must also entail costs to be reliable indicators of male quality (Grafen 1990). However, the nature of the cost of handicap signals is still under debate (Johnstone & Grafen 1993).

As we have just seen the reliability of the information transmitted by any trait acting as sexual signal assumes that it should be somehow costly to produce or/and maintain. Among potential costs associated with signaling, acquiring limited resources (pigments or their precursors) needed for the construction of the signaling traits has often been mentioned, especially in order to explain the evolution of colourful carotenoid signals (Hill 1992).

The '*immunocompetence handicap hypothesis*' (Folstad & Karter 1992, Wedekind 1992) highlighted the endocrine control of honest signalling, suggesting that androgens (such as testosterone) are responsible for the production of male secondary sexual traits while causing immunosuppression. In this model, the cost of being able to express sexual traits is decreased immune function, resulting in greater vulnerability to pathogens. Therefore, only high-quality males possessing 'good genes' could afford to display showy sexual characteristics without suffering reduced fitness from pathogen or parasite attack. According to this theory, cheaters could not spread in the population, since their immunocompetence would be compromised to such an extent by the effects of testosterone that their lifetime reproductive success would be reduced (Folstad & Karter 1992). Two decades later, Roberts et al. (2004) reviewed the studies attempting to find evidence for the supposed immunosuppressive qualities of testosterone. In this meta-analysis, there was no effect of testosterone on direct measures of immunity, but it did increase ectoparasite abundance in several studies. They conclude that the relationships between the endocrine and immune systems are much more complex than was previously supposed, and further studies are required to reveal their consequences in signaling.

Alternatively, authors have suggested that honest signalling may result from the trade-off between the expression of pigments in sexually selected traits and their use in physiological processes such as immunity (that is, trade-off between signal expression and self-maintenance; Owens & Wilson 1999). They propose that oxidative stress (the imbalance between production of reactive oxygen species and availability of antioxidant compounds; Finkel 2000) would have influenced the evolution of pigment-based sexual ornaments. It has been proposed that the proper development of both carotenoid- and melanin-based traits could signal the performance of antioxidants in the integuments. Carotenoids are sensitive to oxidation and can act as antioxidants (McGraw 2006, von Schantz et al. 1999, Hartley & Kennedy 2004) and similarly, melanins could behave as antioxidants and melanocyte development is very sensitive to oxidative stress (McGraw 2006, Moreno & Møller 2006) due to the glutathione, which is one of the most important intracellular antioxidant (Wu et al. 2004) and also serves as an agent regulating the process of melanogenesis (Galván & Alonso-Alvarez 2008).

Even in signals that are thought to be inexpensive to produce, some costs have been invoked to explain how they are maintained as honest signals. Maintenance costs, such as increased risk of predation or adverse social interactions may explain the honesty of these signals (Rohwer & Edward 1981, Krebs & Dawkins 1984, Jonhstone & Norris 1993). Rohwer (1975) first introduced the idea that honesty in the expression of ornamental traits may be maintained by social interactions between individuals (*'social control hypothesis'*). Signals that display social status to conspecifics (so-called badges of status) are often used in intrasexual competition, as well. The major advantage of these signals would be that, by assessing the relative fighting ability of potential opponents early in an interaction, individuals of unequal status competing for limited resources would not need to risk accidental injury or waste energy. (Rohwer 1982). In this manner, frequent testing by conspecifics would uncover cheaters. Indeed, badges of status has been found to correlate with social dominance in several passerine species (Senar 2006). The status signalling hypothesis has been tested in several species with variable

plumage patterns, showing that all types of colour (structural, carotenoid or melanin-based, and even complex combinations of them) can be good status signals. This can be explained by the fact that both status and dominance, as well as signal performance are often correlated with condition (reviewed in Griffith & Pryke 2006).

Secondary sexual signals in birds: types and costs

Ornamental plumage coloration of birds results primarily from either feather microstructure or pigments deposited in the feathers. Structural coloration is produced by the microstructure of the medullary layer of feathers. This microstructure scatters the light giving feathers green, blue, purple, ultraviolet or iridescent coloration (Prum et al. 1999a, b). The colour display produced by feather microstructure usually includes portions of the ultraviolet (UV) range of the electromagnetic spectrum, and UV-reflective plumage is common in many avian taxa (Cuthill et al. 2000; Mullen & Pohland 2008). This type of plumage coloration is invisible to humans (Bennett et al. 1994), but it is well established that most avian species are capable of detecting wavelengths in near-ultraviolet (UV, specifically UV-A) part of the spectrum (320–400 nm; Cuthill 2006). Studies have demonstrated that structural UV signals may be a very sensitive and reliable indicator of the male quality (Keyser & Hill 2000, Zampiga et al. 2004). Female mate choice for males with greater UV reflectance was found in some species (Andersson & Amundsen 1997; Johnsen et al. 1998; Andersson et al. 1998; Bennett et al. 1996; Hunt et al. 1998; Sheldon et al. 1999; Delhey et al. 2003; Siitari et al. 2002). Moreover, studies have shown that structural plumage colour can reliably signal territory quality (Keyser & Hill 2000), reproductive effort and success (Siefferman & Hill 2003, 2005a, 2005b), parasite load (Doucet & Montgomerie 2003) and viability (Sheldon et al. 1999). Besides mate choice, UV colours can also function as signals of social status or for parent-offspring communication (Hill & McGraw 2006; Tanner & Richner 2008).

Since most mammals are blind to UV (Jacobs 1993), the general use of these

signals in birds has led to the suggestion that the evolution of UV vision could have been driven by the need for a avian-specific communication channel advertising unattractiveness to mammals whilst secretly relaying social and sexual information to each other using UV (Guilford & Harvey 1998, Hausmann et al. 2003). It seems, however, that the role of this waveband might be less special than was first imagined (avian predators, for example, can perceive reflectance in this spectrum; Hunt et al. 2001).

Pigment-based bird plumages are the best studied class of feather coloration and have been shown in many species to play an important role in conspecific interactions (Andersson 1994; Hill 2002). They are mainly produced by two different pigment families: carotenoids (yellow-red traits; Goodwin 1984) and melanins (mostly brown-black traits; Jawor & Breitwisch 2003).

Carotenoid pigments are widespread in almost all living organisms and they are responsible for many of the conspicuous animal signals (e.g. pink, red, yellow and orange coloration of hair, feather or skin ornaments). Carotenoids are not toxic (they occur most often as carotenes and xanthophylls) and so animal bodies do not have to dispose of them in any particular way (Rock 1997). In contrast to other kinds of coloration, these pigments cannot be synthesised *de novo* in animals, they can only be obtained by ingestion from the environment (Brush and Power 1976, Goodwin 1984, Olson & Owens 1998, Stradi et al 2001). In birds, dietary carotenoids may either be deposited directly into feathers or chemically modified prior to pigment absorption and deposition in the plumage (Stradi et al 2001).

Carotenoid-based signals are often cited as honest, condition-dependent indicators of individual quality, and in many cases, they are seemingly associated with mate quality and reproductive advantage (Olson & Owens 1998). In several studies, females were found to prefer brighter males, and the intensity of male carotenoid pigmentation was subsequently found to be correlated with some index of vigour. Since carotenoids are scarce in nature (Hill 1991, Hill 1992), and they can only be acquired from the environment, i.e. from food, the most widely discussed hypothesis is that using carotenoids in non-recoverable form (i.e. in dead

tissues, such as scales and feathers) incurs a significant opportunity cost, showing the bearer's foraging skills (Goodwin 1984, Senar & Escobar 2002).

A more recently proposed mechanism suggests that carotenoids could have a detrimental effect on the body (by contributing to the disintegration of cell membranes), therefore, their ingestion is a health risk (Zahavi & Zahavi 1997). On the contrary, most authors suggest that intake of carotenoids might be extremely valuable because of their beneficial physiological functions (Gray 1996, Krinsky 2001). Carotenoids appear to be extremely important in a variety of physiological processes. They can be oxidized or reduced to produce many other carotenoids and their derivatives (e.g. vitamin A). They are thought to be involved in production of steroid hormones that regulate reproduction (Bendich 1993), and in important immunological processes as antioxidants with the potency of free-radical absorption (Olson & Owens 1998, Blount et al. 2003, Krinsky & Yeum 2003). Therefore, carotenoid-based traits might display good antioxidant health status by signalling the excellence of the antioxidant resources (Olson & Owens 1998, von Schantz et al. 1999, Blount et al. 2003). On the other hand, given that oxidation of carotenoids alters or destroys their colour (i.e. bleaches them), preservation of their colour intensity would indicate the possession of efficient means for their protection. So thus, it is not the carotenoids themselves that might be responsible for the antioxidant effect, they rather signal the presence of other (uncoloured) antioxidant resources that are important in immune functions (Hartley & Kennedy 2004).

Many birds develop patches of black or brown coloration that are derived from melanin pigments and serve as sexual or social signals. Most melanin-pigmented animals deposit several types of melanin into their skin, hair and/or feathers (e.g. Prota 1992). In animals, melanin pigments are the end products of a biochemical pathway, they can be *de novo* synthesized from their precursors (the non-essential amino acid tyrosine, or alternatively the essential amino acid phenylalanine which can be converted to tyrosine; Hearing 1993). Tyrosine is one of the most toxic of

the amino acids (Morris 1991), and so the need to metabolize it to a non-toxic form, such as melanin, is essential.

The genetic basis of the melanocortin system is well known (e.g. Mundy 2006, Lin & Fisher 2007). In vertebrates, genetic control in the expression of melanic traits depends on the pro-opiomelanocortin (POMC) gene, which encodes different peptides that are part of the melanocortin system. Most important elements in this system are melanocyte-stimulating hormones (MSH), adrenocorticotrophic hormone (ACTH), melanocortin receptors (MCRs) agouti-signalling (ASIP) and agouti-related (AGRP) proteins (Boswell & Takeuchi 2005).

There was a debate among behavioural ecologists whether melanin-based colour signals are costly to produce. It has been argued that the expression of melanin-based traits are strictly controlled by genes and the resource for developing such trait seems to be unlimited, being less sensitive to environmental factors and overall body condition than carotenoid-based coloration (e.g. Hill & Bawnner 1998, Badyaev & Hill 2000, Bize et al. 2006). Studies that have manipulated levels of parasitism or food intake have generally found melanin-based plumage ornaments to be less responsive to such detrimental factors than carotenoid or structural based coloration, suggesting that such traits may not signal honestly phenotypic quality because their production does not entail a significant fitness cost. (e. g. McGraw & Hill 2000, McGraw et al. 2002, Hill et al. 2004, 2009). Yet, some authors state that melanin-based ornaments are signals of foraging skills. Although melanin pigmentation is not dependent on dietary pigments as is carotenoid pigmentation, individuals must ingest enough of the right type of amino acids to produce maximum color expression, so nutrition has the potential to affect pigmentation. Experiments with captive birds indicate that the availability of calcium (Niecke et al 2003, McGraw 2007), or amino acid precursors to melanin (Poston et al. 2005) could be limiting for the production of melanins (Fargallo et al. 2007a, 2007b). Several experiments have demonstrated that adverse rearing conditions, parasite infections and diet quality influence the expression of different melanin-based

signals (Fitze & Richner 2002, Griffith et al. 2006). Therefore, in spite of strong support for genetic control in melanin production, they might be related to the condition of the bearer, expressing a certain phenotypic plasticity (West-Eberhard 2003, Price 2006, McGraw 2008). Roulin et al. (2008) suggest that the condition-dependent component of the melanin-based signals might be mediated by corticosterone: stress factors (lack of food, etc.) induce a rise in circulating corticosterone which inhibits the secretion factors involved in melanogenesis (e.g. melanocortins and tyrosinase).

Other hypotheses propose that the cost of the melanin-based ornaments is related to the hormones involved in melanogenesis. Thus, both testosterone, often linked to the production of sexually-dimorphic melanic traits (Jawor & Breitwisch 2003, Owens & Short 1995) and melanocyte-stimulating hormone (MSH) promote immunosuppression (Roberts et al. 2004, Evans et al. 2000, Gantz & Fong 2003). The expression of melanin-based traits should be hence costly in terms of higher susceptibility to infections (McGraw 2006, Evans et al. 2000, Moreno & Møller 2006). Moreover, Galván & Alonso-Alvarez (2008) hypothesized that among environmental factors, similarly to carotenoid pigments, oxidative stress would have influenced the evolution of melanin-dependent traits, signaling the ability to cope with it. In vertebrates, low levels of glutathione (often considered as the most important intracellular antioxidant) are needed to promote melanogenesis. Individuals with low enough levels of glutathione, such as those required for melanin production must have sufficient alternative antioxidant resources to counteract the decrease of glutathione levels.

In recent years, a variety of statements have been made regarding differences in the signalling content of melanin and carotenoid-based sexual traits. Animals were believed to utilize the two types of signals differently in their communication with conspecifics, with carotenoid pigmentation involved mostly in female choice, representing the physiological condition of males during moult, and melanin coloration indicating social status (e.g. Kodric-Brown & Brown 1984; Møller

1988; Gray 1996, McGraw & Hill 2000). More recently, however, there have been some very clear demonstrations that there is no clear evidence of a difference between the two signal types (reviewed by Griffith et al. 2006). Carotenoid-based red plumage can also act as a status signal and predict the outcome of experimental aggressive interactions (Pryke et al. 2002; Pryke & Andersson 2003, but see McGraw & Hill 2000). Furthermore, recent studies have shown that even structural-based sexual ornaments predict success in dominance interactions between males (Alonso-Alvarez et al. 2004; Siefferman & Hill 2005a).

2.3b Sexual signals and parental care in birds

In birds with biparental care, the level of male parental assistance when provisioning young may be a very important direct benefit to females, increasing offspring's survival and/or quality. Since parental quality in short-lived species cannot usually be observed in advance of mate choice, the parental quality of a prospective mate must be appraised using indirect cues, such as sexual ornaments (Nisbet 1973). Whether or not bird ornaments are a signal for direct benefits to prospective partners in sexual selection is controversial (Andersson 1994). Sexual selection due to male sexual displays indicating male parenting ability may be entirely phenotypic, or the male trait may evolve to indicate male genotypic quality and females may then gain indirect fitness benefits (Heywood 1989, Hoelzer 1989, Grafen 1990, Price et al. 1993).

Three main hypotheses have been proposed to explain the relationship between male ornament size and parental care. The '*good parent hypothesis*' assumes that male sexual displays (plumage ornaments and song) reliably indicates the ability of males to provide a high level of parental care (e.g. incubating or provisioning the young, feeding the incubating female, or defending the nest; Hoelzer 1989, Qvarnström & Forsgren 1998). If females choose elaborately ornamented males as mates, they will obtain a net direct fitness benefit (Andersson 1994). According to this model, males with larger ornaments will provide more care than less

ornamented ones.

In case of carotenoid-based sexual signals, existing models (Heywood 1989, Hoelzer 1989, Grafen 1990, Price et al. 1993) assumes that variance in male sexual signals directly display differences in their ability to acquire nutrients. Carotenoids can be gained only from the environment, and males that are good at finding food items with a high carotenoid content may signal this ability in a slightly brighter phenotype (eg. Senar & Escobar 2002). Females mating with such males will rear offspring that acquire food with more carotenoids, ensuring offspring of higher phenotypic quality. Female preference for the most brightly coloured males and male brightness will therefore become exaggerated.

In many species where elaborated male signals display intrasexual dominance (as found in many melanin-based traits) females mated with elaborately ornamented males might gain direct benefits in form of high quality resources (e.g. suitable breeding sites, superior territories) monopolised by dominant males. (Qvarnström & Forsgren 1998.)

Alternatively, the '*differential allocation hypothesis*' (Burley 1986) assumes that the reproductive value of a brood is related to the attractiveness of the mates. 'Negotiation' models of biparental care predict stable biparental care when individuals adjust their care facultatively in response to the effort levels of their current mate, such that if one parent reduces its care, the other increases its own effort, but not so much that it completely compensates for the lost care (McNamara et al. 1999, Houston et al. 2005).

So thus, to obtain and keep relatively attractive males (given that sexual traits of males represent honest signals of quality, e.g. they can provide better resources and/or good genes to nestlings), females may allocate elevated reproductive effort to current offspring sired by these males. In return, females may obtain indirect fitness benefit in terms of enhanced viability or/and attractiveness of their offspring. Hence, females would provide more parental care when mated to more ornamented mates. As a response, attractive males are expected to reduce their parental effort in the current brood and save resources for future breeding attempts,

which may result in higher lifetime reproductive success and, in turn, directional selection on secondary sexual characters (Burley 1986). Therefore, this model predicts a negative relationship between both male ornamentation and male paternal care and between parental investments of the two parents as well. Since its formulation, this hypothesis has been supported in various taxa and sexual traits (reviewed by Sheldon 2000), even in case of male differential breeding investment in response to female attractiveness (Ratikainen & Kokko 2010).

The third main hypotheses attempting to explain the relationship between male ornament size and parental care is called the '*trade-off hypothesis*' (Magrath & Komdeur 2003). Regarding that animals frequently face reproductive trade-offs (e.g. between mating and parental effort), this model assumes that more ornamented males provide less parental care because they achieve relatively greater reproductive success by investing to other activities such as mating effort (e.g. pursuing extrapair fertilizations or additional mates in the case of polygynous species) or competition with other males. In this case, unlike the differential allocation theory, there is no direct link between the two parents' current contribution, parental investment of one parent is not adjusted in response to the other's (but see Harrison et al. 2009).

Numerous male secondary sexual traits (both acoustic and visual) have been examined for their putative utility as reliable indicators of male parental competence (e.g. Mountjoy & Lemon 1997, Linville et al. 1998, Buchanan & Catchpole 2000, Candolin 2000). Total parental investment, typically measured in terms of investment to an entire brood, has been found to vary with mate ornamentation in several species, both positively (Hill 1991, Keyser & Hill 2000, Siefferman & Hill 2003) and negatively (e.g. Qvarnström 1997, Sanz 2001, Badyaev & Hill 2002). As proofs for the good parent hypothesis, association between parental investment and carotenoid-based male plumage brightness has been found in several species (e.g. northern cardinal, *Cardinalis cardinalis*; Linville et al 1998, blue tits *Parus caeruleus*; Senar et al 2002). In structural signals, the bright UV blue plumage coloration of adult male eastern bluebirds

(*Sialia sialis*) was positively correlated with male provisioning rates to nestlings (Siefferman & Hill 2003) and male provisioning rates to incubating females as well (Siefferman & Hill 2005c).

In support of the differential allocation theory, females investing more in entire broods when paired to attractive mates were found in several avian species and at various stages of the breeding cycle (e.g. through differential maternal investment in the quality or quantity of eggs produced; Petrie & Williams 1993, Gil et al. 1999, Cunningham & Russell 2000 or through differential parental effort; Burley 1986, 1988, de Lope & Møller 1993, Sheldon 2000). Female blue tits, for example, feed broods at higher rates when mated to males with bright UV coloration (Limbourg et al. 2004) and contributed more to nest defence relative to their mates than do females paired to males with dull UV plumage (Johnsen et al. 2005).

Alternatively, in some case studies where male attractiveness and parental care was also negatively correlated, authors suggested the role for the trade-off hypothesis (collared flycatcher *Ficedula albicollis*; Qvarnström 1997, pied flycatcher *Ficedula hypoleuca*; Sanz 2001, common yellowthroats *Geothlypis trichas*; Pedersen et al. 2006, Mitchell et al. 2007) Yet in other studies, however, none of the mentioned three hypotheses was supported by the results. In bluethroats (*Luscinia svecica*; Smiseth et al. 2001), for example, measures of male and female parental care was not associated with male ornamentation.

2.4 STUDY OBJECTS

2.4a The house sparrow

The house sparrow (*Passer domesticus*) is a member of the *Passer* genus (Old World sparrows) in the family *Passeridae*. It is now the most widely distributed wild bird on the planet (BirdLife International 2010), with several subspecies that are divided in two major clades (the Palearctic *domesticus* and Oriental *indicus* group). It is native to Europe, Asia, and parts of North Africa, but following humans, it has spread throughout the globe since the middle of the 19th century, and has been intentionally or accidentally introduced (mostly the European spp. *P. d. domesticus*) to the Americas, sub-Saharan Africa, New Zealand and Australia, as well as to urban areas in other parts of the world. The northern border of its range fluctuates between 60° and 70° latitude. In the southern hemisphere, all continents have been settled with the exception of tropical South America and Antarctica.

One of the most remarkable attributes of the house sparrow is its close commensalist association with sedentary humans. It is most commonly found in agricultural, urban, or suburban areas, and avoids natural areas such as woodlands, forests, grasslands, and deserts. In cities, towns and villages, even in animal farms, it can be the most abundant bird. This obligate commensalism might have developed independently in the two groups (*domesticus* and *indicus*) after the invention of agriculture in both regions within the last 10.000 years. (Anderson 2006). The house sparrow tends to nest in loose colonies, virtually always in close association with humans. It is primarily a cavity nester, nesting most commonly in holes of buildings or other human structures, holes in trees and nest-boxes. Sometimes it builds its own domed nest onto trees, or occupies the nests of other species (e.g. house martin *Delichon urbica*) and nest platforms of large birds (e.g. white stork *Ciconia ciconia*).

House sparrows are mostly socially monogamous (but see below), with persisting pair bond throughout one breeding season. Pair bonds often remain intact throughout the given breeding season, and sometimes between years (Summers-Smith 1958), but this is probably due primarily to nest site fidelity (the tendency to

utilize the same nest site repeatedly), rather than mate fidelity. Polygyny occurs frequently in sparrows (e.g. Cordero et al. 1999; Griffith et al. 1999b, Veiga 1990, 1990a). Polygynously mated males participate in the breeding activities at the nests of both females (but they tend to favour one of the nests) and can gain increased reproductive success in relation to monogamous ones (Veiga 1990, Griffith et al. 1999b). Additionally, socially monogamous sparrows often participate in extra-pair copulations. Using either minisatellite or microsatellite probes, extra-pair young in the broods were found with similar frequency (7 - 16 %) in several populations (Wetton & Parkin 1991, Cordero et al. 1999, Veiga & Boto 2000, Griffith et al. 1999a, Hankinson 1999). The percentage of broods containing one or more extra-pair offspring varied from 9.3% (Veiga & Boto 2000) to 28.6% (Griffith et al. 1999a). An exception was found on Lundy Island (UK), where only 3.6% of the broods had extra-pair offspring (Griffith et al. 1999a).

Sparrows are reproductively mature in the subsequent season after their year of birth, and most individuals attempt to breed during this first breeding season. Both sexes contribute to care by participating in nest building, defense of the brood, and feeding the nestlings. In our latitude, the breeding season lasts from late April through early to middle August with two or three broods raised. The interbrood interval (the period between the fledging of one brood and the initiation of the next clutch) is 7–10 days (Anderson 2006).

The most common clutch sizes range from three to six eggs in most populations. In most temperate latitude populations, clutch size is affected by advancement of the season (fewer eggs laid late in the season than earlier) and urbanisation (with lower clutch sizes in urban populations than in rural ones) and it tends to increase with latitude (Anderson 2006). The average incubation period of sparrows is 11 – 12 days, eggs are incubated by both parents. Males, however, do not develop a brood patch, but participate in incubation by preventing heat loss during the absence of the female and protecting the eggs from predators or from sparrows prospecting for nest sites. Eggs hatch in the order in which they were laid (Veiga 1990a) and usually with an asynchrony of 24–48 hours (depending on the

clutch size, e.g. Anderson 1994; Seel 1968, Veiga 1990a). Newly hatched chicks are helpless and blind, but they grow and develop rapidly. Both parents feed the nestlings, mostly with insects in the first part and with seed and crops as the nestlings grow older. The nestling period is approximately 14 days, ranging from 13 to 16 days, depending on latitude (Anderson 2006). After leaving the nest, parents (especially males) continue to feed fledglings for several days. After the end of the breeding season, adults join the large flock previously formed by fledged juveniles. Until the next spring, they live in these autumn-winter flocks.

Except for the two migratory subspecies in central Asia (*P. d. bactrianus* and *P. d. parkini*), house sparrows are permanent residents throughout most of their range, and they are also remarkably sedentary. Once established as breeding birds, sparrows rarely disperse to another colony (Summers-Smith 1963). Natal dispersal is also limited, the majority of young sparrows remain in or nearby their natal colony (Altwegg et al. 2000, Anderson 2006). Daily movements of sparrows are similarly short, in both urban and rural populations. Sparrows forage primarily within a 0.5–km radius of their breeding or roosting sites, covering 2–4 km distances in a day (Anderson 2006).

During the last 20–40 years, a widespread decline in numbers of house sparrows was detected in a large part of their extensive range (BirdLife International 2009). Both regional and continental studies suggest that sparrows have decreased in both abundance and distribution in North America, the British Isles, Northern and Western Europe. Numbers have declined by 20%–50%, but in some major urban areas in Great Britain, the decline may have even been more pronounced, amounting to 85%–98.8% (Summers-Smith 1999). In Western Europe this decline parallels similar declines in several other farmland bird species (Donald et al. 2001, Krebs et al. 1999). As an explanation for this recent decline, numerous suggestions have been made. Most likely, changes in agricultural practices in the past decades may have resulted either directly or indirectly in reduced availability of food for house sparrows. Increased mechanization in farming (by replacing the horses with machines), changes in planting practices (by

declining the area of spring plantings) and increasingly efficient harvesting machines (by reducing the crop spillage and wastage) had a negative effect on the food supply of ground-foraging birds in West-Europe and North America. Additionally, increased use of chemicals may also have an indirect effect on sparrows by reducing the amount of insects and weed seeds available. Until now, similar drops in numbers have not been recorded in Central and Eastern Europe, suggesting that density of sparrows remain high in this area.

2.4b Parasites associated with the house sparrow

As one of the most ubiquitous birds, house sparrows and their nests were frequently checked for parasites of any type in the recent past (for a review, see Anderson 2006). Numerous microbial pathogens have been identified including viruses (Arboviruses, *Poxivirus*), bacteria (*Salmonella*, *Escherichia*, *Mycoplasma*, *E. coli*, *Staphylococcus*, *Proteus*, *Streptococcus*, *Bacillus*, *Yersinia*), and fungi (*Candida*). Many of these pathogens cause only a mild viraemia and bacteraemia lasting a few days, but in some cases, microbial infections apparently contribute to illness with severe symptoms (e.g. wart-like growths on the legs, skin and eyes in avian pox) or even embryonic, nestling or adult mortality as well. Infection by protozoan parasites are also frequently reported in sparrows, including parasites that cause avian malaria (*Plasmodium* spp.), toxoplasmosis (*Toxoplasma* spp.), and coccidiosis (*Isospora* spp.). Despite these accounts of sparrow morbidity and mortality due to infection by viruses, bacteria or protozoans, the ultimate effects of these pathogens on sparrow populations are poorly understood. On the contrary, it is well known that the house sparrow (like many other wild birds) can serve as a reservoir for various microbial infections that affect humans or domestic animals (e.g. Moro et al. 2009).

Sparrows are also parasitized by a number of platyhelminths and nematodes, most of which are intestinal tract parasites. Little is known about their effects on sparrows, and virtually nothing is known about their impacts on sparrow populations.

Almost all groups of arthropod ectoparasites were isolated from the birds or their nest, such as mites (see later for details), ticks (*Ixodes*, *Haemaphysalis*, *Amblyomma*), bugs (*Oeciacus*), Mallophagan feather lice (*Brueelia*, *Menacanthus*, *Myrsidea*, *Philopterus*, *Rostrinirmus*) parasitic flies (*Boreallus*, *Carnus*, *Lipoptena*, *Neottiophilum*, *Ornithomyia*, *Ornithoica*, *Protocalliphora*) and fleas (*Ceratophyllus*, *Dasypsyllus*, *Hectopsylla*, *Monopsyllus*, *Nosopsyllus*, *Tarsopsylla*).

This large number of genera and species suggests that sparrow nests support a community of organisms that includes not only parasites of the birds but also various saprophytic organisms, as well as predators and parasites of these two groups (e.g. Kristofik et al. 1993). In most cases, however, only species lists are reported, and no additional information can be gathered about the ectoparasite's ecology, life-history or their effect on the host. Similarly, ectoparasitic bird mites, are commonly reported from house sparrow's nests (Clark & Yunker 1956, Summer-Smith 1963, Phillis 1972, McGoarty and Dobson 1974, Brown & Wilson 1975, Kaczmarek 1991, Anderson 2006), yet there is only one study reporting detailed information on the interactions between the mite parasite and its host (Weddle 2000),

2.4c Badge of the house sparrow

The house sparrows', the most conspicuous sexually dimorphic plumage trait is their melanin-based black throat patch on the chest of males (bib). This trait is seemingly associated with individual quality, social dominance and reproductive advantage. Males with large badges were found dominant over small-badged males in winter flocks (Møller 1987a, Liker & Barta 2002), being in better physical condition (Veiga 1993, Veiga & Puerta 1996, Møller et al. 1996), being more successful in intrasexual competition (Møller 1987b, 1988, 1989, 1990, Veiga 1993) and being preferred by females, at least in some populations (Møller 1988, 1990).

These results indicate that badge size in house sparrow functions as an honest signal, suggesting that some costs are involved in its production or its maintenance.

Some authors addressed the hypothesis that large badges, although being melanin-based, are nutritionally costly to produce. Juvenile male sparrows developed significantly smaller or lighter badges when exposed to limited access to food sources or artificial diet with reduced amino acid precursors essential to melanogenesis during moult (Veiga & Puerta 1996, Poston et al. 2005). Time constraints can entail another type of cost in plumage signal development. Besides structural feathers (e.g. Vágási et al. 2012), expression of melanin-based signals can also be affected by the rate at which moult occurs, as were found by Vágási et al. (2010), showing that sparrows which had undergone an accelerated moult developed smaller badges.

According to the immunocompetence handicap hypothesis (Folstad & Karter 1992, Wedekind 1992), cost of expressing sexual ornaments incurs the immunodepressive effect of androgens needed to develop the traits. Therefore, only high-quality males could afford to display showy sexual traits without suffering reduced fitness by pathogens. Indeed, level of testosterone in house sparrow males was positively correlated with badge size after moult (Gonzalez et al. 2001). Artificially elevated testosterone levels significantly influenced the size of the bib (Evans et al. 2000), antiandrogens, on the contrary, reduced its size, at least in terms of its seasonal exposure (because the white tips of the black feathers of the badge wore off later; Gonzalez et al. 2001). However, no direct evidence of a condition-dependent link between testosterone, melanin synthesis and immunocompetence was found, suggesting that the relationships between endocrine and immune systems are much more complex than was previously supposed. Role for other agents, such as corticosterone (Evans et al. 2000) the lack of oestrogen rather than from the presence of androgens or strict genetic control (Owens and Short 1995) are also suggested.

Besides production costs, other studies tried to reveal the cost of maintenance to explain how sparrow badges are maintained as honest signals. Frequent testing by conspecifics in agonistic interactions (*'social control hypothesis'*; Rohwer 1975) or the elevated cost of increased conspicuousness to visual predators may be such

maintenance costs. Melanin-based black patches and stripes in males of many bird species often correlates with their social status (reviewed by Butcher & Rohwer 1989). In house sparrow which is a typical flocking bird, and used as a model for social selection studies, several authors have investigated dominance relationships in free-living and captive house sparrow flocks (Watson 1970, Møller 1987, Solberg & Ringsby 1997, Tóth et al. 2009). Size of the badge was found the best morphological predictor of dominance rank in male sparrows. Furthermore, males actively use their badge for signaling their status in aggressive encounters with other males (Møller 1987, Veiga 1993, Solberg & Ringsby 1997, Gonzalez et al. 2002, Hein et al 2003). Besides male-male encounters, badge size apparently plays a role as a status signal also in intersexual social interactions. Males with larger black throat patches tended to be dominant regardless of the opponent's sex, that is, large-badged males were more aggressive also toward female flockmates and dominated more females than smaller-badged males, in both free living (Hein et al. 2003) and aviary-held flocks (Liker & Barta 2001).

Although undoubtedly a status signal, exact maintenance costs of this trait are still debated. Low status individuals with artificially enlarged badges did not tend to have more encounters with large-badged males, and these cheaters apparently suffered no physiological costs either, (at least in form of elevated stress-hormone corticosterone level; Gonzalez et al 2002). Similarly, no proof for significant predation cost was found in house sparrows, since individual variation in plumage ornamentation was not associated with predator-related risk taking behaviour and short-term survival (Bókony et al 2008).

Badge size and female choice in house sparrows

The throat patch of male house sparrows has been the focus of several studies that have identified its role as a sexually selected ornament in both intra- and intersexual selection processes. Theories of sexual selection (both the '*good genes*' and the '*direct benefit*' models) usually assume that female preferences for male ornamental traits are fixed and always likely to favour the largest or most extravagant sexual

ornaments. Indeed, a study of house sparrows in Denmark indicated that male bib size is important in female choice, showing strong female preference for large-badged males (Møller 1987, 1988, 1989, 1990). In several other populations, however, there was no specific preference with regard to male ornament size (Veiga 1993, 1995, 1996, Kimball 1996, Cordero et al. 1999), or on the contrary, an apparent preference for small-badged was found (in the Lundy Island population; Griffith et al. 1999, Griffith 2000). Thus, the adaptive significance of badge size variation in male house sparrows and female preference for large badged males remains controversial.

It is still unclear, what benefits females get from preferring large-(or even small) badged males. Females may decide to mate with certain males because they are more attractive (delivering indirect benefits), or provide better resources (territory, parental care or nest defence). In the house sparrow, some attributes of male quality concur with badge size. Large-badged males were found to be in better physical and immunological condition (Veiga 1993, Veiga & Puerta 1996, Møller et al. 1996), breeding earlier in the season (Møller 1989), achieving more nest sites for breeding (Veiga 1993) or more extra-pair copulations (Møller 1987, 1990), having advantages in sperm competition due to larger testes (Møller 1988).

Females were reported to gain direct fitness benefits from large-badged mates in form of increased nestling provisioning (Møller 1988, Voltura et al. 2002) and nest defense (Reyer et al. 1998). Moreover, Voltura et al. (2002) reported higher offspring survival and a greater proportion of chicks fledged from the nests of these males. Similar result was found by Jensen et al. (2004), with large-badged males having greater lifetime reproductive success in form of more recruiting daughters. Moreover, females spent more time at the nest with large-badged males, explained as these males were better able to protect them from harassment by stranger males (Václav et al. 2002).

In contrast, badge-related differences in nest site number and quality did not translate into fitness differences (Møller 1988, Veiga 1993). Similar results were reported by Václav & Hoi (2002), with average-badged males having the earliest

breeding start and largest clutches (but also having the highest hatching failures, resulting similar fledging success than other males). Moreover, in the isolated Lundy Island population, small-badged males were preferred by females as both social and genetic mates and these males produced significantly larger numbers of surviving offspring (Griffith et al. 1999). The reliability of badges as indicators of male age and experience seems to differ among populations because size increases with age in some (Veiga 1993) but not in other locations (Møller 1988).

3 MATERIALS AND METHODS

3.1 Study population: sparrows and their ectoparasites

This thesis is based on field studies that were conducted between 2000 and 2002, in a population of free-living rural house sparrows, inhabiting a milk farm near to Debrecen, Hungary (21° 38' E, 47° 32' N). Sparrows are abundant in this area, maybe due to the abundant food resources (insects for food provisioning and seeds or crops for the parents as well) and many suitable nest sites. They mainly breed in holes and own-built nests in the farm buildings. During the study, 90-100 active nest sites were present in the farm in each breeding season (personal observations). Unfortunately, most of the nests were built into deep holes of the buildings, so thus they were unavailable for the study. At this latitude, sparrows regularly produce three broods per season. They typically begin laying in late April and end breeding in late July. In the majority of the nests of the study area, nestlings were parasitised by various blood-feeding arthropods, mainly mites. These were haematophagous mites of the suborder Mesostigmata in the *Macronyssidae* family, which has been previously found in nests of several passerine birds including the house sparrow (Phillis 1972, McGoarty & Dobson 1974, Brown & Wilson 1975, Weddle 2000). Among the two mite species found, *Ornithonyssus sylviarum* (northern fowl mite; Canestrini & Fanzago 1877) was frequently found on various bird taxa in Europe. *Pellonyssus reedi* (Zumpt & Patterson 1952) was also reported from various bird species (e.g. Clark & Yunker 1956, Baker et al. 1976, Stoehr et al. 2000), until now, however, it was unknown from the European geographic region.

This host-parasite system, together with the easy feasibility of various fieldwork actions (ectoparasite sampling, nestling measurements, observation of parental behaviour) proved a suitable population for investigating several aspects of early nestling development. Fieldwork was carried out in three consecutive years (2000-2002), involving broods of one or two breeding attempts (3rd breeding attempt in 4.1; 2nd and 3rd broods in 4.2; and the 1st and 2nd breeding attempt in 4.3)

3.2 Nestling measurements (4.1, 4.2, 4.3)

Potential nest sites were checked for eggs and nestlings at least three times a week during the breeding seasons, yielding information about the date of egg laying and hatching, as well as about clutch size and nestling age. Nestlings' body parameters were recorded on the 12th day posthatching (that is, when the oldest chick in the brood was 12 days old): body mass with a Pesola spring balance (± 0.1 g), skeletal measures (tarsus and bill size) with a caliper (± 0.1 mm), feather traits (wing and tail length) with a ruler (± 1 mm). At the same time, chicks were provided with a numbered aluminium band. Fledging success was estimated as the brood size on the 12th day after hatching divided by the number of hatched chicks.

Relative age of nestlings within each brood was estimated (only in 4.2) by a toe-clipping marking method: when all chicks hatched in the nest (in nearly all nests, hatching asynchrony of 1-2 days was observed), they were weighed with a Pesola balance (to the nearest 0.1 g) and marked individually by clipping one nail tip. Since nestling age is linearly correlated with body mass in early chick development stages (Summer-Smith 1963), day of hatching was easy to extrapolate. Clipped toes were detectable even on 12 days old chicks.

To assess nestling body condition, residual body mass (RBM) indices were computed as the residuals of a regression of skeletal parameter(s) against body mass (measured when nestlings were 12 day old) using Type II SMA (standard major axis) regression (*line.cis* function in R). For skeletal structural variables, either untransformed tarsus length (in 4.1) or the first principal component of a principal component analysis (PCA) of tarsus and bill length (in 4.2) were chosen. Body mass was log transformed.

3.3 Haematological measures (4.1)

Blood samples for haematological measurements were taken from the brachial vein of each chick, using capillary tubes. For blood cell counts, a drop of blood was smeared on a microscope slide, which was then air-dried, fixed in methanol and stained with May-Grünwald-Giemsa. The rest of the blood sample was centrifuged

for 10 minutes at 10000 rpm to determine haematocrit values. Blood smears were scanned at 1000x magnification following standard procedure. On each smear, erythrocytes, thrombocytes and leukocytes (classified as lymphocytes, monocytes and three families of granulocytes, eosinophils, basophils and heterophils) were count in 40 microscope fields (Campbell 1988). The number of different leukocyte types and thrombocytes related to 10000 erythrocytes were defined as relative counts and used for the analyses.

3.4 Measuring immunocompetence (4.2)

When chicks were 11 days old, they were inoculated with phytohaemagglutinin (PHA, Sigma Chemical Co, St. Louis, Missouri) to assess nestling immunocompetence. This took place with a sub-dermal inoculation of 0.025 mg PHA, dissolved in 0.04 ml saline buffer (PBS), on the left wing web, using an insulin pin. Control inoculation was made with the same volume of PBS on the right wing. The inoculation spots were measured with a thickness gage (Mitutoyo America Co., Aurora, Colorado) on both wings just before the inoculation, as well after 24 (\pm 30 min) hr on day 12. PHA-response was calculated as the swelling caused by PHA minus the swelling on the other wing (Norris & Evans 2000). PHA inoculation is widely used as an indicator of non-specific mitotic immune response (T cell production), causing local swelling via macrophage infiltration and perivascular T cell accumulation (Lochmiller et al. 1993, Martin et al. 2006). While T cell mediated immune response only accounts for one important component of the avian immune system (Roitt et al. 1996, Wakelin 1996), this component is directly related to parasite-mediated nestling mortality (Martin et al. 2001) and the prospects of survival for both nestling and adult birds (Møller & Saino 1994); thus, it is likely to reflect an important aspect of hosts' defense against parasite infection (Martin et al. 2006). This swelling is also easy to measure and has considerable individual variability. On day 12, nestling body parameters, such as body mass and tarsus, wing, and tail lengths were also recorded. Seven nestlings escaped during measurement, some of their measurements are therefore missing.

3.5 Ectoparasite sampling (4.1 and 4.2)

When the oldest nestling in the nest was 12 days old, ectoparasites were collected from each nestling in the brood, simultaneously with nestling measures (on 12 days old chicks). Immediately after the removal from the nest, each nestling was placed in a separate cloth bag that prevented mite escapes. Subsequently, the chicks' body (except the head) was placed into a jar with chloroform vapour for 15 min, to assess individual ectoparasite loads (Fowler & Cohen 1983). To make individual mite loads more precise, the nestlings' head, the jars and carry bags were also thoroughly checked for mites, as well as dead mites tangled into the feathers after the chloroform bath. Parasites were not collected from the nest material. Collected ectoparasites were placed and stored in 96% ethanol and counted later in the laboratory, using a stereomicroscope.

In 4.2, recording the feeding status of mites was also required. This was scored by the colour of their opisthosoma, recording the proportion of mites with red opisthosoma in each brood. These specimens are easy to separate from mites with black opisthosoma, and red opisthosoma colour is a reliable indicator of recent blood feeding (Møller 2000). Duration of ethanol storage had no considerable effect on red colour (Spearman's rank correlation, $\rho = 0.06$, $P = 0.47$).

3.6 Adult bird capture and measurements (4.3)

From the end of April, adult house sparrows were captured with mist-nets dispersed over the study area. Where it was possible, I systematically tried to capture each parent with an electronic trap installed at the entrance of the nests. To avoid nest abandonment with eggs or small chicks, this was performed when the nestlings were 8–13 days old, and mainly in the first breeding season, when no behavioural records were made. In some cases, however, male parents were not yet captured at the time of the behavioural observations at the second breeding attempt. So thus, nest traps were also used in this period, when chicks were 10–12 days old (after all the behavioural samplings).

At first capture, birds were marked with a numbered aluminium ring and a

unique combination of three plastic colour rings to enable individual identification in the field. I weighted them with a Pesola spring balance ($\pm 0.1\text{g}$) and recorded the badge size of males. This was performed with a digital camera, by taking still images from the throat patch of the males, together with a ruler. Photos were converted to grey-scale and measured using the scion image software (Scion Corporation). Areas were measured in pixels and converted to cm^2 using the ruler as standard. Badge size increases with time because of the abrasion of white feather tips concealing the badge (Møller and Erritzoe 1992, Veiga 1996). To avoid seasonal variation of its size, I measured the total badge size by tracing the outline of the black area beneath the white tips. Reliability of badge size measurements was tested by measuring the same badges on two independent photographs that were taken at the same capture event. In each photograph, birds were newly taken in hand. Repeatability (Lessells & Boag 1987) proved very high for badge size measurement ($r = 0.90$, $F_{21,22} = 17.9$, $p < 0.001$).

3.7 Behavioural samplings: provisioning and risk taking (4.3)

I observed the feeding effort of male and female birds in broods of the 2nd breeding attempt, on the 5th and 9th days after the first nestling has hatched (D5 and D9). Parental feeding of nestlings was recorded using a camouflaged video camera mounted 2-3 m from the focal nests, during the normal feeding period (09.00-17.00). Sampling times were randomized on the successive observation days: when the first sampling (D5) was conducted before 12.00, the second one (D9) was then conducted after 12.00.

During all behavioral sampling, I recorded which parent (male or female) visited the nest, its arrival and departure times. Feeding rates of adults were calculated by counting the numbers of feeding visits per 60 minutes to the nest, following an initial acclimation period (latency was the time until first entering by any parent). After each behavioural sample, number of chicks present in the nest was counted.

Since weather conditions might largely influence parental behaviour (Finlay

1971, Turner 1984), their occurrent effect on feeding activity had to be controlled for. Therefore, before conducting behaviour analyses I examined the effects of several environmental factors (daily temperature, number of sunny hours, amount of rainfall, all information gathered from Hungarian Meteorological Service) on parental care behaviours.

To assess parental risk taking behaviour of the sparrows, I recorded the parents' reaction to a predator model. When the oldest offspring in the nest was 8 days old (D8), feeding parents were exposed to a stuffed weasel (*Mustela nivalis*) model, fixed in crouching position ca. 20-30 cm below the nest, facing the entrance. After placing the predator at the focal nest, the observer immediately left and recorded the behaviour of the parents from a hide 30–50 m away, using spotting scopes. The models were exposed for about 10–15 minutes, until both parents had noticed it (the response to the predator dummy was usually an intense mobbing, together with parents of the neighbouring nests). When both parents were detected by means of their colour rings among the mobbing birds, the model was removed by the observer. As a measure of risk taking, I used the time between predator removal and the first entry into the nest by each parent (return time; e.g. Dale et al. 1996). The first bird visiting the nestbox was deemed the risk taker, the second one the follower. I continued observing until both parents entered the nest. The data were omitted if only one parent was present during the observation (max. 60 min.). Parental responses to the predator model were also recorded using a camouflaged digital video camera, mounted 2-3 meters away from the nest entrance. My observations confirmed that the parents enter the nestbox after predator removal to feed the nestlings, but never in the presence of the predator. The behavioural observations were conducted throughout the day (09.00–17.00 hours) within the normal feeding time, in June and July, 2002. Each sparrow pair was subjected to the same experimental procedure and tested only once. The model was not exposed during rain. All parents were socially monogamous when their feeding behaviours was also observed.

3.8 Statistical procedures

Measures of parasite distribution, such as prevalence, mean and median intensity, mean abundance and aggregation indices (D discrepancy index and the k exponent of the negative binomial distribution) were calculated with the Quantitative Parasitology 2.0 software (Rózsa et al. 2000). Confidence intervals of 95% are given for all of these descriptive statistics. All other analyses were performed with the R statistical computing environment (Ihaka & Gentleman 1996, R Development Core Team).

To detect the physiological effects of nest mites on developing house sparrows (in 4.1), correlational analyses were performed with nonparametric Spearman rank method. Since chicks from the same brood cannot be considered as independent sample points, brood mean values were used for all variables. In these analyses, mite loads in a given brood were characterised with mean intensity (calculated as the total number of mites collected from one brood divided by the number of chicks found in the nest), and were log transformed before statistical testing. Significance levels were adjusted with Bonferroni corrections for multiple comparisons.

To analyse intra-brood patterns of mite distributions (in 4.2), two parasite variables were calculated for each nestling: (1) total number of mites and (2) proportion of mites with recent blood meal. Total mite number exhibited a negative binominal distribution, it, therefore, was log transformed before entering in the statistical models.

To detect mite preference patterns within a brood, and to control for effects of potentially confounding variables (such as breeding attempt or brood effect), linear mixed-effect models were built (lme function in R; Pinheiro & Bates 2000). Since nestling's data from the same brood cannot be treated as independent data points, brood was included as a random effect. Breeding attempt (2nd vs 3rd) and nestling variables, i.e., body mass and tarsus length as surrogates of body size, and wing and tail length as proxies for feather development, and PHA-response as a measure of immunocompetence, were included as fixed effects. When I investigated

relationships between a particular nestling trait and mite parameters, other nestling variables were added sequentially (as fixed effects) to the models in various combinations, and I tested whether the effects of other variables altered the results.

To examine the relationship between the males' ornamental traits and their parental efforts (in 4.3), and to control for effects of potentially confounding variables (such as time of breeding, brood size, environmental conditions), linear models were used. Environmental and nestling variables were added sequentially to the models in various combinations, and I tested whether the effects of other variables altered the results. Variables with non-normal distributions were log transformed before entering in the statistical models. Altogether 32 breeding pairs were included in the analyses. Correlations between parental behaviours were performed with parametric and no-parametric correlation tests depending on the distributional properties of the variables. Furthermore, since relationships between badge size and other variables were reported as nonlinear (curvilinear; Václav & Hoi 2002, besides using real badge size values, analyses were also performed using absolute deviations from the mean badge size, to test whether males with average-sized badges are doing better or worse than the rest of males.

4. RESULTS

4.1 Effects of haematophagous mites on nestling house sparrows

In this study I investigated whether intense loads of nest-dwelling blood-sucking mites affect condition and health state of developing house sparrow nestlings. (in altogether 100 chicks in 25 broods of the 3rd breeding attempt).

Mites in the house sparrow nests

Two haematophagous mite species were found on nestling house sparrows. A few specimens were identified as *Ornithonyssus sylviarum*, but the majority of the specimens belonged to the species *Pellonyssus reedi*. Because both species are similar regarding their size, feeding habits and life cycle, I did not analyse their effects on chicks separately (Clark & Yunker 1956, Combs & Lancaster 1965).

Brood size varied from 2 to 6 chicks, with an average of 4.0 (1.08) nestling. I found no evidence of nestling mortality due to parasitism or starvation. Parasite prevalence was 1.0 (95% confidence limits are 0.9637 and 1.0), that is, mites were found in each nest. Abundance of mites in the nests varied remarkably, with a range of 6-1998 mites per nest. The average intensity was 37.3 mites per nestling (95% confidence limits are 15.8 and 59.1). Median intensity was 8 mites per chick with 95% confidence limits from 6 to 8 mites.

Impact of mites on nestling house sparrows

Clutch size was not related to the total number of parasites in the nest ($r_s = -0.064$, $p = 0.76$), and likewise fledging success was also unrelated to parasite load ($r_s = -0.126$, $p = 0.548$). After Bonferroni correction, I found no significant effects of ectoparasites on body mass, body condition, or other measured biometric variables of nestling sparrows, such as tarsus, wing and tail length, however in wing measures, there was an explicit trend for negative correlation (Table 1, Fig. 2 - 7).

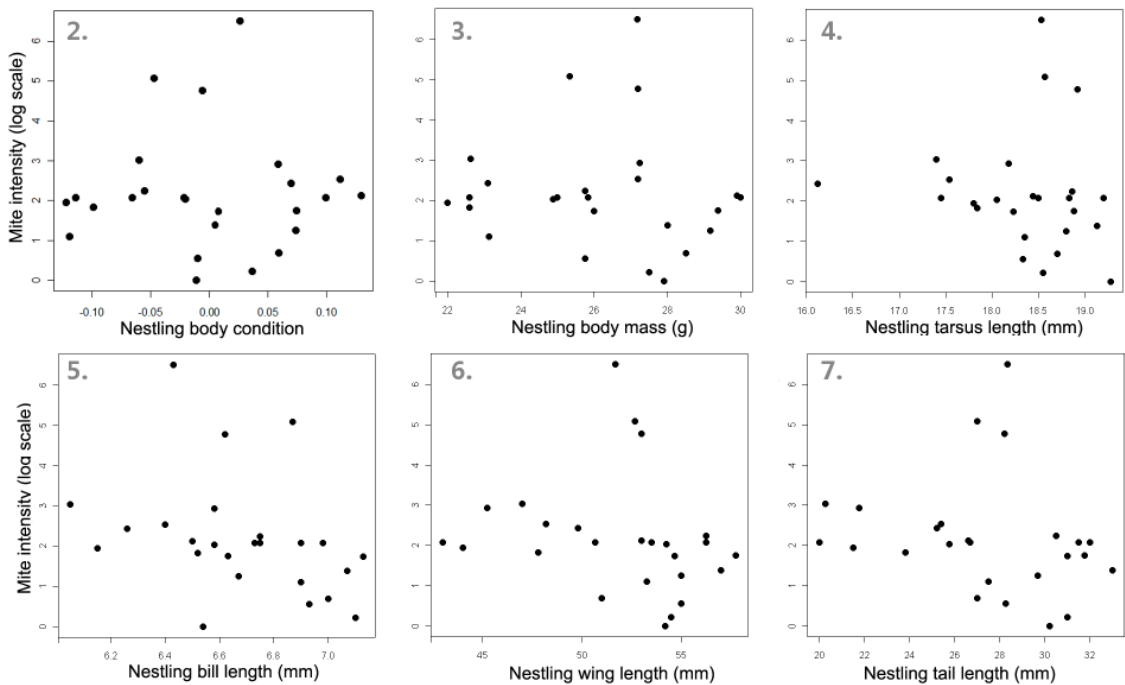


Figure 2 - 7. House sparrow nestling body parameters in relation to mite intensity. Mite numbers are log transformed, data points are mean values per brood.

Among the measured haematological variables, there was a strong positive correlation between mite intensity and the number of thrombocytes in the peripheral blood (Table 1, Fig. 8). Heterophil granulocytes also showed a marginally significant positive correlation with mite intensity (Table 1, Fig. 13). On the other hand, the heterophil granulocyte/lymphocyte ratio, a common measure of stress was not related to the mite infection ($r_s = 0.183$, $p = 0.38$), along with another stress measure method, the leukocyte/red blood cell (RBC) ratio ($r_s = 0.215$, $p = 0.301$). Similarly, mite intensity was not related to the relative number of lymphocytes and monocytes in the peripheral blood, and this was also the case for two families of granulocytes, the eosinophils and basophils (Table 1, Fig. 10 - 12). Additionally, I found a significant decrease in the haematocrit values of the nestling sparrows with increasing mite intensity (Table 1, Fig. 9).

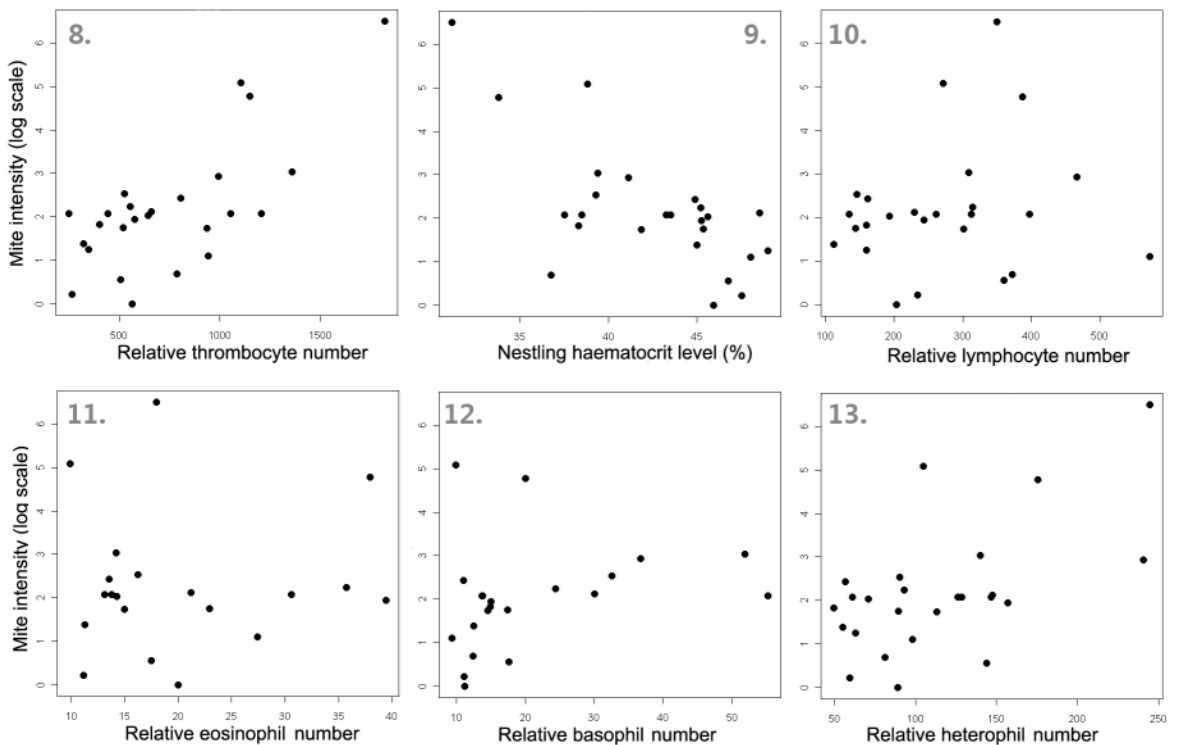


Figure 8 - 13. Relationship between measured haematological variables and mite intensity of sparrow nestlings. Mite numbers are log transformed, data points are mean values per brood.

		rho	P
Body parameters*	Body condition	0.03	0.86
	Body mass	-0.2	0.33
	Tarsus length	-0.24	0.238
	Bill length	-0.5	0.011
	Wing length	-0.43	0.03
	Tail length	-0.37	0.068
Haematological variables**	Haematocrit	-0.558	0.004*
	Thrombocytes	0.57	0.003*
	Heterophils	0.48	0.015
	Eosinophils	0.001	0.995
	Basophils	0.42	0.052
	Lymphocytes	0.173	0.408
	Monocytes	0.105	0.614

Table 1. Correlations between mite intensity and some measured variables in house sparrow chicks (all values reported are brood means; Spearman rank correlations, N= 25 broods).

*There were no significant results after Bonferroni correction. ($\alpha = 0.01$)

**Significant at the 0.05 level after Bonferroni correction. ($\alpha = 0.0071$)

There was a significant correlation between haematological variables that were affected by mite parasitism. Thrombocytes and heterophile granulocytes were positively correlated ($r_s = 0.66$, $p < 0.001$), while haematocrit levels negatively correlated with both thrombocytes ($r_s = -0.527$, $p = 0.007$) and heterophils ($r_s = -0.27$, $p = 0.018$; Fig. 14 - 16).

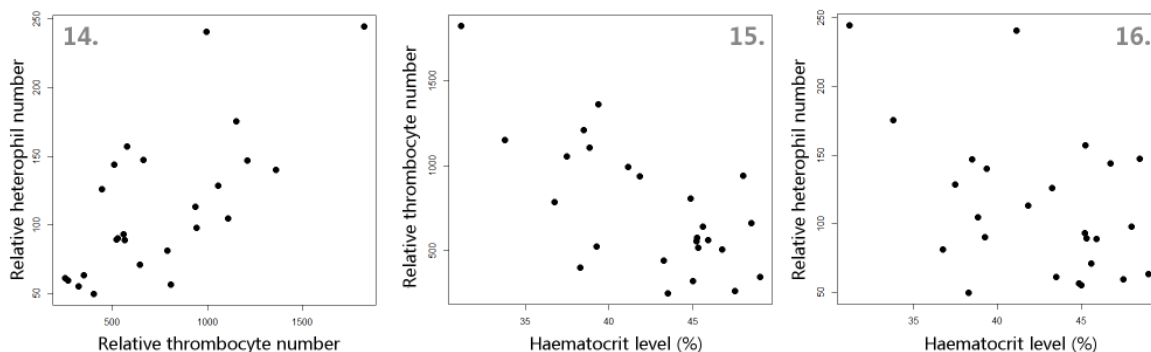


Figure 14 - 16. Relationship between haematological variables that were correlated with mite intensities. Data points are mean values per brood.

DISCUSSION

Here I report the results of an observational study on the impact of natural levels of haematophagous mite infection on nestling house sparrow hosts. A crucial point of this investigation was whether ectoparasitic mite infections have any physiological and health consequences, causing a detrimental impact on the chicks.

Mite infection apparently affected the blood profile of young sparrows. Mite intensity showed a significant positive correlation with heterophils, but not with other leukocytes participating in immune responses, such as lymphocytes and eosinophils. In addition, there was a strongly significant positive correlation between thrombocyte number and parasite load. Another conspicuous consequence of mite parasitism was a definite anaemia, manifesting in low haematocrit levels in the chicks suffering from high mite intensity.

Changes in blood profile could be ascribed to many factors, such as pathogens

or intense physical activity. In face of its aspecificity, blood smear analyses are widely used in many empirical works, mainly because it is a simple method to gain information about general physiological processes, including immune responses. There is however still uncertainty in the interpretation of blood profile results. For instance, it is not evident whether low levels of circulating white blood cells indicate a relative healthy individual, or a depleted leukocyte pool caused by persistent infection. Similarly, elevated leukocyte numbers may indicate an activated immune system or lowered immunocompetence (Owens & Wilson 1999).

Heterophils are involved in fighting the infection in the bloodstream via non-specific phagocytosis of pathogens and dead tissue parts. Peripheral heterophylia is a widely recorded symptom recurring in almost any kind of stress, inflammation and infection (Maxwell 1993, Parslow 1994). Immunologically reactive components of mite saliva may cause such an aspecific inflammatory reaction as a consequence of frequent bites. Therefore, because of the obvious relationship between mite load and relative heterophil number, I suggest that *Pellonyssus* and *Ornithonyssus* infections were associated with an increased stress level and acute phase of inflammation in the nestling sparrows.

Lymphocytes are immune cells that assist in the recognition and destruction of many types of pathogens. In some avian taxa, an increase in lymphocytes and heterophils is thought to be a typical response to infectious disease (Campbell 1988). Furthermore, decline in the lymphocyte level is assumed to be an indicator of general stress or immunosuppression caused by pathogens, and changes in heterophil/lymphocyte ratio are thought to have the same background (Maxwell 1993). Blood smear analyses however didn't show this decline in lymphocyte number, even in the most heavily parasitized broods. Consequently, there was no evidence for such suppression in the immune functions by the parasitic mites.

Thrombocytes are mostly involved in processes of haemostasis (Campbell 1998). High levels of thrombocytes therefore suggest an activated haemostatic function, which may be the result of the frequent injuries caused by the blood feeding of mites. Finally, haematocrit values associated with mite loads show that

these ectoparasites cause anaemia in their host due to depletion of the erythrocyte pool, as was also found in other studies investigating the effects of mites on bird hosts (Merino & Potti 1995, Potti et al. 1999, Stoehr et al. 2000, Morrison & Johnson 2002). This form of physiological handicap may have detrimental fitness consequences in the fledging period, because difficulties in oxygen uptake and transport may result in lower foraging ability and increased predation risk (Phillips et al. 1985, Clark 1991). On the whole these haematological results suggest that haematophagous mites mainly activate non-specific immune responses in sparrow chicks. Their detrimental physiological effects consist primarily of inflammatory processes and anaemia because of the depletion of the erythrocyte pool.

Contrary to the blood profile variables, my results suggest that blood-sucking *Pellonyssus* and *Ornithonyssus* mites may have no strong immediate detrimental effect on growth and survival in sparrow chicks. First, intensity of mite infestation seemed not to induce chick mortality and decrease in fledging success. Second, general measures of chick body size such as tarsus, bill, wing, and tail length showed little or no affection by mite numbers. Third, nestling body mass was also unrelated to intensity of infections. Nestling's body mass at fledging is an important fitness component because it considerably affects offspring survival in the post-fledging period (Lindström 1999). In accordance with many studies reporting decreased body weight due to ectoparasitic mites (Møller 1990, 1990b, Clayton & Tompkins 1995, Morrison & Johnson 2002), Weddle (2000) found a negative effect of *Pellonyssus reedi* on sparrow nestling body mass in house sparrows. The same effect by this mite species was shown in an experimental study with nestling house finches (*Carpodacus mexicanus*), along with the possibility of mite-induced mortality (Stoehr et al. 2000).

It is not clear why this study failed to find such detrimental effects of mites in regard to chick growth and fledging success. One reason may be that differences among the studies may reflect population differences, e.g. either in the susceptibility of sparrows to infection or in the virulence of the parasitic mites. Second, environmental conditions, (climate, food available) can significantly

modify the outcome of the parasite's detrimental effects. Under poor circumstances, parasites affect their nestling hosts usually stronger than in a good habitat or a good year (Allander 1998, Møller 2002). Favourable conditions permit the parents to compensate their harmful effects to some degree, ensuring good nutritional status with elevated food provisioning (Perrin et al. 1996, Tripet & Richner 1997, Tripet et al. 2002, Merino & Potti 1998, O'Brien & Dawson 2008). The study area on the milk farm seems to be a highly appropriate habitat for sparrows, with overabundant food sources, where parents can easily provide the necessary amount of food to ensure the good nutritional status. In addition, the study may happen to have been conducted in a favourable year. These possibilities call for further testing, preferentially by experimental manipulations of parental efforts and parasite loads on nestling sparrows.

4.2 Within-brood distribution of nest mites suggest their adaptive host-abandonment

In this part of the thesis I attempted to reveal factors and mechanisms that shape intranest distribution of macronyssid fowl mites on house sparrow nestlings.

Altogether 26 nests with 107 chicks and 25 nests with 95 chicks in the 2nd and 3rd breeding attempt were investigated, respectively. Five pairs had nests in both breeding attempts. In these cases, data from 1 breeding attempt (with the lesser brood size, to minimize data loss) were excluded, so altogether a data set of 188 house sparrow nestlings from 46 nests was analysed.

Mite distribution within house sparrow broods

The most common ectoparasite found on nestling sparrows was *Pellonyssus reedi* (syn. *Pellonyssus passerii*; Clark & Junker 1956). Other ectoparasites were also collected in low numbers from some chicks, including another nest-dwelling mesostigmatid mite species (53 specimens of *Ornithonyssus sylviarum*; Canestrini & Fanzago 1877), feather lice (three specimens of *Brueelia subtilis*; Nitzsch 1874, one specimen of *Menacanthus eurysternus*; Burmeister 1838) and fleas (*Ceratophyllus gallinae*; Schrank 1803, altogether 23 specimens in 10 nests).

All ectoparasites other than *Pellonyssus reedi* were excluded from the analyses. In mesostigmatid mites, only feeding forms are found on nestlings (non-feeding stages dwell in the nest material) thus, my sampling represents only this subpopulation of mites.

In total, 12213 specimens of *Pellonyssus reedi* were collected from the 2nd and 3rd breeding attempts. Prevalence of this mite in the nests was 1.0 in both breeding attempts, i.e., all investigated broods were infected with mites. Parasite burdens of the broods (total number of mites found in one brood) varied considerably, because mite distributions were highly aggregated in both breeding attempts, showing typical negative binomial distributions (Fig. 17). In the 2nd breeding attempt, mite number found in a brood ranged from 2 to 1482, with a mean abundance of 167.5.

In 3rd broods, mean abundance was 314.4, with mite loads ranging from 2 to 1636.

When analysing individual mite loads of nestlings, I found similarly high mite prevalences and aggregation indices both in the 2nd and 3rd broods (index of discrepancy and the k value of the negative binomial distribution; Table 2). Similarly to between-brood patterns, parasite burden of individual nestlings was also highly variable: mites found on one nestling ranged 0 to 713 on 2nd brood chicks and 0 to 769 on 3rd brood chicks.

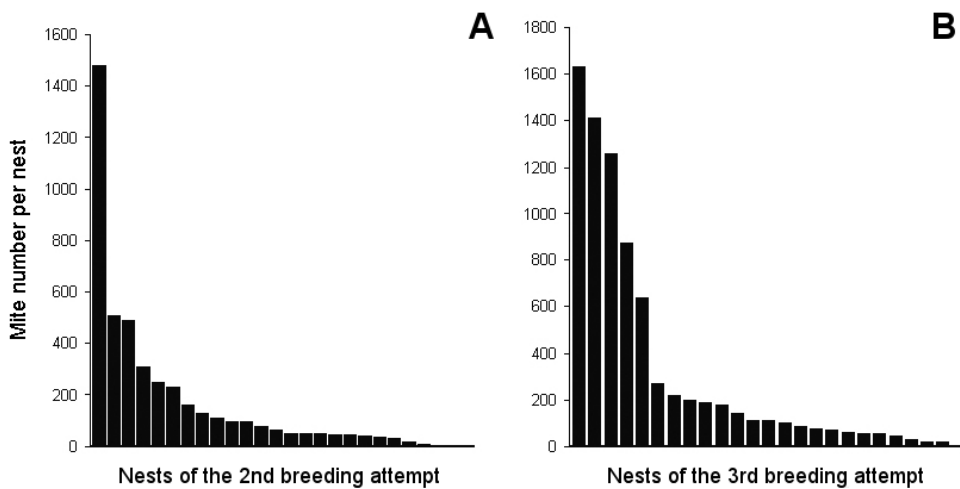


Figure 17. Mite abundance in the sparrow nests of the 2nd (A) and 3rd (B) broods (N= 26 and 25, respectively)

	2nd brood's nestling	3rd broods' nestling	both broods
No. broods	26	25	51
Mean brood size	4.26 (0.96)	4 (1.08)	4.13 (1.02)
No. nestling	98	90	188
Mite number per nest	2-1482	2-1636	
Mite number per nestling	0-713	0-769	
Prevalence	0.92 (0.85 - 0.96)	0.97 (0.92 – 0.99)	0.95 (0.91- 0.97)
Mean intensity	43.99 (27 – 62.56)	84.53 (56.76 – 113.06)	63.63 (46.41 – 78.86)
Median intensity	17 (11 – 22)	28 (22 – 39)	22 (17 – 25)
Mean abundance	40.7 (25.05 – 58.79)	82.75 (56.08 – 111.8)	60.48 (44.65 – 75.53)
D (discrepancy)	0.703	0.675	0.706
K of neg.binom.distr.	0.5	0.59	0.51

Table 2. Measures of parasitism by *Pellonyssus reedi* mites on individual house sparrow nestlings. 95% confidence interval values are given in parentheses, except brood size where mean and SD are shown.

Factors affecting nestlings' mite loads

I found a strong seasonal effect on infestation levels, nestling sparrows of the 3rd breeding attempt having significantly more mites than nestlings in the 2nd broods (linear mixed-effect model, $F_{1,44} = 5.85$, $p = 0.019$). This effect of seasonality was controlled for in all subsequent analyses.

Among nestling parameters, body condition and body mass were unrelated to mite load ($F_{1,134} = 1.66$ and 0.55 , $p = 0.19$ and 0.65 ; Fig. 18). This was also the case when controlling for tarsus length, feather length parameters and/or PHA-response in various combinations ($F_{1,110 - 1,127} = 0.06 - 2.83$, $p = 0.09 - 0.79$). The measure of skeletal size, i.e. tarsus length, was also unrelated to mite numbers ($F_{1,134} = 0.003$, $p = 0.95$; Fig. 19), even after removing effect of body mass, feather length and/or immunity ($F_{1,110 - 1,131} = 0.06 - 2.80$, $p = 0.09 - 0.64$). Similarly, PHA-response was unrelated to mite load ($F_{1,120} = 2.06$, $p = 0.15$; Fig. 20), and this result remained unchanged when I controlled for body mass, tarsus length, and feather parameters ($F_{1,110 - 1,116} = 0.57 - 2.10$, $p = 0.37 - 0.79$).

Both of the feather length traits showed a negative correlation with mite numbers (wing length: $F_{1,133} = 6.67$, $p = 0.01$; tail length: $F_{1,133} = 12.41$, $p < 0.001$; Fig. 21 and 22). That is, within a brood, chicks with longer wing and tail feathers had fewer mites than nestlings with less developed feathers. In wing length, this negative correlation remained when I controlled for body condition, mass, tarsus length and/or immunity effects ($F_{1,117 - 1,126} = 5.79 - 11.43$, $p = 0.001 - 0.017$), but disappeared when tail length was added to the model ($F_{1,124} = 0.001$, $p = 0.97$). The negative correlation between mite number and tail length remained significant when controlling for body size and immunity parameters ($F_{1,111 - 1,126} = 11.80 - 18.56$, $p = 0.000 - 0.006$), as well as for wing length ($F_{1,132} = 8.35$, $p = 0.004$). Relative nestling age also had a significant effect on individual mite load, older chicks having significantly less mites than their younger nest-mates ($F_{1,140} = 5.81$, $p = 0.02$). This correlation was not influenced by removing the effect of body condition, body size (body mass and tarsus) and/or PHA-response on mite loads ($F_{1,111 - 1,126} = 5.40 - 4.63$, $p = 0.020 - 0.037$), but disappeared after feather traits (wing and tail length) were included in the model ($F_{1,131} = 1.24$, $p = 0.26$).

When nestling age was added to the models, the effects of the analysed nestling parameters remained unchanged: body condition, body mass, tarsus length and PHA-response were unrelated to mite load of nestlings ($F_{1,119 - 1,133} = 0.1 - 0.71$, $p = 0.19 - 0.74$) and there was no change in the significant negative correlation between feather developmental parameters and mite number (wing length: $F_{1,132} = 5.25$, $p = 0.023$, tail length: $F_{1,132} = 8.38$, $p = 0.004$).

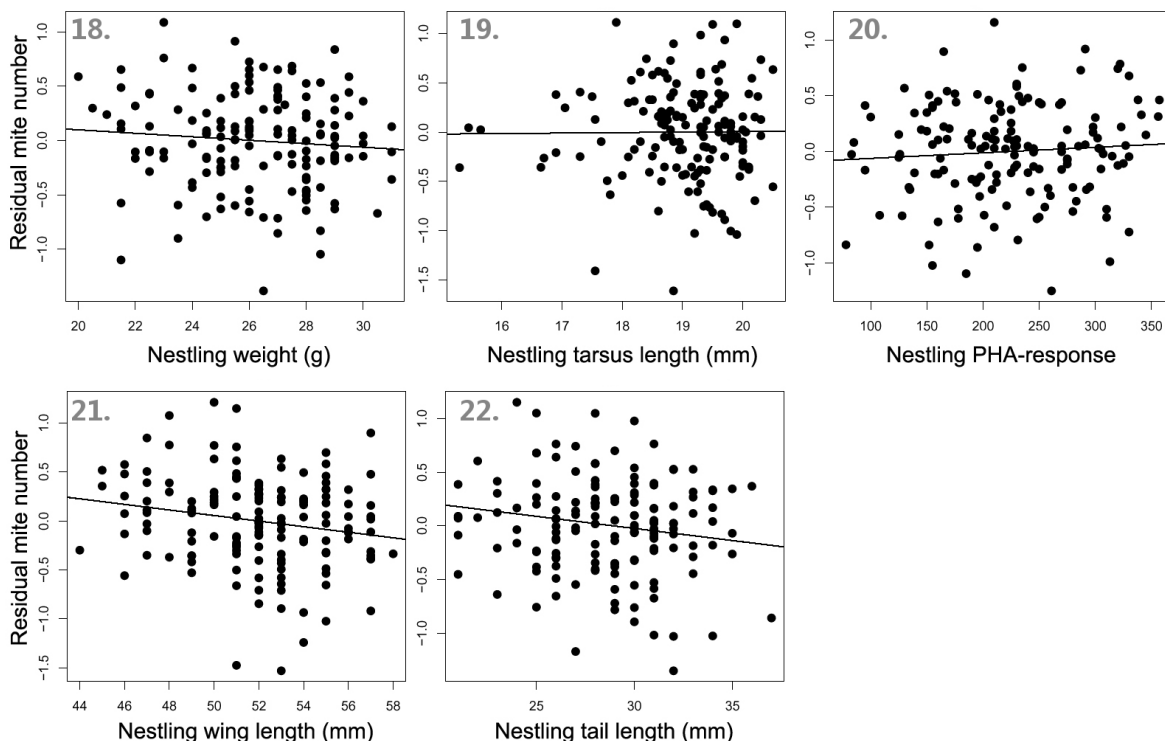


Figure 18 - 22. Correlation between total mite number and various nestling parameters of sparrow chicks. In each case, effects of breeding attempt and other nestling parameters are statistically controlled for (N = 188 nestlings).

Factors affecting proportion of recently fed mites

Altogether 3962 mites were counted with a red opisthosoma. That is, 32,4% of the collected parasites had recently fed, in average. Proportion of these mites was not affected by breeding attempt ($F_{1,44} = 0.38$, $p = 0.53$) and nestling age ($F_{1,132} = 0.14$, $p = 0.70$). Body condition, body mass, tarsus length, and PHA-response of nestlings were also unrelated to the proportion of recently fed mites ($F_{1,114 - 1,126} = 0.13 - 1.37$, $p = 0.31 - 0.71$), and these results remained the same after controlling for other nestling variables and age ($F_{1,103 - 1,119} = 0.03 - 2.55$, $p = 0.22 - 0.98$). Feather development traits were also unrelated to red opisthosoma mite proportion when analysed separately. Tail length (but not wing length), however, was positively related to the proportion of red opisthosoma mites after controlling for body size and immunity parameters ($F_{1,124} = 4.028$, $p = 0.04$). This means that

chicks with longer retrices had more red opisthosoma mites than chicks with shorter ones. This relation was not influenced when wing length and age effects were controlled for ($F_{1,103} = 5.15$, $p = 0.02$).

DISCUSSION

The results of this study did not indicate that the within-brood distribution of *Pellonyssus reedi* fowl mites on house sparrow nestlings around fledging time was related to those host characteristics that are often suggested as being preferred by parasites. Several studies reported preferences for large (older) nestlings by some parasite species (Darolová et al. 1997, Dawson & Bortolotti 1997, Roulin et al. 2003, Simon et al. 2003), and suggested that such hosts may provide better feeding conditions or safer habitat than the smaller ones. In contrast with these studies, I did not find any relationship between mite number and body mass or tarsus length of nestlings. Mite preference for better plumage cover on nestlings with more developed feathers was also not the case since the opposite pattern was found. Furthermore, these measurements of nestlings were also unrelated to the proportion of recently fed mites, which suggests that mites do not have higher feeding success on larger hosts than on smaller ones (at least within the range of body size variation that occurred in the studied broods).

Other studies suggest that the distribution of parasites may be related to individual differences in host susceptibility (Møller 1990, Lochmiller 1996, Christe et al. 1998, Roulin et al. 2003, Simon et al. 2003). For example, ectoparasites often stimulate host immunoregulatory and effector pathways that may raise an effective defense via blocking blood meal acquisition (e.g. Nazario et al. 1998, Wang et al. 1998). Consequently, intra-brood differences of such immune responses might be reflected in different ratios of blood-fed mites on different chicks (Møller 2000). In this study, however, neither mite loads nor the proportion of red opisthosoma mites were related to nestling immunity as measured by their T-cell responses.

We, on the other hand, found clear negative relationships between nestling sparrows' age and feather development and their parasite loads. This finding may

indicate that mites abandon nestling close to fledging. Avoiding old nestling might be advantageous if the removal from the nest by the fledging young seriously decrease the future reproductive prospect of the mites. Although relatively little is known about the life history of *Pellonyssus reedi*, pieces of circumstantial evidence support this assumption. The closely related macronyssid haematophagous mites need the nest material for successful breeding: mating and egg laying takes place in the nest, the non-feeding developmental stages inhabit mainly the nest material, and even feeding protonymph and adult forms rest in the nest material between the feeding periods (Clark & Yunker, 1956).

Consequently, mites abandoning mature chicks can continue to feed on the unfledged nestling and reproduce for some extra time, because older sparrow nestling may leave the nest days before their younger siblings (Anderson 2006, my personal observations). Furthermore, mites remaining in the nest could continue to reproduce during the development of subsequent sparrow broods in their original nest or a nest nearby. Mites remaining on a fledged bird might miss these opportunities and are probably obliged to postpone their reproduction for the next year. As mites reproduce quickly (as indicated by the increasing population size during the breeding season; Masan & Kristofik 1995, Stoehr et al. 2000, Szabó et al. 2002, Garvin et al. 2004) this one-year delay in reproduction might be very costly.

This argument is supported by the observation that mites dwell in (or nearby) the nest between two breeding attempts, when no hatched nestling are present (Clark & Yunker 1956). In the house sparrow, the nestling of the 2nd, 3rd or 4th breeding attempts hatch 7-10 days after the last chick of the previous attempt had fledged (Anderson 2006, my personal observations). Mites can definitely endure this period starving (or even feeding on the incubating parents; Axtell & Arrends 1990). The fact that the population size of fowl mites increases during the breeding season in several passerine hosts (Masan & Kristofik 1995, Pacejka et al. 1996, Stoehr et al. 2000, Szabó et al. 2002, Garvin et al. 2004, this study) may also support the idea that parasite individuals can successfully survive the periods

between successive broods. Mites even can search for new hosts in the sparrow colony when the original nest is not used for further breeding by sparrows. For example, the closely related *Ornithonyssus* and *Dermanyssus* mites are reported to leave the nest and looking for new hosts when left behind in an empty nest (Axtell & Arrends 1990, Mullens et al. 2001). Such a behaviour may also be feasible for *Pellonyssus* mites: e.g. in the milk farm population sparrows built their nests mainly in holes under the roof, and these nests holes were often very close (20-30 cm) to each other.

Being removed from the nest by fledglings may be less costly for mites in terms of survival. In the study of Clark & Yunker (1956), specimens of *P. reedi* were found on free-living house sparrows throughout the year. Thus, it is likely that *Pellonyssus* mites are able to survive on adult host for longer periods but it might be unlikely that these mites can reproduce during their stay on the hosts.

The mechanism by which *Pellonyssus* mites could perceive the development stage of their host is an open question. However, the possibility of such mechanisms is exemplified by other arthropods, e.g. by commensalist feather mites whose host-abandonment behaviour is well-studied. Since these latter organisms have special requirements of temperature and humidity, they are coerced to attach tightly to their host, with the possibility to die if they fall out on moulting feathers (Dubinin 1951). During moult, they seem to be able to perceive (via the vibration of the feathers ready to fall out, or via the altered airflow caused by the vibrating feathers) and leave the moulting feather by climbing onto the surrounding feathers already moulted or scheduled to moult later (Jovani & Serrano 2001, Pap et al. 2005).

For *P. reedi*, I found that feather development was the best explanatory variable of mite loads. As feather development may be a good predictor of fledging time in sparrows (nestling are able to fly when their wing lengths reach about 50 mm, Summers-Smith 1963), it may serve as a cue to induce the mites' avoidance or abandonment behaviour. For instance, the mites' effort when moving from the nest material to the body surface of nestling may depend on the length and density of

feathers, and mites may give up above a specific level of such efforts. This idea might be supported by the finding that the proportion of recently fed mites increases with feather length, given that feeding takes considerable time. If this is the case, then mites already on the nestling fed while the income of mites with empty stomach diminishes. The process could then result in a positive relation between feather length and the proportion of mites with red stomach. Note, however, that the latter result can also be explained by density-dependent processes. For instance, on highly infested nestling, mites may compete for food to a greater extent, making their feeding success lower than on nestling with low ectoparasite burden. In my case, chicks with more developed feathers had relatively less mites, and on such a host competitive interactions among parasites may be reduced, resulting in a higher proportion of successfully fed mites. It is unknown, however, whether feeding success of mites is really related to population density within the range of population sizes that occurred in this study.

In conclusion, I did not find evidence for that mite would prefer nestling with large body size or weak immunity. On the other hand, my study suggest that *P. reedi* mites may avoid or abandon nestling around the time of their fledging, which may play an important role in shaping mite distribution within the broods. This behavioural response would allow the mites to remain in the nest and to continue feeding and reproducing during the development of unfledged chicks of current or subsequent breeding events. To verify this argument, however, more data are needed on the life history of the mites during their full life cycle. The results presented here, nevertheless, imply that, in the last days of nestling age, within-brood parasite distributions on avian hosts not necessarily represent preferences, and should not be compared with distributions measured in other developmental stages of nestling.

4.3 Paternal investment is unrelated to badge size in house sparrows

In this study I investigated whether aspects of parental quality of house sparrow males (in form of nestling provisioning, risk-taking and nestling quality) is related to their secondary sexual trait, allowing females to gain direct benefits when choosing mates on their basis. This study was carried out in June and July 2002, involving broods of the 1st and 2nd breeding attempt. Behavioural sampling was made only on the 2nd breeding nests. In this breeding season, clutch size at hatching ranged between 3-6 nestlings (4.88 in average), and 1-6 nestlings (4.23) on day 12, near to fledging. In this year, ectoparasitic mites were found only in three broods, these were excluded from analyses.

Provisioning behaviour

On both D5 and D9, female feeding rates were higher (3.06 h^{-1} and 4.28 h^{-1} in average) than of the males' (2.54 h^{-1} and 3.35 h^{-1}), but this difference was only marginally significant on D5 (paired Wilcoxon test; $V = 343$, $p = 0.06$; Fig. 23A) and non-significant on D9 ($V = 317$, $p = 0.18$; Fig. 23B). Both males and females had higher provisioning rates on D9 than on D5, this increase was significant only in females ($V = 107$, $p = 0.017$) but not in males ($V = 175$, $p = 0.36$).

In females, none of the measured weather conditions (daily temperature, number of sunny hours, rainfall) affected the feeding rate ($F_{1,29} = 0.001 - 0.31$, $p = 0.57 - 0.99$). Similarly, time of day, start of breeding and clutch size were unrelated to provisioning activities on both D5 ($F_{1,29} = 0.002 - 2.46$, $p = 0.12 - 0.95$) and D9 ($F_{1,29} = 0.12 - 1.85$, $p = 0.18 - 0.72$).

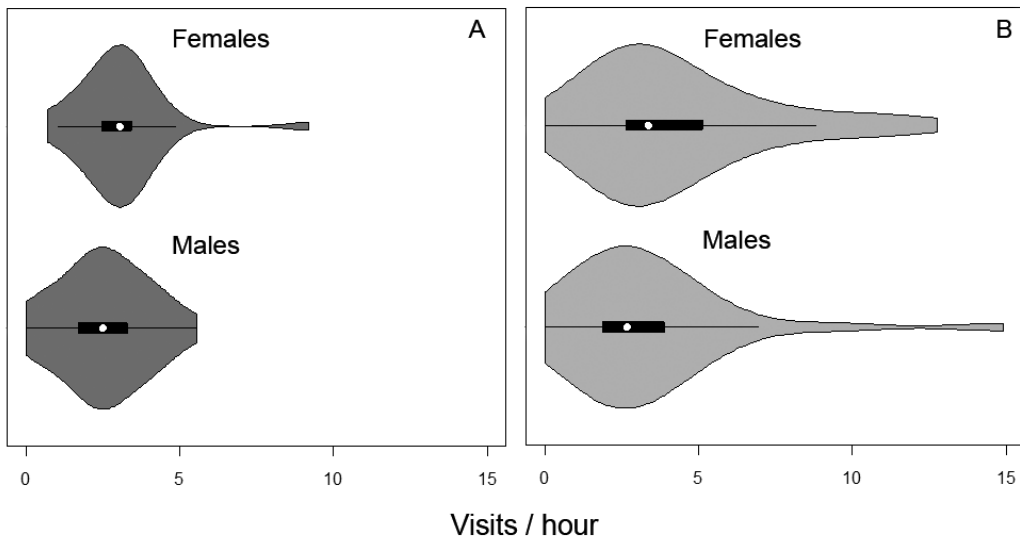


Figure 23. Feeding rates (nest visits in 60 minutes) of the parents on D5 (a) and D9 (b), displayed with violin plots.

Male provisioning, however, was negatively influenced by both daily temperature and number of sunny hours on D5 ($F_{1,29} = 5.13$ and 4.83 , $p = 0.030$ and 0.035) but not on D9 ($F_{1,29} = 0.29$ and 0.04 , $p = 0.59$ and 0.82). Note that these two measures of weather conditions were highly correlated on both D5 and D9 (Spearman's rank correlation, $p < 0.001$ in both cases). Rainfall and time of the day had no effect on male feeding activity ($F_{1,29} = 0.17 - 0.39$, $p = 0.53 - 0.67$). Feeding activity of males on D5 decreased in clutches that hatched later in the season ($F_{1,29} = 5.98$, $p = 0.043$), but this trend was not present on D9 ($F_{1,29} = 0.74$, $p = 0.39$). Number of the nestlings in the brood had an effect on male feeding rates on D9 ($F_{1,29} = 5.18$, $p = 0.030$), that is, male parents delivered more food to larger clutches. This was, however, not true for D5 nests ($F_{1,29} = 0.04$ and 0.62 , $p = 0.83$ and 0.43).

Parental feeding effort was associated with growth of the chicks, but this was noticeable only in the second part of the nestling period. Cumulative feeding rate of fathers and mothers measured on D5 had no influence on body condition and body size variables measured on D12 ($F_{1,29} = 0.0009 - 1.59$, $p = 0.52 - 0.92$), on

D9, however, feeding effort positively correlated with nestling body mass and tarsus size ($F_{1,29} = 6.55$ and 9.091 , $p = 0.015$ and 0.005 ; Fig. 24 - 25). This trend was also present (although non-significantly) in body condition ($F_{1,29} = 3.15$, $p = 0.09$; Fig. 26). Male contribution to nestling development was nonsignificant, since nestling condition and size on D12 was uncorrelated with both feeding effort of the fathers ($F_{1,29} = 0.0005$ – 1.71 , $p = 0.2$ – 0.89), and male shares of total parental provisioning ($F_{1,29} = 0.003$ – 2.6 , $p = 0.11$ – 0.86).

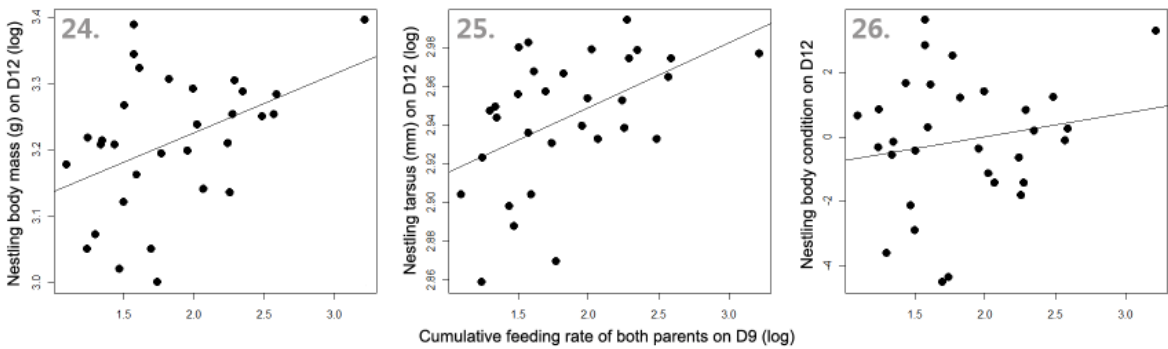


Figure 24 - 26. Effect of cumulative provisioning of both parents on nestling growth, measured on D9.

Badge size of males was unrelated to their provisioning activity in both feeding records ($F_{1,28} = 0.02$ and 0.29 , $p = 0.88$ and 0.59 , respectively; Fig. 27AB), and this was also the case when corrected for factors affecting male feeding rates (see above; $F_{4,24} = 0.001$ and 0.12 , $p = 0.73$ and 0.96). Feeding rates of average-badged males were similar to large- or little-badged ones ($F_{1,28} = 0.27$ and 2.84 , $p = 0.60$ and 0.11), even when controlled for clutch size ($F_{2,26} = 0.18$ and 2.02 , $p = 0.67$ and 0.17).

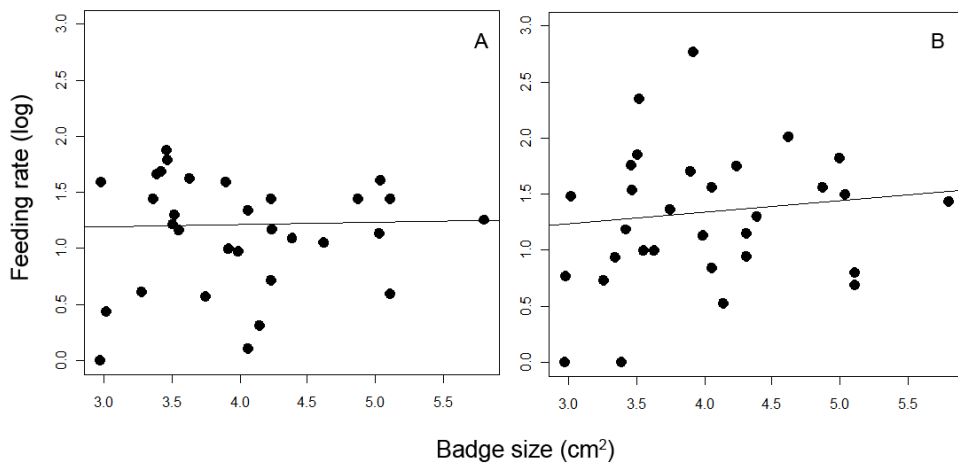


Figure 27. Badge size and feeding rates of male sparrows on D5 (A) and D9 (B).

Similarly, female provisioning behaviour wasn't affected by male ornament size ($F_{1,28} = 0.76$, $p = 0.39$ on D5 and $F_{1,28} = 0.54$, $p = 0.46$ on D9). Feeding rates were similar in mothers mated to average-badged fathers and mothers mated to extremely-sized ones ($F_{1,28} = 0.12$, $p = 0.72$ on D5 and $F_{1,28} = 0.50$, $p = 0.48$ on D9). In general, there was no correlation between male and female provisioning behaviour, neither on D5 (Pearson correlation; $t = 1.35$, $p = 0.18$), nor on D9 ($t = 0.34$, $p = 0.73$).

Risk taking

Return time (the time between predator dummy removal and the first entry into the nest) varied considerably between parents in both sexes (51 to 3120 seconds in males and 39 to 1803 seconds in females; Fig. 28).

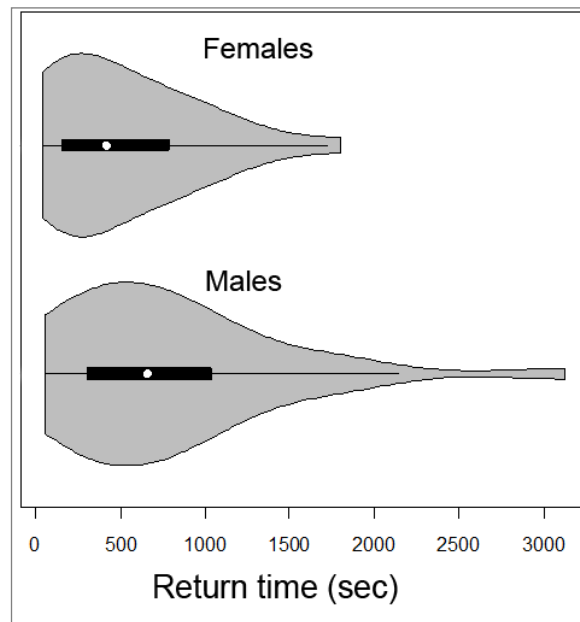


Figure 28. Return time in sparrow parents, displayed with violin plots.

There was a trend for females being more risky, their return time was shorter (542 sec. in average), than of fathers (756.7 sec), although this difference was insignificant (Wilcoxon test, $W = 267.5$, $p = 0.203$). Similarly, females were (also not significantly) more often the risk takers (the bird that first entered the nest), males rather tended to be the followers (in 19/32 broods; binomial test, $p = 0.21$). Return time was affected by clutch size in both sexes. Males with larger broods entered their nest in significantly shorter time after the predator dummy removal ($F_{1,28} = 6.90$, $p = 0.014$). This trend was also present in females, although not significantly ($F_{1,27} = 2.25$, $p = 0.14$).

Risk-taking behaviour of fathers was unrelated to their badge size ($F_{1,28} = 0.99$, $p = 0.33$; Fig. 29), even after correcting for clutch size ($F_{2,26} = 0.209$, $p =$

0.65). This result remained when the single outlier (3120 sec) was excluded from the data ($F_{1,27} = 0.11$, $p = 0.73$). Return time of males with average badge sizes was similar to large-badged or little-badged ones ($F_{1,28} = 1.16$, $p = 0.29$), even when controlled for clutch size ($F_{2,26} = 0.84$, $p = 0.37$). In addition, badge size was similar in risk taker and follower males (3.98 and 3.96 cm³, respectively; Welch two sample t-test, $t = 0.047$, $p = 0.96$).

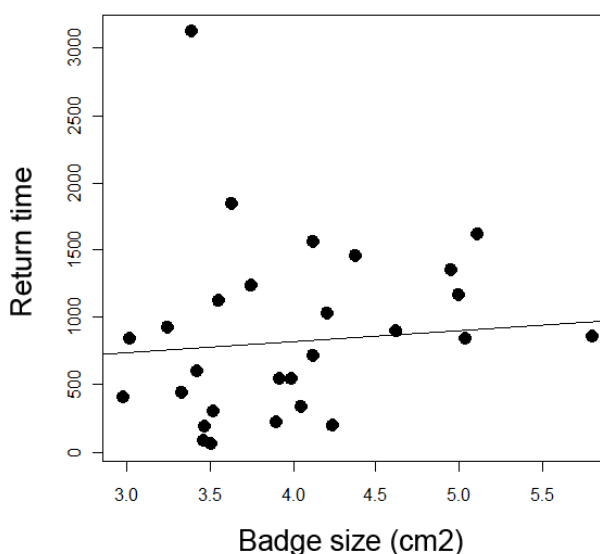


Figure 29. Badge size and return time of sparrow fathers.

Return time of females was also unrelated to the sexual ornament of their male partners ($F_{1,27} = 1.74$, $p = 0.20$), and similarly, risk taking behaviour was similar in mothers mated with average-sized and extremely-sized males ($F_{1,27} = 0.03$, $p = 0.86$). Return rates of mothers and fathers within the same pair were not correlated (Pearson correlation; $t = 0.59$, $cor = 0.13$, $p = 0.55$).

When different measures of parental efforts were set together, female individuals acted more consistently. Their two records of provisioning behaviour were correlated (feeding rates on D5 and D9; Pearson correlation; $t = 2.54$, $cor =$

0.43, $p = 0.016$), while in males, this correlation was not present ($t = -0.15$, $\text{cor} = -0.02$, $p = 0.87$). In both males and females, risk taking behaviour and D5 provisioning was uncorrelated ($t = -0.02 - 0.35$, $\text{cor} = 0.004 - 0.07$, $p = 0.72 - 0.98$), but risk taking and D9 feeding was positively correlated in both sexes ($t = 2.32 - 2.40$, $\text{cor} = 0.42 - 0.44$, $p = 0.02 - 0.024$),

Direct reproductive success of caring males was independent of their badge size, since there was no badge size-related difference in clutch sizes prior to fledging on D12 ($F_{1,28} = -1.49$, $p = 0.37$), and clutch sizes were similar in average-badged and extremely-badged males ($F_{1,28} = -0.85$, $p = 0.23$). Similarly, badge size seemed to have no influence on nestling development, either. Nor nestling body condition ($F_{1,28} = 1.68$, $p = 0.21$) nor any of the measured nestling parameters (body weight, tarsus and bill length, wing and tail size) recorded on D12 were affected by the badge size of fathers ($F_{1,28} = 0.01 - 1.90$, $p = 0.18 - 0.91$), and there were no differences between nestlings of average badged and extremely-badged fathers ($F_{1,28} = 0.03 - 1.81$, $p = 0.18 - 0.85$).

DISCUSSION

Early development of altricial birds is largely influenced by parental care. Parental food provisioning is the chief factor affecting growth and survival of altricial bird nestlings (Lack 1954, 1968, Martin 1987, MacColl & Hatchwell 2004), while nest defense might ensure this growth and survival when nest predators are present (Andersson et al. 1980, Knight & Temple 1986).

In biparental species where males contribute actively to the rearing of offspring, male parental quality has often been invoked as a key element in mate choice. If substantial individual variation occurs in quality of parental performance of available males, selection favours female preference for males that are good fathers (Trivers 1972, Searcy 1982, Parker 1983). Given that females of short-lived birds with temporary social bonds may be unable to correctly assess male parental quality at the time of pairing, sexually-selected traits that indicate parental quality

in males might evolve, as predicted by theoretical models (Wolf et al. 1997, Kokko 1998).

Although several studies support the idea that a melanin-based bib in house sparrows is a condition-dependent trait (Jawor and Breitwisch 2003, Griffith et al. 2006), latest results suggest that the bib size of male house sparrows is currently under little or, at most, weak sexual selection. In a recently published meta-analysis, Nakagawa et al. (2007) attempted to assess the role and function of this plumage signal, disentangling the versatile results of the latest three decades. This meta-analysis confirmed the role of the bib as a badge of status and partly as indicator of age and quality. On the contrary, it provided little evidence for sexual selection acting on bib size, as both parental care (nestling provisioning and incubation) and reproductive success failed to show significant relationship with this trait.

Similarly, this work also failed to find any association between badge size and various components of male parental care in house sparrows, suggesting that there is no direct benefit of choosing large-badged males as social partner. Large-badged fathers don't provide more and take no greater risk than other males. Moreover, their reproductive success is similar (in form of fledging success and nestling size at fledging) to smaller-badged ones. Therefore, '*good parent*' model of sexual selection (Hoelzer 1989) cannot be supported on the basis of this data.

Given that theory suggest strong female preferences for good fathers when (1) male parental investment largely influence offspring fitness and (2) males are highly variable, but (3) consistent in their parental contributions (Trivers 1972, Searcy 1982, Parker 1983), house sparrow would be a good model animal meeting this requirements. Specifically, in house sparrows, similarly to other bird species (e.g. Bart & Tornes 1989, Dickinson & Weathers 1999), male assistance was found to be essential in maximising reproductive success (Schwagmeyer 2003), with short-term fitness gains (clutch size and fledging success) attributable mainly to male effort in chick feeding. Moreover, Schwagmeyer et al. also reported

remarkable individual consistency across time in house sparrow males: variation in male parental provisioning at one stage of the nestling cycle was highly predictable from the previous behaviour of the individuals, rather than the mates' current behaviour, both during the rearing time of the same nest (2002), and across broods (2003). This consistency was absent in females, with much less variation in their parental performance. Similar results are reported by Freeman-Gallant & Rothstein (1999) in Savannah sparrow (*Passerculus sandwichensis*), where males, but not females, were consistent in provisioning rates across years.

In this study, total parental deliveries (at least in the later nestling phase) correlated with nestling body mass and size at fledging. That is, this type of parental effort was transformed into measurable fitness gain, given that fledging body mass highly affects long-term nestling survival and recruitment (Gustafsson & Sutherland 1988, Haywood & Perrins 1992; also in house sparrows; Schwagmeyer & Mock 2008). Male contribution, however, was not that essential in nestling development, as found in previous studies. Moreover, there was indeed considerable variation in male parental competence, that is, both 'good fathers' and 'bad fathers' were present in the study population, and their parental performance was consistent (at least in the second part of nestling period) concerning the various activities. Although female individuals behaved more consistently than males (in both the two records of provisioning rates and risk taking and D9 provisioning), fathers that were good at risk taking on D8 were also good providers on D9 (but there was no consistency in their early (D5) and late (D9) provisioning behaviour).

Alternatively, elevated level of parental provisioning might be the response (and not the cause) to the bigger nestling size, or to a more intense begging of chicks in better condition. Since these results come from an observational study, in this case, causes and effects can't be identified.

In general, parental performance of house sparrows is suggested to follow a 'sealed bid' process, rather than a pattern that can be described by 'negotiation models' (Schwagmeyer et al. 2002). In negotiation models of biparental care,

individuals are expected to adjust their parental care in response to the effort of their current mate, predicting an inverse relationship between the parents' contribution (McNamara et al. 1999, McNamara et al. 2003). In a 'sealed bid' process, however, instead of facultatively adjusting their own provisioning to partner's contributions, individuals behave as if they had committed to a certain level of parental care at the outset, such that they may modify their contribution according to brood age, prey abundance, etc. This pattern was found in several bird species, including house sparrows; (Sanz et al. 2000, Schwagmeyer et al. 2002) and similar pattern can be concluded also in this population (although there was no specific experiment to test it), where feeding rates of mothers and fathers were not correlated.

The observed behavioural patterns suggest that predictions of the '*differential allocation theory*' (Burley 1986) didn't come true, either. That is, that large-badged males weren't more appreciated by females, at least females did not adjust their effort to the attractiveness of their mates. Female feeding rates and risk taking weren't related to the badge size of their partners, suggesting that (similarly to direct fitness gains) there are no indirect genetic benefits when choosing males with more elaborated signals. Moreover, the third main hypothesis attempting to explain the relationship between parental care and male ornament size was also failed in my case. Since large-badged males provided no less effort than little-badged ones as predicted by theory, '*trade-off*' (Magrath & Komdeur 2003) model (to invest more in fitness-maximizing activities other than care) also failed to explain these data.

To conclude, in contrast with the statements of field studies reporting positive correlation between badge size and male shares of risk-taking and nestling provisioning (Reyer et al. 1998, Voltura et al. 2002), these results suggest that badge size is probably not a signal that females can rely on when assessing real parental ability. This is congruent with one of the main conclusions in Nakagawa et al.'s (2007) meta-analysis, namely that badge size of house sparrows is under weak

sexual selection.

In this case, however, sparrow females might use clues other than plumage ornaments when assessing male parental quality. Early paternal activities that can be explored and judged by females at the time of pairing even in a non-territorial bird (e.g. nest building and guarding) could serve as such signal. Yet, Hoi et al. (2003) found no relationship between intensity of early (nest building and nest guarding) and later (late incubation, brooding and provisioning) paternal effort, suggesting that early performance do not seem to be honest indicators of later paternal effort in the house sparrow, either. Therefore, exact patterns of mate-choice decisions in house sparrow females remains an open question.

5.1 SUMMARY

In altricial birds, early development constitute an important and critical period, with extremely rapid growth and high energetic demands. During this time, rearing conditions may have both short- and long-term consequences, influencing fledging condition, survival, physiology, behaviour and reproductive performance in adulthood.

Since nestlings of altricial birds are defenseless and nutritionally dependent and they rely totally on their parents in this period, parental care (e.g. nutrition effort and defense) is one of the most important among these conditions. In biparental caring birds, parental efforts may depend on both individual quality and the interplay between the caring parents. Male sexual ornaments might serve as a cue in female choice as signals that honestly indicates male parenting ability. However, male sexual displays might signal also other (e.g. genetic) benefits, females mated with more/less ornamented males might therefore adjust their own parental effort to the reproductive value of their actual partner. So thus, early development of the nestlings is influenced also by the outcome of these parental decisions.

Even in case of beneficial environment and megfelelő parental investment, the presence of parasites can during offspring development can ruin a good start in life. Nest-dwelling arthropod ectoparasites that are adapted to feed on developing birds might have radical consequences on both short and long-term fitness, given that nestlings are exposed to them in a sensitive period of energy demanding fast growth and development. These ectoparasites may have a number of detrimental effects on nestlings, (e.g. loss of nutrients, tissue damage, immune reactions, or transmission of micropathogens) often impairing nestling growth and development and resulting offspring in poor condition at fledging.

The impact of nest-dwelling ectoparasites on nestling quality, however, may vary considerably due to variation in environmental factors, offspring quality, and individual parasite load. Parasite infestation of a given chick in a brood is usually

explained either by the parasites' preference for certain kinds of host characteristics, or by individual differences in offspring's susceptibility to parasites. Beside these factors (at least in short life-cycle parasites), avoidance of certain nestlings can give an alternative approach to understand within-brood variance in ectoparasite infection.

In this thesis, I present the results of three observational field studies that concern two important biotic factors during early life of house sparrows: parasitism and parental assistance. Field studies were conducted between 2000 and 2002, in a population of free-living rural house sparrows, inhabiting a milk farm near to Debrecen, Hungary. In the majority of the nests, nestlings were parasitised by blood-feeding Macronyssid mites (*Ornythonyssus sylviarum* and *Pellonyssus reedi*).

In the first study I investigated whether intense loads of nest-dwelling blood-sucking mites affect condition and health state of developing house sparrow nestlings. Natural levels of ectoparasitic blood-sucking mites had no significant negative effect on body condition and size of fledgling sparrows. Health state of developing chicks was, however, influenced by mite parasitism, by affecting their blood profile (by activating inflammatory processes) and causing anaemia.

In the second study I attempted to reveal factors and mechanisms that shape intranest distribution of macronyssid fowl mites on house sparrow nestlings. Body size and condition played no role in shaping within-brood distribution pattern of nest-dwelling mites. Instead, intranest variance of mites was found correlating with developmental status (age and feather development) of sparrow chicks, indicating that mites abandon nestling close to fledging to avoid removal from the nest. Identification and abandonment of mature nestlings that are ready to fledge could be adaptive for the parasites, allowing them to stay in the nest and continue reproduction. Contrary to many studies where within-brood variance in parasite burdens are explained by the parasites' preferences for certain kinds of host characteristics, this result suggests that this type of behavioural adaptation

(avoidance instead of preference) may also significantly shape intranest distribution of parasites - at least in certain types of parasites and in certain developmental status of hosts.

In the third study I investigated whether aspects of parental quality of house sparrow males (in form of nestling provisioning, risk-taking) as well as nestling quality and intranest survival is related to their secondary sexual trait (badge size), allowing females to gain direct benefits when choosing mates on their basis. Parental contribution (nestling provisioning and risk-taking) of male sparrows during the intranest phase of offspring development was not associated with body condition and fledging success of their chicks. Moreover, both paternal and maternal investment in a social pair was independent of the male's badge size, suggesting that both direct (according to the good parent hypothesis) and indirect (according to the differential allocation hypothesis) fitness benefits for the females are independent of this trait, and that badge size is probably not a signal that females can rely on when assessing real parental ability in house sparrows.

5.2 ÖSSZEFOGLALÁS

A fészeklakó madarak életének első szakasza nagyon fontos és érzékeny periódus, melyet rendkívüli mértékű növekedés és az ezzel járó nagy energiaigény jellemez. A fejlődés ezen ideje alatti behatások nagymértékű, rövid- és hosszú távú, következményekkel járhatnak, jelentősen befolyásolva a fiókák egészségi állapotát, kirepüléskori kondícióját, rövid és hosszú távú túlélését, valamint reprodukív képességeit. Mivel a fészeklakó fiókák önállóan nem tudnak táplálkozni, kiszolgáltatottak a fészekpredátoroknak és teljesen a nevelő szülőkre vannak hagyatkozva ebben a periódusban, a korai hatások egyik legfontosabbika a szülői gondoskodás. Ennek a gondoskodásnak a mértéke és minősége a biparentálisan gondozó madarak esetén a szülők aktuális egyedi állapotától valamint a szülőpár közti interakcióktól is függ.

A hímek másodlagos nemi jellegei őszintén jelezhetik a nőtények számára viselőjük szülői képességeit/hajlandóságát. Mivel ezek a szignálok egyéb, a nőtények számára hasznos tulajdonságokkal (pl. genetikai minőség) is összefügghetnek, a tojók az aktuális párjuk reprodukív értékéhez igazíthatják saját szülői befektetéseik mértékét. A fiókák fejlődése így nem független a szülők ilyen döntésinek kimenetelétől sem.

A kedvező feltételek és a megfelelő szülői gondoskodás megléte sem biztosíték azonban a gondtalan fejlődésre. Egyes ízeltlábú fészeklakó ektoparaziták kimondottan a fejletlen fiókákon történő táplálkozáshoz alkalmazkodtak, és mivel az intenzív növekedéssel és nagy energiaigénnyel járó érzékeny korai szakaszban károsítják a fiókákat, komoly negatív következményeik lehetnek rövid és hosszú távon egyaránt. Az ektoparaziták mind közvetlen (pl. tápanyagok elvesztése, szöveti károsodás, gyulladásos folyamatok és más káros élettani hatások), mind pedig közvetett (költséges immunfunkciók generálása, mikropatogének terjesztése) módon hátráltathatják a fiókák fejlődését és növekedését, rossz kirepüléskori kondíciót és egészségi állapotot eredményezve, ezzel is csökkentve a kirepülés utáni túlélési esélyüket.

A fészekparaziták káros hatásának mértéke (egyéb tényezők mellett) nagyban függ a parazitáltság mértékétől. Az, hogy egy adott fészekaljban miképpen oszlanak el a paraziták az együtt nevelkedő (és ezért egyidejű táplálékforrást jelentő) fiókákon, vagyis egy adott fiókára milyen parazitaterhelés jut, azt többféle módon is próbálták már magyarázni. A paraziták preferálhatnak bizonyos fiókákat, mert azok relatíve jobb táplálékforrást jelentenek, vagy fogékonyabbak, vagyis gyengébb immunválaszt adnak a parazitákra. A korábbi kutatások azonban a preferenciára irányultak, és nem foglalkoztak azzal, hogy bizonyos fiókákat (amelyek valamilyen szempontból kockázatosak lehetnek a paraziták számára) érdemes lehet elkerülni.

PhD dolgozatomban három terepi vizsgálat eredményeit mutatom be, melyekben két biotikus tényezőnek, az ektoparazitáknak és a szülői gondoskodásnak a korai fejlődésre kifejtett hatását vizsgáltam házi verebek fiókáiban. A vizsgálatokat egy Debrecen melletti tehenészet területén élő háziveréb-populációban végeztem 2000 és 2002 között. A fészkek többségében a Macronyssidae családba tartozó fészeklakó vérszívó atkák (főleg *Pellonyssus reedi*, valamint *Ornithonyssus sylviarum*) éltek a fiókákon.

Az első tanulmányban a vérszívó fészeklakó atkáknak a fejlődő verébfiókák kondíciójára és egészségi állapotára kifejtett hatását vizsgáltam. Az fiókákon talált paraziták száma nem befolyásolta a kirepüléskori kondíciójukat és méretüket, viszont a fiziológiai állapotukat igen. A nagyfokú parazitáltság gyulladós folyamatokat (aszpecifikus immunreakciókat) és anémiát okozott a fiókákban.

A második vizsgálat a háziveréb-fiókákat parazitáló vérszívó atkák fészekaljon belüli eloszlásának okait próbálta kideríteni. A fiókák mérete (tömeg és csüd hossz) és kondíciója nem állt összefüggésben a fiókák egyedi parazitáltságával. Az atkák tápláltsági állapotának vizsgálata is azt mutatta, hogy a jobb kondícióban lévő, nagyobb fiókák nem jelentenek jobb táplálékforrást. Viszont a fiókák fejlettségi állapota (koruk és tollazatuk mérete) szignifikánsan befolyásolta a rajtuk talált atkák számát: a fejlettebb tollazatú és idősebb fiókákon

kevesebb atka táplálkozott, mint kevésbé fejlett testvéreiken. Ez arra utalhat, hogy a kirepülés előtt álló fiókákat elkerülik a paraziták. Az ilyen fiókákön való tartózkodás (legalábbis a gyors életmenetű atkák számára) kockázatos lehet, mivel a fészekből kikerülve elveszíthetik a fészek adata előnyöket (nagy szaporodási potenciál, kedvező és biztonságos környezet). Így a fejlett, kirepülés előtt álló fiókák felismerése és aktív elhagyása adaptív viselkedés lehet a paraziták számára, biztosítva a fészekben maradásukat. Vagyis ellentétben sok korábbi vizsgálattal, amelyekben a paraziták fészekaljon belüli eloszlását bizonyos fiókák (jobb táplálékforrást vagy rosszabb immunitást jelentő egyedek) iránt való preferenciával magyarázták, én bizonyos fiókák elkerülésének fontosságát hangsúlyozom.

A harmadik terepi vizsgálat arra próbált választ találni, hogy a hím házi verebek szülői erőfeszítései (etetési és kockázatvállalási viselkedése) és fiókáik kirepülési sikere kapcsolatban áll-e a begyfoltméretükkel, vagyis hogy a begyfoltméret lehet-e olyan másodlagos nemi jelleg, aminek figyelembe vételével a nőstények közvetlen haszonra tehetnek szert párválasztáskor (a 'jó szülő hipotézis' szerint), vagy esetleg párjuk reprodukív értékéhez igazítják saját szülői befektetéseik mértékét (a 'differenciális befektetés hipotézis' szerint). A hímek kirepülés előtti etetési viselkedése és kockázatvállalása nem függött össze a fiókák kirepüléskori kondíciójával és kirepülési sikerével. Ráadásul sem a hímek, sem a tojók szülői erőfeszítései nem korreláltak a hím begyfoltjának méretével. Így a begyfalt ebben a fajban (legalábbis a vizsgált populációban) valószínűsíthetően nem olyan nemi jelleg, aminek mérete megbízhatóan jelzi a tojók számára viselőjük szülői képességeit vagy hajlandóságát. Arra sem találtunk bizonyítékot, hogy a begyfalt tükrözne valamilyen indirekt reprodukív hasznót, ami alapján párt választva a tojóknak érdemes lenne saját szülői befektetésüket megnövelni.

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