

Charles University in Prague

Faculty of Science

Department of Zoology



Adam Dušek

**Maternal Investment Strategy in Model Monotocous and
Polytocous Mammals: A Life-History Perspective**

Ph.D. Thesis

Supervisor: Prof. Ing. Luděk Bartoš, DrSc.

Supervisor Specialist: Doc. RNDr. Pavel Stopka, PhD.

Prague, 2011

Declaration:

I hereby confirm that I have written the present Ph.D. thesis myself, using only the referenced sources. This Ph.D. thesis, neither its substantial part, was not submitted to gain another or the same academic title.

In Prague, May 12, 2011

Adam Dušek

Content

Acknowledgements	iv
Abstract	1
Abstrakt	2
Introduction	3
I. Dušek, A., Bartoš, L. & Švecová, L. 2007. The effect of a mother's rank on her offspring's pre-weaning rank in farmed red deer. <i>Applied Animal Behaviour Science</i> , 103: 146–155.	
II. Drábková, J., Bartošová, J., Bartoš, L., Kotrba, R., Pluháček, J., Švecová, L., Dušek, A. & Kott, T. 2008. Sucking and allosucking duration in farmed red deer (<i>Cervus elaphus</i>). <i>Applied Animal Behaviour Science</i> , 113: 215–223.	
III. Dušek, A., Bartoš, L. & Sedláček, F. Mixed sex allocation strategies in a polytocous mammal, the house mouse (<i>Mus musculus</i>). <i>Behavioral Ecology and Sociobiology</i> , under review.	
IV. Dušek, A., Bartoš, L. & Sedláček, F. 2010. Developmental instability of ano-genital distance index: implications for assessment of prenatal masculinization. <i>Developmental Psychobiology</i> , 52: 568–573.	
Discussion	8
Maternal Investment in Red Deer	8
Maternal Investment in House Mouse	9
Conclusion.....	12
References	13

Acknowledgements

First and foremost, my special thanks belong to my long-time supervisor, mentor, and friend, Luděk Bartoš for his unfailing encouragement, keen insight, endless patience, and giving me the freedom to independently work on my own research topics.

I am also very grateful to my supervisor specialist, and friend, Pavel Stopka for his generosity, great inspiration, and support to continue in my long-term research.

I would also like to thank to my former supervisor, and friend, František Sedláček for his kindness, caring, knowledge, and giving me the opportunity to engage in long-term research.

Many thanks belong to all my coauthors for the help in preparing experiments, data collection and analysis, creativity, inspiration, stimulating discussions, criticism, and writing the articles: Luděk Bartoš, František Sedláček, Jorga Drábková, Ludmila Švecová, Jitka Bartošová, Jan Pluháček, Radim Kotrba, and Tomáš Kott. Special thanks belong to my dear colleague, and very nice person, late Ludmila Švecová for her help in preparing the data for the analysis.

I would also like to express my thanks to my colleagues from various institutions, in particular from the Institute of Animal Science, the Charles University, and the University of South Bohemia, without whose help, support, inspiration and criticism the writing of this Ph.D. thesis would have been impossible: Sven Krackow, Douglas B. Meikle, Lee C. Drickamer, Mertice M. Clark, John G. Vandenberg, Frederick S. vom Saal, Oldřich Nedvěd, Petr Šimeček, Jan Zrzavý, George A. Bubenik, Trevor de Vries, Pavel Klír, Věra Pípalová, Ludmila Hyánková, Milan Marounek, Zdeněk Volek, Radko Rajmon, Dominika Formanová, Loren D. Hayes, Emil Tkadlec, Hynek Burda, Daniel Frynta, Tomás Landete-Castillejos, Romana Stopková, Petr Janovský, Vratislav Kšáda, Marek Špínka, Marie Šimečková, Petra Lantová, Michaela Zelenková, Dita Ungrová, Josef Fulka Jr., and Valerius Geist.

I am very thankful to all institutions and foundations that found my research worth of being supported financially: the Institute of Animal Science, the Czech Science Foundation, the Charles University, and the University of South Bohemia.

Last but not least, I would like to convey my heartfelt gratitude to my parents and my brother for offering me their encouragement and their loving support.

Abstract

The litter size is one of the most important determinants of mammalian life-histories. Depending on the size of the litter, the mammals can be divided into two main groups: (1) the monotocous mammals, producing only one offspring per litter; and (2) the polytocous mammals, producing more than one offspring per litter. This life-history dichotomy entails different strategies whereby the mammalian females may optimize their maternal investment. The aim of this Ph.D. thesis is to show variation in the maternal investment strategies of monotocous and polytocous mammals from a life-history perspective. In order to address this issue, I investigated the strategy of maternal investment in the red deer (*Cervus elaphus*), representing a typical monotocous mammal, and the house mouse (*Mus musculus*), representing a typical polytocous mammal. From a life-history perspective, the red deer, producing no more than one litter per year, can be viewed as a model of “K-selected species”, while the house mouse, producing up to ten litters per year, can be viewed as a model of “r-selected species”. The red deer and the house mouse are ideal model organisms for this type of research also because they both are representatives of the most common mammalian mating system – the simultaneous polygyny. A general assumption of the maternal investment theory is that in this mating system the maternal investment is optimized mainly to maximize reproductive success of male offspring. Both in the red deer and the house mouse, the females optimized their maternal investment according to their state. One way whereby the females optimized their investment was by controlling the offspring’s intrauterine growth and date of birth. In addition, the investment tactics partly varied according to the sex of the offspring. In both species, the females tended to provide more investment to male than female offspring, but their investment tactics fundamentally differed depending on the species-specific life-history. The red deer females seemed to optimize their investment mainly to maximize the offspring competitiveness. By contrast, the house mouse females seemed to optimize their investment mainly to maximize the offspring number. In addition, the house mouse females showed a great phenotypic plasticity which may be an adaptation to a colonizing life strategy. The present Ph.D. thesis thus (1) shows the importance of a life-history perspective for understanding the variation in the maternal investment strategies of monotocous and polytocous mammals, and (2) challenges a general assumption of the maternal investment theory that in polygynous mammals the maternal investment is optimized mainly to maximize reproductive success of male offspring.

Abstrakt

Velikost vrhu je jedním z nejdůležitějších faktorů určujících životní historii savců. Podle velikosti vrhu mohou být savci rozděleni na dvě základní skupiny: (1) monotokní savci, kteří produkují vrhy pouze s jedním mládětem, a (2) polytokní savci, kteří produkují vrhy s více mláďaty. Tato dichotomie vedla k rozrůznění strategií, kterými samice savců optimalizují svou mateřskou investici. Cílem této disertační práce je ukázat rozdílnost strategií mateřské investice monotokních a polytokních savců z pohledu teorie životní historie. Pro tento účel byla zkoumána strategie mateřské investice u jelena lesního (*Cervus elaphus*), typicky monotokního savce, a myši domácí (*Mus musculus*), typicky polytokního savce. Z pohledu teorie životní historie představuje jelen lesní, který produkuje ne více než jeden vrh ročně, modelového “K-stratéga”. Naopak myš domácí, která může produkovat až deset vrhů za rok, představuje modelového “r-stratéga”. Jelen lesní a myš domácí jsou ideálními modelovými organismy pro tento typ výzkumu i proto, že oba tyto druhy jsou zástupci vůbec nejvíce rozšířeného reprodukčního systému savců – simultánní polygynie. Obecným předpokladem teorie mateřské investice je, že v tomto reprodukčním systému matky optimalizují svou investici hlavně proto, aby maximalizovaly reprodukční úspěch svých samčích potomků. Jak u jelena lesního, tak u myši domácí samice optimalizovaly svou mateřskou investici podle své kondice. Jedním ze způsobů, kterými optimalizovaly svou investici, byla kontrola prenatalního růstu a data porodu potomka. Navíc investiční taktiky samic částečně závisely na pohlaví potomka. U obou zkoumaných druhů měly samice tendenci investovat více do samčích než samičích potomků. Zdá se však, že jejich investiční taktiky se zásadním způsobem lišily podle druhově specifické životní historie. Samice jelena lesního optimalizovaly svou investici hlavně k maximalizaci konkurenceschopnosti svých potomků. Naproti tomu samice myši domácí optimalizovaly svou investici především k maximalizaci počtu svých potomků. U samic myši domácí byla navíc pozorována velká fenotypová plasticita, která může být adaptací na kolonizační způsob života. Předkládaná disertační práce tak (1) ukazuje důležitost teorie životní historie pro pochopení rozdílnosti strategií mateřské investice monotokních a polytokních savců a (2) zpochybňuje obecně uznávaný předpoklad teorie mateřské investice, že samice polygynních savců optimalizují svou mateřskou investici hlavně proto, aby maximalizovaly reprodukční úspěch svých samčích potomků.

Introduction

The class *Mammalia* (the mammals) represents one of the most diverse and diversified taxons of animals at all. The modern placental mammals occupy almost every environment on the Earth, from the oceans to the air, from the South to the North Pole (Nowak 1999; Wilson & Reeder 2005). One of the main reasons for this evolutionary success is their great adaptability (Bronson 1985, 1989; Feldhamer et al. 1999). During the evolutionary process of natural selection, the mammals adopted various life-history tactics (reviewed in Stearns 1976; Clutton-Brock 1988) that enabled them to maximize lifetime reproductive success, i.e., the total number of offspring per lifetime. However, these tactics are not invariable, but depend on various contextual factors (including genetic, morphological, physiological, behavioral and environmental conditions). These conditions are usually referred to as the organism's state (McNamara & Houston 1996).

The body size is one of the most important factors that influenced the evolution of mammalian life-histories (Stearns 1983; Charnov 1991, 2001; Millar & Hickling 1991). In general, the small species tend to produce more than one offspring per litter, whereas the large species tend to produce only one offspring per litter (Eisenberg 1981; Stearns 1983; Read & Harvey 1989). Carranza (1996) was the first who suggested that this life-history dichotomy may be partly caused by sexual size dimorphism. Most mammals are typically polygynous, i.e., one male mates with two or more females (Clutton-Brock 1989). In this mating system, large body size may be more important for male than female reproductive success (Trivers 1972; Ralls 1977; Lande 1980; Clutton-Brock et al. 1981; Andersson 1994). Since the parental investment per individual offspring generally increases with the decreasing size of the litter (Smith & Fretwell 1974), it is possible that as the sexual size dimorphism increased, the sexual selection for large male body size might reduce the optimal litter size (Lloyd 1987). The optimization of parental investment thus might significantly contribute to the above-mentioned polarization in mammalian life-histories (Morris 1987; Isaac 2005).

This life-history polarization can be best illustrated by the “r- and K-selection theory” originally proposed by MacArthur and Wilson (1967), and further elaborated by Pianka (1970; but see also Boyce 1984). According to this theory, “r-selection” represents the selection in populations favoring rapid population growth, and “K-selection” represents the selection in saturated environments favoring ability to compete and to avoid predation. The theory assumes that “r-selection” is typical for the species living in an unstable environment that tend to produce many, “cheap” offspring, whereas “K-selection” is typical for the species

living in a relatively stable environment that tend to produce few, “expensive” offspring. Although some species can be referred to as “r- or K-selected species”, the majority of the species represent a mosaic of life-history traits from both these reproductive extremes. From a within-species perspective, mammalian males can be viewed as “r-selected reproducers” and females as “K-selected reproducers” (Hrady 2000). Mainly for this complexity, some authors (e.g., Stearns 1977, 1992) questioned the general validity of the “r- and K-selection theory”. Yet despite its limited validity, the “r- and K-selection theory” (MacArthur & Wilson 1967; Pianka 1970; Boyce 1984) still remains a very useful concept for the understanding of the between-species life-history variation (Lombardi 1998; Feldhamer et al. 1999; Begon et al. 2006).

As well as the optimization of parental investment influenced the evolution of mammalian life-histories, this process, on the contrary, influenced the evolution of parental investment (reviewed in Clutton-Brock 1991). Trivers (1972) defined the parental investment as “*any investment by the parent in an individual offspring that increases the offspring’s chance of surviving (and hence reproductive success) at the cost of the parent’s ability to invest in other offspring*”. In general, the total investment available increases with the quality of the parent (Gadgil & Bossert 1970; Hirshfield & Tinkle 1975; Morris 1987). Due to this relation, the quality of the offspring also tends to increase with the quality of the parent (Leimar 1996; Mousseau & Fox 1998). However, the parental investment per individual offspring does not only depend on the total investment available, but also on its effectiveness in individual’s fitness returns. There is a lower threshold below which no offspring can survive, and an upper threshold above which an additional investment has no effect on offspring fitness (Morris 1996).

From a life-history perspective, the optimization of parental investment varies depending on the size of the litter (Lack 1948; Smith & Fretwell 1974; Charnov & Ernest 2006). The monotocous species, producing single-offspring litters, are generally under stronger selection pressure for an effective parental investment than the polytocous species, producing multi-offspring litters (see e.g., Köhl et al. 2007). In most mammals, this selection pressure is, moreover, enhanced by a female uniparental care (i.e., parental care provided only by female: Clutton-Brock 1991; Lombardi 1998; Feldhamer et al. 1999). In the monotocous mammals, the parental investment is the most effective (Mock & Parker 1997). By contrast, in the polytocous mammals, the mothers must divide their investment among several offspring (Lazarus & Inglis 1986). If all their offspring have a similar demand and probability of survival, the mothers should partition their investment equally. However, if some offspring

have a greater demand or a higher probability of survival than others, the mothers should preferentially favor this offspring or, contrariwise, the marginal offspring (Morris 1987). Such preferential investment implies a parent-offspring conflict (Trivers 1974) and a sibling competition (Brockelman 1975; Lessells 2002; Stockley & Parker 2002). The same effects can also be observed in the monotocous mammals, but in such taxa the sibling competition is sequential (Mock & Parker 1997).

Although the fundamental difference between the monotocous and polytocous mammals entails different investment tactics, all these tactics are state-dependent (McNamara & Houston 1996; Lindström 1999). The investment of the parents can be adjusted according to their sex, condition, age, social rank, nutritional state, health status, and quality of the habitat in which they live (Bronson 1989; Clutton-Brock 1991; McNamara & Houston 1996; Morris 1998). The reason for this behavior is the selection for an optimal parental investment (Morris 1985, 1987) and minimal reproductive costs (Williams 1966; Bell 1980; Clutton-Brock 1991). In order to cope with both these tasks, the parents can adjust their investment with respect to the offspring size (Smith & Fretwell 1974; Morris 1985, 1987; Lloyd 1987), sex (Clutton-Brock et al. 1981; Charnov 1982; Clutton-Brock & Iason 1986; Cockburn et al. 2002; Navara & Nelson 2009; West 2009), and number (Lack 1948; Mountford 1968; Smith & Fretwell 1974; Morris 1985, 1987). In polygynous mating system (i.e., where a male mates with several females), which is typical for most mammals, parents are supposed to invest more heavily in sons than daughters (Trivers & Willard 1973; Clutton-Brock et al. 1981). The reason for this is that in this mating system extra parental investment may have a larger effect on the fitness returns from sons than daughters. On the other hand, when the offspring's quality is strongly determined by the quality of the mother, the high-quality daughters may have a higher reproductive value (i.e., age-specific expectation of all present and future offspring: Fisher 1930) than the high-quality sons, even though their reproductive success may be much lower (Leimar 1996).

Depending on the state, mammalian females can optimize their reproductive effort (i.e., the proportional allocation of available time and energy to reproduction: Gadgil & Bossert 1970) during the whole period of parental investment (i.e., from conception to weaning). The reproductive optimization is a continuous process. However, since the mother's reproductive optimum can vary during the period of parental investment (Morris 1998; Sikes 1998), from an individual's perspective, the reproductive optimization can be rather perceived as a discrete process during which each decision affects the investment tactic until the next decision step. There are two critical ontogenetic periods during which these decisions can occur: (1)

pregnancy (i.e., from conception to birth; e.g., Bruce 1959; Austad & Sunquist 1986; Gosling 1986; Lycett & Dunbar 1999; Bartoš et al. 2011), and (2) lactation (i.e., from birth to weaning; e.g., Day & Galef 1977; Gandelman & Simon 1978; McClure 1981; Green & Rothstein 1991; Andersen et al. 2011). The lactation period can be, moreover, subdivided into two further periods (Langer 2008). First, the period when the offspring ingests exclusively milk. And second, the period when both milk and solid food are taken. Under an optimal investment tactic, the sequence of maternal decisions maximizes the expected reproductive value of all offspring at the end of the parental investment period, i.e., at weaning (McNamara & Houston 1996).

In addition to this complexity, mammalian mothers may optimize their offspring's phenotype by influencing the interactions between the offspring and its peers. These interactions may be influenced both prenatally and postnatally, and include, for example, inter-embryonic steroid leakage (vom Saal 1989; vom Saal et al. 1999; Ryan & Vandenberg 2002; Uller 2006), sibling competition (Mock & Parker 1997; Stockley & Parker 2002; Drummond 2006; Hudson & Trillmich 2008), allonursing-induced milk competition (Riedman 1982; Packer et al. 1992; Hayes 2000; Roulin 2002), and social rank acquisition (Holekamp & Smale 1991; McNamara & Houston 1996). The importance of all these interactions is obvious because the conditions experienced during early development (i.e., from conception to developmental maturity) can influence the animal's life-history (Huntingford & Turner 1987; Henry & Ulijaszek 1996; Desai & Hales 1997; Lindström 1999; Stockley & Parker 2002). Since the effect of early developmental conditions may persist over generations (Clark et al. 1993; Champagne 2008), these interactions can significantly contribute to parental inclusive fitness.

The aim of this Ph.D. thesis is to show variation in the maternal investment strategies of monotocous and polytocous mammals from a life-history perspective. In order to address this issue, I investigated the strategy of maternal investment in the red deer (*Cervus elaphus*) and the house mouse (*Mus musculus*). Both the red deer and the house mouse are ideal model organisms for this type of research. The red deer, usually producing one offspring per litter (Clutton-Brock et al. 1982), represents a typical monotocous mammal. By contrast, the house mouse, producing, on average, four to eight offspring per litter (Berry 1970; Berry & Bronson 1992), represents a typical polytocous mammal. In addition, from a life-history perspective (MacArthur & Wilson 1967; Pianka 1976), the red deer, producing no more than one litter per year (Clutton-Brock et al. 1982), can be viewed as a model of "K-selected species", while the house mouse, producing up to ten litters per year (Berry 1970; Berry & Bronson 1992), can be

viewed as a model of “r-selected species”. On the other hand, the red deer and the house mouse share several common features. Both these species are modern placental mammals (Liu et al. 2001; Madsen et al. 2001; Murphy et al. 2001) living in groups with social hierarchy (Berry 1970; Clutton-Brock et al. 1982), their mating system is simultaneous polygyny (i.e., a male may associate with several females at once: Clutton-Brock 1989), and due to great adaptability they both can occupy almost every environment on the Earth (Bronson 1984; Geist 1998; Wilson & Reeder 2005). Furthermore, both these species represent typical members of their own taxonomic groups (the red deer: *Artiodactyla*; the house mouse: *Rodentia*), which are model taxa in themselves (Alderton 1996; Geist 1998; Baskin & Danell 2003; Wolff & Sherman 2007).

This Ph.D. thesis is based on four original studies, two on deer and two on mice. Three of these studies have been published and one is under review. The objective of the studies was: (I) to test the effect of a mother’s rank on her offspring’s pre-weaning rank in the red deer; (II) to discriminate between the sucking and allosucking (i.e., non-maternal sucking) behavior of the red deer according to the sucking duration; (III) to test the effect of a mother’s condition on the variation in offspring sex ratio (sons to daughters) in the house mouse; and (IV) to assess postnatal developmental stability of female ano-genital distance index (widely used as a marker of natural prenatal masculinization; i.e., natural process of sexual differentiation, induced by prenatal androgens, resulting in a male-like phenotype) in the house mouse. The data were collected in the experimental facilities belonging to the Institute of Animal Science (Praha, Czech Republic) and the University of South Bohemia (České Budějovice, Czech Republic).

**I. The Effect of a Mother's Rank on Her Offspring's Pre-weaning
Rank in Farmed Red Deer**

Adam Dušek, Luděk Bartoš, Ludmila Švecová

Applied Animal Behaviour Science, 103: 146–155

2007

**II. Sucking and Allosucking Duration in Farmed Red Deer
(*Cervus elaphus*)**

**Jorga Drábková, Jitka Bartošová, Luděk Bartoš, Radim Kotrba, Jan
Pluháček, Ludmila Švecová, Adam Dušek, Tomáš Kott**

Applied Animal Behaviour Science, 113: 215–223

2008

**III. Mixed Sex Allocation Strategies in a Polytocous Mammal, the
House Mouse (*Mus musculus*)**

Adam Dušek, Luděk Bartoš, František Sedláček

Behavioral Ecology and Sociobiology, under review

**IV. Developmental Instability of Ano-Genital Distance Index:
Implications for Assessment of Prenatal Masculinization**

Adam Dušek, Luděk Bartoš, František Sedláček

Developmental Psychobiology, 52: 568–573

2010

Discussion

Maternal Investment in Red Deer

The selection on offspring competitiveness resulted in various investment tactics whereby the red deer mothers support their offspring. The studies presented in this Ph.D. thesis showed that there are generally two types of support that the offspring can receive. The offspring can be supported either by its own mother or by another offspring mother. The first of these studies (Dušek et al. 2007) showed that the red deer mothers transmitted their social rank to their pre-weaning offspring. The mothers affected the formation of dominance relationships among their offspring both (1) directly by intervening on behalf of their offspring, and (2) indirectly through the offspring birth body weight, timing of delivery and the aggression directed towards the peers of their offspring. The second of these studies (Drábková et al. 2008) showed that the red deer hinds nursed (1) not only their own calves but also the non-filial calves, (2) some non-filial calves more frequently than others, and (3) the preferred non-filial male calves for a longer time than the preferred non-filial female calves. From the offspring's point of view, both the maternal and non-maternal support corresponds to an investment optimum that maximizes the offspring's reproductive value (Pianka 1976; Morris 1985, 1987; McNamara & Houston 1996).

The findings of Dušek et al. (2007) indicate that the main function of the “maternal rank inheritance” is the optimization of parental investment. Due to this process, the mothers can maintain their investment as effective as possible. The offspring of dominant mothers may gain maximum access to resources (Holekamp & Smale 1991), while the offspring of subordinate mothers may be saved from an ineffective fighting with their peers (Huntingford & Turner 1987). The composite effect of the offspring's birth weight and the offspring's birth date (Dušek et al. 2007) suggests that one way the red deer mothers optimize their parental investment is by controlling the offspring intrauterine growth and date of delivery (Clutton-Brock et al. 1982; Landete-Castillejos et al. 2000b, 2009; Coulson et al. 2003; Veiberg et al. 2004). This optimization may have significant effect on both male (Clutton-Brock et al. 1982; Coulson et al. 1997; Kruuk et al. 1999; Loison et al. 1999) and female (Clutton-Brock et al. 1986; Langvatn et al. 1996; Loison et al. 1999) reproductive value. In addition, since sex did not affect the offspring's rank (Dušek et al. 2007), it seems that the “inheritance” of maternal rank is important for both male and female red deer calves.

On the other hand, the findings of Drábková et al. (2008) indicate that the non-maternal nursing is more important for male than female red deer calves. Due to the non-maternal nursing, the offspring may compensate for inadequate milk supply from the mother (Landete-Castillejos et al. 2000a; Bartoš et al. 2001; Dušek & Bartoš 2006; Drábková et al. 2008) or gain competitive advantage over its peers (Dušek & Bartoš 2006; Dušek et al. 2007), which can have a greater impact on male than female reproductive value (see Trivers 1972). The non-maternal nursing could evolve through the kin selection and/or reciprocal altruism (Riedman 1982; Roulin 2002). Both these possibilities may explain why some non-filial male calves were allonursed for a longer time than others (Drábková et al. 2008), and also why the milk hinds, i.e., females with a surviving calf, attacked other calves more often than the yield hinds, i.e., females without a calf (Dušek et al. 2007). Thus, in “K-selected” mammals with alloparental care, like the red deer, the main function of the non-maternal nursing may be to provide a sufficient milk supply for maintaining optimal parental investment.

With respect to the importance of competitiveness for male reproductive success (Trivers 1972), one could assume that both the maternal and non-maternal support will be more important for the red deer males than females (Trivers & Willard 1973; Clutton-Brock et al. 1981). This assumption was supported by Clutton-Brock et al. (1984) showing that dominant mothers produced significantly more sons than subordinates, and that maternal rank had a greater effect on the breeding success of sons than daughters. On the other hand, because the red deer females stay within their natal group, whereas the males disperse from it (Clutton-Brock et al. 1982; Baskin & Danell 2003), one could argue that both the maternal (e.g., “rank inheritance”) and non-maternal support may be important for daughters as well. This assumption was also supported by Clutton-Brock et al. (1986) showing an association between the rank of the mother and that of her adult daughter. Nevertheless, since this association was relatively weak, it seems that, in the red deer, the mother’s rank is more important for male than female fitness (Hewison & Gaillard 1999). Either way, the above-mentioned contrasting findings (Clutton-Brock et al. 1984, 1986) illustrate the complexity of this issue, and indicate antagonistic selection for optimal investment in sons and daughters (Leimar 1996; Wade et al. 2003; Wilson et al. 2005; Foerster et al. 2007).

Maternal Investment in House Mouse

The selection on rapid population growth resulted in various investment tactics whereby the house mouse mothers optimize the phenotype of their offspring. The studies presented in

this Ph.D. thesis focused on two types of phenotypic optimization relevant for polytocous mammals. The first study (Dušek et al. under review) investigated the condition-dependent optimization of litter composition. For this aim, a mother's condition at mating was experimentally decreased by pre-mating food restriction. The food-restricted mothers produced larger litters with a higher proportion of daughters than the control mothers. By contrast, the control mothers optimized size- and sex-specific composition of the litter according to their weight at mating. In addition, this study showed that of the food-restricted mothers partly coped with the pre-mating food restriction. The evidence for this was provided (1) by an increase in the proportion of sons in the litter with the increasing maternal weight loss (during the period of food restriction), (2) by a positive effect of food restriction-delayed delivery date on the offspring birth weight, and (3) by a lower pre-weaning offspring mortality in the food-restricted than control group. The second study (Dušek et al. 2010) investigated to what extent the female phenotype is determined by natural prenatal masculinization. To assess this effect, a repeatability of the ano-genital distance index (proposed by Vandenberg & Huggett 1995) during the postnatal ontogeny was tested. The index showed poor repeatability, thus indicating a relatively small effect of natural prenatal androgens on the female phenotypic development.

The findings of Dušek et al. (under review) show a great reproductive plasticity of the house mouse. A number of previous studies have shown that the female mice optimize their parental investment by adjusting size (Berry 1970; Bronson 1979; König & Markl 1987; Ylönen et al. 2003) and sex ratio (proportion of male births: Wright et al. 1988; Meikle & Thornton 1995; Krackow & Burgoyne 1998; Rosenfeld et al. 2003; Cameron et al. 2008) of their litters. The study of Dušek et al. (under review) is, however, the first to show that an optimal composition of the litter may be a result of (1) greater production costs for sons than daughters, (2) maternal environmental conditions before mating, and (3) maternal ability to cope with adverse conditions. The results indicate that (1) under stable conditions, the female mice may vary the size and sex ratio of their litters to maximize the fitness returns from sons and daughters (as predicted by Williams 1979), (2) under changeable conditions, the female mice may favor cheaper daughters to maximize the number of successful (surviving) offspring (as predicted by Myers 1978), and (3) the female mice are able to cope with adverse environmental conditions (*sensu* Mendl & Deag 1995) and, even under changeable conditions, may favor more expensive sons. Since the maternal food restriction did not reduce the offspring birth weight but delayed the offspring birth date (Dušek et al. under review), it seems that one way the female mice optimize sex-differential investment is by controlling the

date of conception and sex-specific embryonic growth (Bronson & Marsteller 1985; Krackow 1995; Krackow et al. 2003; Mao et al. 2010).

In polytocous mammals, such as the house mouse, the postnatal phenotype of the female may be affected not only directly by parental investment, but also indirectly by sex-specific sibling interactions, including the inter-embryonic steroid leakage (Uller 2006). Due to this, the reproductive value of the female is partly a result of her prenatal androgen milieu, mainly influenced by her intrauterine position relative to the members of the same or opposite sex (Clark & Galef 1995b; vom Saal et al. 1999; Ryan & Vandenberg 2002). Since the intrauterine position of the female is determined by the size and sex ratio of the birth litter (vom Saal 1981; Clark & Galef 1990; Clark et al. 1991), which, in turn, can be affected by her mother's prior intrauterine position (Clark et al. 1993, 1997; Vandenberg & Huggett 1994; Clark & Galef 1995a; Ryan & Vandenberg 2002), the optimization of litter composition may have a significant effect on the reproductive profile of female offspring (vom Saal & Bronson 1978; vom Saal & Moyer 1985; Clark et al. 1986, 1993). From a life-history perspective, one of the most important questions is whether this effect is permanent or not. The findings of Dušek et al. (2010) indicate that, at least in female genital morphology, the effect of natural prenatal androgens is not permanent. Assuming that the natural prenatal androgens do not permanently affect either other phenotypic traits, one can speculate that they have only a limited effect on the female reproductive profile.

The variation in investment tactics observed by Dušek et al. (under review) suggests that the offspring's reproductive success (Clutton-Brock 1988) is optimized under stable conditions, while the offspring's reproductive value (Fisher 1930) is optimized under changeable conditions. Once again, these findings illustrate the complexity of this issue, and indicate antagonistic selection for optimal investment in sons and daughters (Leimar 1996; Wade et al. 2003; Wilson et al. 2005; Foerster et al. 2007). However, since the offspring sex ratio was optimized along with the size of the litter, it is possible that the main function of both these tactics is to maximize the offspring number. The selection for a high reproductive output could also be a reason why the female mice showed so great phenotypic plasticity (Dušek et al. 2010, under review). This plasticity can be an adaptation to a colonizing life strategy which has to cope with variable environment and high mortality (Berry 1970; Bronson 1979, 1984; König & Markl 1987; König et al. 1988).

Conclusion

Both in the red deer and the house mouse, the females optimized their maternal investment according to their state. One way whereby the females optimized their investment was by controlling the offspring's intrauterine growth and date of birth. In addition, the investment tactics partly varied according to the sex of the offspring. In both species, the females tended to provide more investment to male than female offspring, but their investment tactics fundamentally differed depending on the species-specific life-history. The red deer females seemed to optimize their investment mainly to maximize the offspring competitiveness. By contrast, the house mouse females seemed to optimize their investment mainly to maximize the offspring number. In addition, the house mouse females showed a great phenotypic plasticity which may be an adaptation to a colonizing life strategy. The present Ph.D. thesis thus (1) shows the importance of a life-history perspective for understanding the variation in the maternal investment strategies of monotocous and polytocous mammals, and (2) challenges a general assumption of the maternal investment theory (Trivers & Willard 1973; Clutton-Brock et al. 1981) that in polygynous mammals the maternal investment is optimized mainly to maximize reproductive success of male offspring.

References

- Alderton, D. 1996. Rodents of the World. Blandford, London.
- Andersen, I. L., Naevdal, E. & Boe, K. E. 2011. Maternal investment, sibling competition, and offspring survival with increasing litter size and parity in pigs (*Sus scrofa*). Behavioral Ecology and Sociobiology, doi 10.1007/s00265-010-1128-4.
- Andersson, M. 1994. Sexual Selection. Princeton University Press, Princeton.
- Austad, S. N. & Sunquist, M. E. 1986. Sex-ratio manipulation in the common opossum. Nature, 324: 58–60.
- Bartoš, L., Bartošová, J., Pluháček, J. & Šindelářová, J. 2011. Promiscuous behaviour disrupts pregnancy block in domestic horse mares. Behavioral Ecology and Sociobiology, doi 10.1007/s00265-011-1166-6.
- Bartoš, L., Vaňková, D., Hyánek, J. & Šiler, J. 2001. Impact of allosucking on growth of farmed red deer calves (*Cervus elaphus*). Animal Science, 72: 493–500.
- Baskin, L. & Danell, K. 2003. Ecology of Ungulates: A Handbook of Species in Eastern Europe and Northern and Central Asia. Springer, Berlin.
- Begon, M., Harper, J. L. & Townsend, C. R. 2006. Ecology: From Individuals to Ecosystems, 4th edn. Blackwell Publishing, Malden.
- Bell, G. 1980. The costs of reproduction and their consequences. American Naturalist, 116: 45–76.
- Berry, R. J. 1970. The natural history of the house mouse. Field Studies, 3: 219–262.
- Berry, R. J. & Bronson, F. H. 1992. Life history and bioeconomy of the house mouse. Biological Reviews of the Cambridge Philosophical Society, 67: 519–550.
- Boyce, M. S. 1984. Restitution of r- and K-selection as a model of density-dependent natural selection. Annual Review of Ecology and Systematics, 15: 427–447.
- Brockelman, W. Y. 1975. Competition, fitness of offspring, and optimal clutch size. American Naturalist, 109: 677–699.
- Bronson, F. H. 1979. The reproductive ecology of the house mouse. Quarterly Review of Biology, 54: 265–299.
- Bronson, F. H. 1984. The adaptability of the house mouse. Scientific American, 250: 116–125.
- Bronson, F. H. 1985. Mammalian reproduction: an ecological perspective. Biology of Reproduction, 32: 1–26.
- Bronson, F. H. 1989. Mammalian Reproductive Biology. University of Chicago Press,

Chicago.

- Bronson, F. H. & Marsteller, F. A. 1985. Effect of short-term food deprivation on reproduction in female mice. *Biology of Reproduction*, 33: 660–667.
- Bruce, H. M. 1959. An exteroceptive block to pregnancy in the mouse. *Nature*, 184: 105.
- Cameron, E. Z., Lemons, P. R., Bateman, P. W. & Bennett, N. C. 2008. Experimental alteration of litter sex ratios in a mammal. *Proceedings of the Royal Society B Biological Sciences*, 275: 323–327.
- Carranza, J. 1996. Sexual selection for male body mass and the evolution of litter size in mammals. *American Naturalist*, 148: 81–100.
- Champagne, F. A. 2008. Epigenetic mechanisms and the transgenerational effects of maternal care. *Frontiers in Neuroendocrinology*, 29: 386–397.
- Charnov, E. L. 1982. *The Theory of Sex Allocation*. Princeton University Press, Princeton.
- Charnov, E. L. 1991. Evolution of life history variation among female mammals. *Proceedings of the National Academy of Sciences of the United States of America*, 88: 1134–1137.
- Charnov, E. L. 2001. Evolution of mammal life histories. *Evolutionary Ecology Research*, 3: 521–535.
- Charnov, E. L. & Ernest, S. K. M. 2006. The offspring-size/clutch-size trade-off in mammals. *American Naturalist*, 167: 578–582.
- Clark, M. M. & Galef, B. G. 1990. Sexual segregation in the left and right horns of the gerbil uterus: “The male embryo is usually on the right, the female on the left” (Hippocrates). *Developmental Psychobiology*, 23: 29–37.
- Clark, M. M. & Galef, B. G. 1995a. A gerbil dam’s fetal intrauterine position affects the sex ratios of litters she gestates. *Physiology & Behavior*, 57: 297–299.
- Clark, M. M. & Galef, B. G. 1995b. Prenatal influences on reproductive life history strategies. *Trends in Ecology & Evolution*, 10: 151–153.
- Clark, M. M., Galef, B. G. & vom Saal, F. S. 1991. Nonrandom sex composition of gerbil, mouse, and hamster litters before and after birth. *Developmental Psychobiology*, 24: 81–90.
- Clark, M. M., Karpiuk, P. & Galef, B. G. 1993. Hormonally mediated inheritance of acquired characteristics in Mongolian gerbils. *Nature*, 364: 712.
- Clark, M. M., Spencer, C. A. & Galef, B. G. 1986. Reproductive life history correlates of early and late sexual maturation in female Mongolian gerbils (*Meriones unguiculatus*). *Animal Behaviour*, 34: 551–560.

- Clark, M. M., Vonk, J. M. & Galef, B. G. 1997. Reproductive profiles of adult Mongolian gerbils gestated as the sole fetus in a uterine horn. *Physiology & Behavior*, 61: 77–81.
- Clutton-Brock, T. H. 1988. *Reproductive Success: Studies of Individual Variation in Contrasting Breeding Systems*. University of Chicago Press, Chicago.
- Clutton-Brock, T. H. 1989. Mammalian mating systems. *Proceedings of the Royal Society of London B Biological Sciences*, 236: 339–372.
- Clutton-Brock, T. H. 1991. *The Evolution of Parental Care*. Princeton University Press, Princeton.
- Clutton-Brock, T. H., Albon, S. D. & Guinness, F. E. 1981. Parental investment in male and female offspring in polygynous mammals. *Nature*, 289: 487–489.
- Clutton-Brock, T. H., Albon, S. D. & Guinness, F. E. 1984. Maternal dominance, breeding success and birth sex ratios in red deer. *Nature*, 308: 358–360.
- Clutton-Brock, T. H., Albon, S. D. & Guinness, F. E. 1986. Great expectations: dominance, breeding success and offspring sex ratios in red deer. *Animal Behaviour*, 34: 460–471.
- Clutton-Brock, T. H., Guinness, F. E. & Albon, S. D. 1982. *Red Deer, Behavior and Ecology of Two Sexes*. Edinburgh University Press, Edinburgh.
- Clutton-Brock, T. H. & Iason, G. R. 1986. Sex ratio variation in mammals. *Quarterly Review of Biology*, 61: 339–374.
- Cockburn, A., Legge, S. & Double, M. C. 2002. Sex ratios in birds and mammals: can the hypotheses be disentangled? *In*: I. C. W. Hardy (Ed.). *Sex Ratios: Concepts and Research Methods*, 1th edn. Pp. 266–286. Cambridge University Press, Cambridge.
- Coulson, T., Albon, S., Guinness, F. E., Pemberton, J. & Clutton-Brock, T. H. 1997. Population substructure, local density, and calf winter survival in red deer (*Cervus elaphus*). *Ecology*, 78: 852–863.
- Coulson, T., Kruuk, L. E. B., Tavecchia, G., Pemberton, J. M. & Clutton-Brock, T. H. 2003. Estimating selection on neonatal traits in red deer using elasticity path analysis. *Evolution*, 57: 2879–2892.
- Day, C. S. D. & Galef, B. G. 1977. Pup cannibalism: one aspect of maternal behavior in golden hamsters. *Journal of Comparative and Physiological Psychology*, 91: 1179–1189.
- Desai, M. & Hales, C. N. 1997. Role of fetal and infant growth in programming metabolism in later life. *Biological Reviews of the Cambridge Philosophical Society*, 72: 329–348.
- Drábková, J., Bartošová, J., Bartoš, L., Kotrba, R., Pluháček, J., Švecová, L., Dušek, A. & Kott, T. 2008. Sucking and allosucking duration in farmed red deer (*Cervus elaphus*).

- Applied Animal Behaviour Science, 113: 215–223.
- Drummond, H. 2006. Dominance in vertebrate broods and litters. *Quarterly Review of Biology*, 81: 3–32.
- Dušek, A. & Bartoš, L. 2006. The effect of the birth weight on the calf's allosucking success in the red deer (*Cervus elaphus*) supports the compensation hypothesis. *In*: L. Bartoš, A. Dušek, R. Kotrba & J. Bartošová-Víchová (Eds.). *Advances in Deer Biology: Deer in a Changing World*. Pp. 132–133. Research Institute of Animal Science, Prague.
- Dušek, A., Bartoš, L. & Sedláček, F. 2010. Developmental instability of ano-genital distance index: implications for assessment of prenatal masculinization. *Developmental Psychobiology*, 52: 568–573.
- Dušek, A., Bartoš, L. & Sedláček, F. Mixed sex allocation strategies in a polytocous mammal, the house mouse (*Mus musculus*). *Behavioral Ecology and Sociobiology*, under review.
- Dušek, A., Bartoš, L. & Švecová, L. 2007. The effect of a mother's rank on her offspring's pre-weaning rank in farmed red deer. *Applied Animal Behaviour Science*, 103: 146–155.
- Eisenberg, J. F. 1981. *The Mammalian Radiations: A Study in Evolution and Adaptation*. Athlone, London.
- Feldhamer, G. A., Drickamer, L. C., Vessey, S. H. & Merritt, J. F. 1999. *Mammalogy: Adaptation, Diversity, and Ecology*. WCB McGraw-Hill, Boston.
- Fisher, R. A. 1930. *The Genetical Theory of Natural Selection*. Clarendon Press, Oxford.
- Foerster, K., Coulson, T., Sheldon, B. C., Pemberton, J. M., Clutton-Brock, T. H. & Kruuk, L. E. B. 2007. Sexually antagonistic genetic variation for fitness in red deer. *Nature*, 447: 1107–U9.
- Gadgil, M. & Bossert, W. H. 1970. Life historical consequences of natural selection. *American Naturalist*, 104: 1–24.
- Gandelman, R. & Simon, N. G. 1978. Spontaneous pup-killing by mice in response to large litters. *Developmental Psychobiology*, 11: 235–241.
- Geist, V. 1998. *Deer of the World: Their Evolution, Behaviour, and Ecology*. Stackpole Books, Mechanicsburg.
- Gosling, L. M. 1986. Selective abortion of entire litters in the coypu: adaptive control of offspring production in relation to quality and sex. *American Naturalist*, 127: 772–795.
- Green, W. C. H. & Rothstein, A. 1991. Sex bias or equal opportunity? Patterns of maternal investment in bison. *Behavioral Ecology and Sociobiology*, 29: 373–384.

- Hayes, L. D. 2000. To nest communally or not to nest communally: a review of rodent communal nesting and nursing. *Animal Behaviour*, 59: 677–688.
- Henry, C. J. K. & Ulijaszek, S. J. 1996. *Long-term Consequences of Early Environment: Growth, Development and the Lifespan Developmental Perspective*. Cambridge University Press, Cambridge.
- Hewison, A. J. M. & Gaillard, J. M. 1999. Successful sons or advantaged daughters? The Trivers–Willard model and sex-biased maternal investment in ungulates. *Trends in Ecology & Evolution*, 14: 229–234.
- Hirshfield, M. F. & Tinkle, D. W. 1975. Natural selection and the evolution of reproductive effort. *Proceedings of the National Academy of Sciences of the United States of America*, 72: 2227–2231.
- Holekamp, K. E. & Smale, L. 1991. Dominance acquisition during mammalian social development: the “inheritance” of maternal rank. *American Zoologist*, 31: 306–317.
- Hrdy, S. B. 2000. *Mother Nature: Maternal Instincts and How They Shape the Human Species*. Ballantine Books, New York.
- Hudson, R. & Trillmich, F. 2008. Sibling competition and cooperation in mammals: challenges, developments and prospects. *Behavioral Ecology and Sociobiology*, 62: 299–307.
- Huntingford, F. & Turner, A. 1987. *Animal Conflict*. Chapman and Hall, New York.
- Isaac, J. L. 2005. Potential causes and life-history consequences of sexual size dimorphism in mammals. *Mammal Review*, 35: 101–115.
- König, B. & Markl, H. 1987. Maternal care in house mice. I. The weaning strategy as a means for parental manipulation of offspring quality. *Behavioral Ecology and Sociobiology*, 20: 1–9.
- König, B., Riester, J. & Markl, H. 1988. Maternal care in house mice (*Mus musculus*). II. The energy cost of lactation as a function of litter size. *Journal of Zoology*, 216: 195–210.
- Krackow, S. 1995. The developmental asynchrony hypothesis for sex ratio manipulation. *Journal of Theoretical Biology*, 176: 273–280.
- Krackow, S. & Burgoyne, P. S. 1998. Timing of mating, developmental asynchrony and the sex ratio in mice. *Physiology & Behavior*, 63: 81–84.
- Krackow, S., Schmidt, T. A. & Elepfandt, A. 2003. Sexual growth dimorphism affects birth sex ratio in house mice. *Proceedings of the Royal Society of London B Biological Sciences*, 270: 943–947.

- Kruuk, L. E. B., Clutton-Brock, T. H., Rose, K. E. & Guinness, F. E. 1999. Early determinants of lifetime reproductive success differ between the sexes in red deer. *Proceedings of the Royal Society of London B Biological Sciences*, 266: 1655–1661.
- Kühl, A., Mysterud, A., Erdnenov, G. I., Lushchekina, A. A., Grachev, I. A., Bekenov, A. B. & Milner-Gulland, E. J. 2007. The “big spenders” of the steppe: sex-specific maternal allocation and twinning in the saiga antelope. *Proceedings of the Royal Society B Biological Sciences*, 274: 1293–1299.
- Lack, D. 1948. The significance of litter-size. *Journal of Animal Ecology*, 17: 45–50.
- Lande, R. 1980. Sexual dimorphism, sexual selection, and adaptation in polygenic characters. *Evolution*, 34: 292–305.
- Landete-Castillejos, T., García, A., Carrión, D., Estevez, J. A., Ceacero, F., Gaspar-López, E. & Gallego, L. 2009. Age-related body weight constraints on prenatal and milk provisioning in Iberian red deer (*Cervus elaphus hispanicus*) affect allocation of maternal resources. *Theriogenology*, 71: 400–407.
- Landete-Castillejos, T., García, A., Garde, J. & Gallego, L. 2000a. Milk intake and production curves and allosuckling in captive Iberian red deer, *Cervus elaphus hispanicus*. *Animal Behaviour*, 60: 679–687.
- Landete-Castillejos, T., García, A., Molina, P., Vergara, H., Garde, J. & Gallego, L. 2000b. Milk production and composition in captive Iberian red deer (*Cervus elaphus hispanicus*): effect of birth date. *Journal of Animal Science*, 78: 2771–2777.
- Langer, P. 2008. The phases of maternal investment in eutherian mammals. *Zoology*, 111: 148–162.
- Langvatn, R., Albon, S. D., Burkey, T. & Clutton-Brock, T. H. 1996. Climate, plant phenology and variation in age of first reproduction in a temperate herbivore. *Journal of Animal Ecology*, 65: 653–670.
- Lazarus, J. & Inglis, I. R. 1986. Shared and unshared parental investment, parent-offspring conflict and brood size. *Animal Behaviour*, 34: 1791–1804.
- Leimar, O. 1996. Life-history analysis of the Trivers and Willard sex-ratio problem. *Behavioral Ecology*, 7: 316–325.
- Lessells, C. M. 2002. Parentally biased favouritism: why should parents specialize in caring for different offspring? *Philosophical Transactions of the Royal Society of London B Biological Sciences*, 357: 381–403.
- Lindström, J. 1999. Early development and fitness in birds and mammals. *Trends in Ecology*

- & Evolution, 14: 343–348.
- Liu, F. G. R., Miyamoto, M. M., Freire, N. P., Ong, P. Q., Tennant, M. R., Young, T. S. & Gugel, K. F. 2001. Molecular and morphological supertrees for eutherian (placental) mammals. *Science*, 291: 1786–1789.
- Lloyd, D. G. 1987. Selection of offspring size at independence and other size-versus-number strategies. *American Naturalist*, 129: 800–817.
- Loison, A., Langvatn, R. & Solberg, E. J. 1999. Body mass and winter mortality in red deer calves: disentangling sex and climate effects. *Ecography*, 22: 20–30.
- Lombardi, J. 1998. *Comparative Vertebrate Reproduction*. Kluwer Academic Publishers, Boston.
- Lycett, J. E. & Dunbar, R. I. M. 1999. Abortion rates reflect the optimization of parental investment strategies. *Proceedings of the Royal Society of London B Biological Sciences*, 266: 2355–2358.
- MacArthur, R. H. & Wilson, E. O. 1967. *Theory of Island Biogeography*. Princeton University Press, Princeton.
- Madsen, O., Scally, M., Douady, C. J., Kao, D. J., Debry, R. W., Adkins, R., Amrine, H. M., Stanhope, M. J., De Jong, W. W. & Springer, M. S. 2001. Parallel adaptive radiations in two major clades of placental mammals. *Nature*, 409: 610–614.
- Mao, J., Zhang, X., Sieli, P. T., Falduto, M. T., Torres, K. E. & Rosenfeld, C. S. 2010. Contrasting effects of different maternal diets on sexually dimorphic gene expression in the murine placenta. *Proceedings of the National Academy of Sciences of the United States of America*, 107: 5557–5562.
- McClure, P. A. 1981. Sex-biased litter reduction in food-restricted wood rats (*Neotoma floridana*). *Science*, 211: 1058–1060.
- McNamara, J. M. & Houston, A. I. 1996. State-dependent life histories. *Nature*, 380: 215–221.
- Meikle, D. B. & Thornton, M. W. 1995. Premating and gestational effects of maternal nutrition on secondary sex ratio in house mice. *Journal of Reproduction and Fertility*, 105: 193–196.
- Mendl, M. & Deag, J. M. 1995. How useful are the concepts of alternative strategy and coping strategy in applied studies of social behaviour? *Applied Animal Behaviour Science*, 44: 119–137.
- Millar, J. S. & Hickling, G. J. 1991. Body size and the evolution of mammalian life histories.

- Functional Ecology, 5: 588–593.
- Mock, D. W. & Parker, G. A. 1997. *The Evolution of Sibling Rivalry*. Oxford University Press, Oxford.
- Morris, D. W. 1985. Natural selection for reproductive optima. *Oikos*, 45: 290–293.
- Morris, D. W. 1987. Optimal allocation of parental investment. *Oikos*, 49: 332–339.
- Morris, D. W. 1996. State-dependent life histories, Mountford's hypothesis, and the evolution of brood size. *Journal of Animal Ecology*, 65: 43–51.
- Morris, D. W. 1998. State-dependent optimization of litter size. *Oikos*, 83: 518–528.
- Mountford, M. D. 1968. The significance of litter-size. *Journal of Animal Ecology*, 37: 363–367.
- Mousseau, T. A. & Fox, C. W. 1998. The adaptive significance of maternal effects. *Trends in Ecology & Evolution*, 13: 403–407.
- Murphy, W. J., Eizirik, E., Johnson, W. E., Zhang, Y. P., Ryderk, O. A. & O'Brien, S. J. 2001. Molecular phylogenetics and the origins of placental mammals. *Nature*, 409: 614–618.
- Myers, J. H. 1978. Sex ratio adjustment under food stress: maximization of quality or numbers of offspring? *American Naturalist*, 112: 381–388.
- Navara, K. J. & Nelson, R. J. 2009. Prenatal environmental influences on the production of sex-specific traits in mammals. *Seminars in Cell & Developmental Biology*, 20: 313–319.
- Nowak, R. M. 1999. *Walker's Mammals of the World*, 6th edn. Johns Hopkins University Press, Baltimore.
- Packer, C., Lewis, S. & Pusey, A. 1992. A comparative analysis of non-offspring nursing. *Animal Behaviour*, 43: 265–281.
- Pianka, E. R. 1970. On r- and K-selection. *American Naturalist*, 104: 592–597.
- Pianka, E. R. 1976. Natural selection of optimal reproductive tactics. *American Zoologist*, 16: 775–784.
- Ralls, K. 1977. Sexual dimorphism in mammals: avian models and unanswered questions. *American Naturalist*, 111: 917–938.
- Read, A. F. & Harvey, P. H. 1989. Life history differences among the eutherian radiations. *Journal of Zoology*, 219: 329–353.
- Riedman, M. L. 1982. The evolution of alloparental care and adoption in mammals and birds. *Quarterly Review of Biology*, 57: 405–435.

- Rosenfeld, C. S., Grimm, K. M., Livingston, K. A., Brokman, A. M., Lamberson, W. E. & Roberts, R. M. 2003. Striking variation in the sex ratio of pups born to mice according to whether maternal diet is high in fat or carbohydrate. *Proceedings of the National Academy of Sciences of the United States of America*, 100: 4628–4632.
- Roulin, A. 2002. Why do lactating females nurse alien offspring? A review of hypotheses and empirical evidence. *Animal Behaviour*, 63: 201–208.
- Ryan, B. C. & Vandenberg, J. G. 2002. Intrauterine position effects. *Neuroscience and Biobehavioral Reviews*, 26: 665–678.
- Sikes, R. S. 1998. Unit pricing: economics and the evolution of litter size. *Evolutionary Ecology*, 12: 179–190.
- Smith, C. C. & Fretwell, S. D. 1974. The optimal balance between size and number of offspring. *American Naturalist*, 108: 499–506.
- Stearns, S. C. 1976. Life-history tactics: a review of the ideas. *Quarterly Review of Biology*, 51: 3–47.
- Stearns, S. C. 1977. The evolution of life history traits: a critique of the theory and a review of the data. *Annual Review of Ecology and Systematics*, 8: 145–171.
- Stearns, S. C. 1983. The influence of size and phylogeny on patterns of covariation among life-history traits in the mammals. *Oikos*, 41: 173–187.
- Stearns, S. C. 1992. *The Evolution of Life Histories*. Oxford University Press, Oxford.
- Stockley, P. & Parker, G. A. 2002. Life history consequences of mammal sibling rivalry. *Proceedings of the National Academy of Sciences of the United States of America*, 99: 12932–12937.
- Trivers, R. L. 1972. Parental investment and sexual selection. *In*: B. Campbell (Ed.). *Sexual Selection and the Descent of Man, 1871–1971*. Pp. 136–179. Aldine, Chicago.
- Trivers, R. L. 1974. Parent-offspring conflict. *American Zoologist*, 14: 249–264.
- Trivers, R. L. & Willard, D. E. 1973. Natural selection and parental ability to vary the sex ratio of offspring. *Science*, 179: 90–92.
- Uller, T. 2006. Sex-specific sibling interactions and offspring fitness in vertebrates: patterns and implications for maternal sex ratios. *Biological Reviews*, 81: 207–217.
- Vandenberg, J. G. & Huggett, C. L. 1994. Mother's prior intrauterine position affects the sex ratio of her offspring in house mice. *Proceedings of the National Academy of Sciences of the United States of America*, 91: 11055–11059.
- Vandenberg, J. G. & Huggett, C. L. 1995. The anogenital distance index, a predictor of the

- intrauterine position effects on reproduction in female house mice. *Laboratory Animal Science*, 45: 567–573.
- Veiberg, V., Loe, L. E., Mysterud, A., Langvatn, R. & Stenseth, N. C. 2004. Social rank, feeding and winter weight loss in red deer: any evidence of interference competition? *Oecologia*, 138: 135–142.
- vom Saal, F. S. 1981. Variation in phenotype due to random intrauterine positioning of male and female fetuses in rodents. *Journal of Reproduction and Fertility*, 62: 633–650.
- vom Saal, F. S. 1989. Sexual differentiation in litter-bearing mammals: influence of sex of adjacent fetuses in utero. *Journal of Animal Science*, 67: 1824–1840.
- vom Saal, F. S. & Bronson, F. H. 1978. In utero proximity of female mouse fetuses to males: effect on reproductive performance during later life. *Biology of Reproduction*, 19: 842–853.
- vom Saal, F. S., Clark, M. M., Galef, B. G., Drickamer, L. C. & Vandenberg, J. G. 1999. Intrauterine position phenomenon. *In*: E. Knobil & J. D. Neill (Eds.). *Encyclopedia of Reproduction*. Pp. 893–900. Academic Press, New York.
- vom Saal, F. S. & Moyer, C. L. 1985. Prenatal effects on reproductive capacity during aging in female mice. *Biology of Reproduction*, 32: 1116–1126.
- Wade, M. J., Shuster, S. M. & Demuth, J. P. 2003. Sexual selection favors female-biased sex ratios: the balance between the opposing forces of sex-ratio selection and sexual selection. *American Naturalist*, 162: 403–414.
- West, S. A. 2009. *Sex Allocation*. Princeton University Press, Princeton.
- Williams, G. C. 1966. Natural selection, the costs of reproduction, and a refinement of Lack's principle. *American Naturalist*, 100: 687–690.
- Williams, G. C. 1979. The question of adaptive sex ratio in outcrossed vertebrates. *Proceedings of the Royal Society of London B Biological Sciences*, 205: 567–580.
- Wilson, A. J., Pilkington, J. G., Pemberton, J. M., Coltman, D. W., Overall, A. D. J., Byrne, K. A. & Kruuk, L. E. B. 2005. Selection on mothers and offspring: whose phenotype is it and does it matter? *Evolution*, 59: 451–463.
- Wilson, D. E. & Reeder, D. M. 2005. *Mammal Species of the World: A Taxonomic and Geographic Reference*, 3rd edn. Johns Hopkins University Press, Baltimore.
- Wolff, J. O. & Sherman, P. W. 2007. *Rodent Societies: An Ecological and Evolutionary Perspective*. University of Chicago Press, Chicago.
- Wright, S. L., Crawford, C. B. & Anderson, J. L. 1988. Allocation of reproductive effort in

Mus domesticus: responses of offspring sex ratio and quality to social density and food availability. *Behavioral Ecology and Sociobiology*, 23: 357–365.

Ylönen, H., Jacob, J., Runcie, M. J. & Singleton, G. R. 2003. Is reproduction of the Australian house mouse (*Mus domesticus*) constrained by food? A large-scale field experiment. *Oecologia*, 135: 372–377.