

MONOGAMY

Mating Strategies and Partnerships in Birds, Humans and Other Mammals

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CHAPTER 1

Monogamy: past and present

Ulrich H. Reichard

MONOGAMY APPROACHED

Scientists have been interested in social monogamy in animals for a long time (cf. Wickler & Seibt, 1983; Dewsbury, 1988). By the end of the Victorian era, animal monogamy was already intuitively fascinating perhaps because it seemed to mirror most closely the living ideal of western, industrialised societies: human monogamy as reflected in an early description of social monogamy as 'animal marriage' (Wundt, 1894). Part of social monogamy's attractiveness probably stemmed from both the assumed and postulated mutual faithfulness of the individuals in these partnerships. Unfortunately, *social* monogamy, which primarily describes a demographic, close spatial and behavioural relationship between one male and one female, has often been mixed both with exclusive mating as well as joint reproduction and biparental care of offspring. This historical conflation has resulted in misunderstandings and disagreement about the biological meaning of the 'monogamy phenomenon' as well as conflicting expectations and interpretations among scientists about selective forces and behavioural traits associated with it (cf. Wickler & Seibt, 1983; Murray, 1984; Mock, 1985; Dewsbury, 1988; Mock & Fujioka, 1990; Gubernick, 1994).

Variation in duration and levels of monogamous partnerships

The definition of *social* monogamy is that a female and a male each have only a single partner of the opposite sex at a time (cf. Black, 1996; Gowaty, 1996a). The temporal component is important for understanding socially monogamous partnerships because only few sexually reproducing organisms truly establish a unique, holistic, monogamous lifetime-partnership in which partnership duration equals the partners' remaining lifespan (i.e., Southgate et al., 1998). The overwhelming majority of socially monogamous animals and humans however practice serial or sequential social monogamy,

i.e., if a first partner dies, or is otherwise lost, another partner will be accepted (Wickler & Seibt, 1983).

Socially monogamous partnerships are highly variable in duration along a continuous time axis. They may be long-term and last until one partner dies (pair-living mammals: Hendrichs, 1975; Getz et al., 1987; Sommer, chapter 7; Sun, chapter 9; birds: some geese, ducks, and swans: Black et al., 1996; Williams & McKinney, 1996). Or they may be rather short-term, the result of active partnership termination and pairing with a new partner while the old partner is still alive. Active partnership termination and pairing with a new partner occurs in mammal species, including humans, with short- and long-term socially monogamous partnerships (e.g., Blurton Jones et al., 2000; Marlowe, 2000; Sommer & Reichard, 2000), and also in birds (Desrochers & Magrath, 1996; Catry et al., 1997; Hatchwell et al., 2000). Relatively short, socially monogamous partnerships characterise some bird species in which all pair relationships break up at the end of each breeding season and pairing with a new partner the following year is not uncommon (McKinney, 1986; Ens et al., 1996; Ligon, 1999). At the short-term end of the duration continuum, partnerships are found that only fulfil the minimal temporal requirement for social monogamy. Conventionally, this scenario has been that of a male and female staying together for at least a single breeding season (cf. Wittenberger & Tilson, 1980; Birkhead & Møller, 1996), including a considerable post-fertilisation period during which a recognisable pair relationship is maintained.

Besides temporal variation of pair relationships usually subsumed under the umbrella category 'monogamous', surprising behavioural and genetic mating system variations across levels of monogamous relationships have been revealed over the past two decades (Mock, 1985; Black, 1996; Hughes, 1998). Contrary to the early assumption of sexual exclusivity between socially paired individuals, it is now evident that sperm competition can also play a prominent role in

partnerships of socially monogamous individuals, who may interact sexually and reproduce with multiple partners (Birkhead & Møller, 1998; Petrie et al., 1998).

The advent of new molecular techniques in the mid-1980s (Jeffreys et al., 1985) gave rise to a deepened understanding of the structure of monogamous mating systems (cf. Hughes, 1998). For the first time, it became possible to distinguish between social and genetic mating systems based on the assignment of genetic parentage. Genetic parentage analyses fundamentally changed our perception about the biological meaning(s) of social monogamy (cf. Birkhead & Møller, 1996; Møller, chapter 2). Triver's (1972) had foreseen what is now recognised as a common male reproductive strategy when he predicted that pair-living males would cooperate with a female partner to raise offspring and maintain social monogamy, but copulate and reproduce with additional females. Soon after Triver's (1972) claim, the first observational evidence confirmed the flexible mating patterns of pair-living individuals. Copulations outside social pair relationships of otherwise pair-living individuals were recorded and became quickly known as extra-pair copulations or EPCs (e.g., Bray et al., 1975; Beecher & Beecher, 1979; Gladstone, 1979; McKinney et al., 1984; Birkhead et al., 1987; Møller, 1988b). But not only pair-living males search for EPC opportunities to increase their reproductive success. Far from being passive recipients of male extra-pair advances, there is growing evidence that socially monogamous females often play an active role in structuring sexual and reproductive relationships (cf. Hrdy, 1986; Gowaty, 1996b). Pair-living females seek sexual contact with social and extra-pair partners (Kempnaers et al., 1992; Sheldon, 1994; Smiseth & Amundsen, 1995; Kempnaers, 1997; Otter et al., 1998; Berteaux et al., 1999; Hasselquist & Sherman, 2001), often control the sexual activities (Møller, 1988b; Wagner, 1992; Ahnesjö et al., 1993; Wagner, chapter 6) and probably the paternity of their offspring (Birkhead & Møller, 1993; Gowaty, 1996a; Pizzari & Birkhead, 2000; Shellman-Reeve & Reeve, 2000).

It was, however, not until the new molecular techniques were developed and applied that the occurrence of extra-pair fertilisations (EPFs) and the evolutionary significance of flexible mating behaviours of pair-living males and females were fully acknowledged. Alternative mating strategies of socially monogamous birds are now considered to be a widespread, regular phenomenon, forming an integral part of socially monogamous

male and female reproductive strategies (reviews in Birkhead & Møller, 1992, 1995, 1996; Møller, 1998, 2000; Hasselquist & Sherman, 2001). Besides birds, monogamous social pairing combined with flexible reproduction has been observed in diverse animals, including socially monogamous lizards (Bull et al., 1998) and cooperative and/or pair-living mammals (Keane et al., 1994; Sillero-Zubiri, 1996; Goossens et al., 1998; Spencer et al., 1998; Fietz et al., 2000).

A brief word on terminology

Behavioural and genetic studies of socially monogamous birds (cf. Birkhead & Møller, 1992) and mammals (e.g., Reichard, 1995; Fietz et al., 2000) have convincingly demonstrated that in a majority of contexts an uncritical use of the simple term 'monogamous' to describe and understand relationships of pair-living species is inadequate (Gowaty, 1996a). It ignores the flexibility, variability, and complexity of different levels of relationships between socially monogamous animals. The language that is needed is one that openly and precisely reveals our knowledge about male-female relationships at the social-, sexual-, and genetic levels in order to be able to identify the evolutionary consequences of variations in social association. This is particularly important where the social, sexual and reproductive system of a pair-living species does not coincide (cf. Hughes, 1998).

This book uses a consistent terminology to reflect the complexity and current knowledge of, and the intended focus on monogamous male-female relationships. *Social monogamy* refers to a male and female's social living arrangement (e.g., shared use of a territory, behaviour indicative of a social pair, and/or proximity between a male and female) without inferring any sexual interactions or reproductive patterns. In humans, social monogamy equals monogamous marriage. *Sexual monogamy* is defined as an exclusive sexual relationship between a female and a male based on observations of sexual interactions. Finally, the term *genetic monogamy* is used when DNA analyses can confirm that a female-male pair reproduce exclusively with each other. A combination of terms indicates examples where levels of relationships coincide, e.g., sociosexual and sociogenetic monogamy describe corresponding social and sexual, and social and genetic monogamous relationships, respectively. Lastly, the term *monogamous social system* is used synonymously with social monogamy, and the term *monogamous mating*

system is synonymous with known monogamous sexual and genetic relationships.

DEVELOPING A THEORETICAL FRAMEWORK: PATHWAYS TO SOCIAL MONOGAMY

Far from being a unitary phenomenon with a simple evolutionary explanation, social monogamy is multifaceted, having evolved along different pathways in different animal lineages. Three components influence the occurrence of social monogamy: the amount of paternal care, the access mode to resources, and partner choice. A clear grasp of the importance of each of these factors, and how they interact and influence each other, provides the necessary foundation for understanding the different routes to social monogamy. Such a framework is outlined in Figure 1.1. The three bold arrows in the Figure point back and forth between the three main components of social monogamy's evolution (paternal care, resource access, mate choice), indicating that these factors influence each other. The smaller arrows link the main steps leading to social monogamy. Because interactions between factors promoting the evolution of social monogamy are complex, it is not useful to connect with small arrows all the possible influences on the steps or specific conditions leading to social monogamy. This complexity seems to be particularly true for paternal care, which can influence the evolution of social monogamy at different stages and to various degrees (see The importance of paternal care, below). Therefore, an absence of connecting arrows does not equal an absence of a link between factors or conditions. For all pathways outlined in Figure 1.1 it was assumed that social monogamy would be the resulting, visible outcome of the compromise between the sexes' interests in maximising their own reproduction (cf. Davies, 1991, 1992; Chapman & Partridge, 1996).

The importance of paternal care

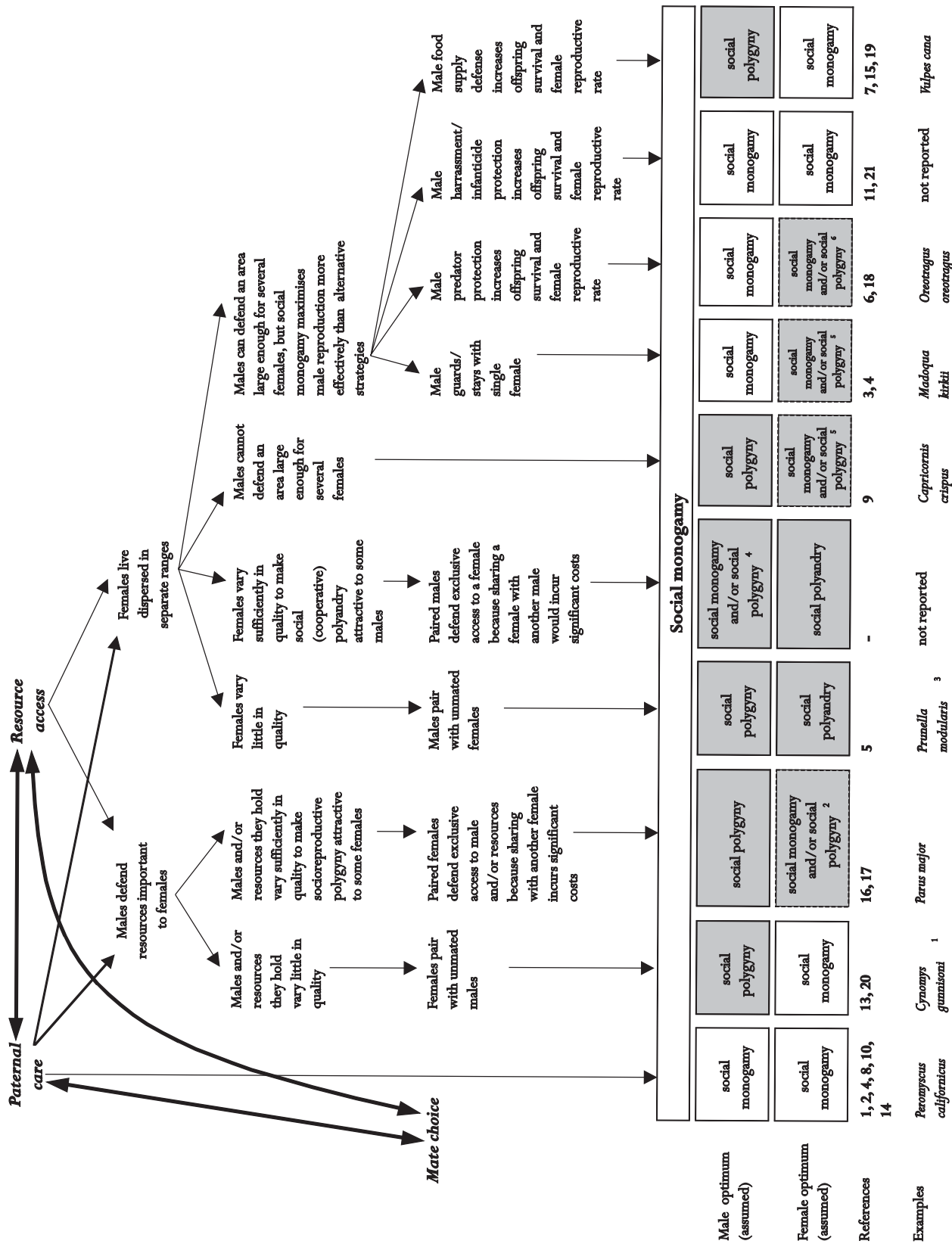
It has repeatedly been suggested that the need for biparental care lead to socially monogamous pairs (Lack, 1968; Ligon, 1999; Burley & Johnson, 2002). When a female cannot rear young successfully without the direct help (e.g., feeding, carrying, warming) of a male, social monogamy is likely to become the reproductive strategy that best maximises male and female fitness (Kleiman, 1977; Wittenberger & Tilson, 1980; Kleiman & Malcolm,

1981; Malcolm, 1985; Birkhead & Møller, 1996). This hypothesis attracted much attention, probably because it is in socially monogamous species that biparental care is more common and obvious, particularly in birds (Gowaty, 1996c), although it also occurs in some small mammals (Gubernick, 1984; Gubernick & Teferi, 2000). Biparental care has also been suggested as one important factor explaining the prevalence of human social monogamy (Marlowe, 2000). The hypothesis originally postulated that male care could not be shared between offspring/broods of several females without decreasing either female or both adults' reproductive success below what could be achieved under a monogamous parenting system. Where male care can be shared socioreproductive polygyny may develop. When male contributions to infant survival are critical, biparental care and social monogamy may become the straightforward parenting and social systems.

Additionally, even where paternal care is not critical for offspring survival and females can raise some offspring alone, paternal care may influence female mate choice at a later stage along the pathways leading to social monogamy. Under conditions where males occupy separate territories and naturally vary in quality, e.g., parenting ability, a male's parenting potential may become important for female mate choice. Females choosing parenting males as mates may increase paternal care and increasingly constrain males to social monogamy (Burley & Johnson, 2002). Aspects of male care may also be important in situations when monogamously paired females are confronted with the arrival of another female. If social monogamy maximises female reproductive success, paired females may base their decision to aggressively enforce social monogamy on the importance of and hence potential loss of paternal care when male assistance has to be shared with a second female (Slagsvold & Lifjeld, 1994). Such examples illustrate how intimately resource access strategies (males occupy separate ranges), paternal care, and mate choice (paired females benefit from social monogamy and prevent polygynous parenting) will often be linked along pathways to social monogamy.

Resource access and mate choice

Males do not provide a measurable amount of paternal care in all socially monogamous animal lineages (Clutton-Brock, 1991). In fact, direct male care is absent in the majority of socially monogamous mammals



Paternal care

Resource access

Mate choice

Males defend resources important to females

Females live dispersed in separate ranges

Males and/or resources they hold vary little in quality

Females vary little in quality

Males and/or resources they hold sufficiently in quality to make socioreproductive polygyny attractive to some females

Males pair with unmated males

Paired females defend exclusive access to male and/or resources because sharing with another female incurs significant costs

Paired males defend exclusive access to a female because sharing a female with another male would incur significant costs

Males can defend an area large enough for several females, but social monogamy maximises male reproduction more effectively than alternative strategies

Male guards/stays with single female

Male predator protection increases offspring survival and female reproductive rate

Male harassment/infanticide protection increases offspring survival and female reproductive rate

Male food supply defense increases offspring survival and female reproductive rate

Social monogamy

social monogamy	social monogamy	social monogamy and/or social polygyny 4	social polygyny	social monogamy and/or social polygyny 5	social polyandry	social monogamy and/or social polygyny 6	social monogamy and/or social polygyny 3	social monogamy and/or social polygyny 9	social monogamy and/or social polygyny 5	social polyandry	social monogamy and/or social polygyny 16, 17	social monogamy and/or social polygyny 13, 20	social monogamy	social monogamy and/or social polygyny 1, 2, 4, 8, 10, 14
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Male optimum (assumed)

Female optimum (assumed)

References: 1, 2, 4, 8, 10, 14

Examples: *Peromyscus californicus* 1, *Cynomys gunnisoni* 1, *Prunella modularis* 3, *Parus major*, *Falco sparverius* 3, *Caprimulgus crispus* 9, *Madoqua kirki* 3, 4, *Oreotragus oreotragus* 6, 18, not reported 11, 21, *Vulpes cana* 7, 15, 19

(Komers & Brotherton, 1997). When Komers and Brotherton (1997) tested the relationship between paternal care, female dispersion, and social monogamy across mammals they did not find the expected three-way interaction between the three character states, nor a two-way interaction, either between paternal care and female grouping or paternal care and mating system, and finally, no single effect of paternal care. Further analyses revealed that social monogamy in mammals probably evolved significantly more often in the absence of paternal care than in its presence and that the associated evolution between the two character states of paternal care and social monogamy presumably occurred by chance when social monogamy was already present. The authors concluded that paternal care was a poor predictor of social monogamy, a finding already independently suggested for primates by Wright (1990), Tardif (1994), and Dunbar (1995). With decreasing importance of paternal care, the evolution of social monogamy may increasingly depend on how resources necessary for males and females to reproduce are distributed and which strategies individuals follow to maximise their reproduction.

Generally, differential investment in gametes, i.e., anisogamy (Parker et al., 1972) is thought to set the stage for the evolution of sex-specific reproductive strategies (but see Snowdon, 1997). It is males who invest little in gametes and produce mobile sperm, whereas females make substantial energetic contributions to each gamete and produce large, nutritious eggs. Because of the inequality in gamete production, the difference in the

potential reproductive rates of males and females is significant (Clutton-Brock & Parker, 1992): A male can usually fertilise many more eggs than a single female can develop to ovulation. Consequently, for most females access to resources important for successful, regular egg development limit their reproductive success (Trivers, 1972). Hence, females are expected to follow strategies that best maximise their resource access, which often equals their access to food (Janson, 1992). Ecological factors have been suggested as the major influence on the distribution of females (Emlen & Oring, 1977; Clutton-Brock & Harvey, 1977; Clutton-Brock, 1989). When resources occur in relatively small patches, uniformly distributed in time and space, and predation pressure is low, females may be able to afford to live nongregariously to minimise feeding competition (Alexander, 1974; Wrangham, 1980; van Schaik, 1983).

In contrast to females, male reproduction is less dependent on access to food resources but is limited primarily by access to fertile females (Bateman, 1948; Trivers, 1972; Clutton-Brock, 1989), hence male spatial distribution often follows female spatio-temporal distribution (Andelman 1986; Altmann, 1990; Mitani et al., 1996). At first glance, the evolution of social monogamy may then be understood as a function of females living in exclusive ranges and males mapping their lives onto these females. However, although females living separate from each other represents an important precondition for the evolution of social monogamy in mammals (Komers & Brotherton, 1997; van Schaik & Kappeler, chapter 4), it is not a sufficient explanation

Figure 1.1. Pathways to social monogamy.

Key to references: 1 Arcese, 1989; 2 Bart & Tornes, 1989; 3 Brotherton & Rhodes, 1996; 4 Clutton-Brock, 1991; 5 Davies, 1992; 6 Dunbar & Dunbar, 1980; 7 Geffen & Macdonald, 1992; 8 Gubernick & Teferi, 2000; 9 Kishimoto & Kawamichi, 1996; 10 Kleiman, 1977; 11 McKinney, 1986; 12 Moehlman, 1989; 13 Pribil & Picman, 1996; 14 Ribble, chapter 5; 15 Rutberg, 1983; 16 Slagsvold, 1983; 17 Slagsvold & Lifjeld, 1994; 18 Sommer, 2000; 19 Sun, chapter 9; 20 Travis et al., 1995, 1996; 21 van Schaik & Dunbar, 1990

¹ In Gunnison's prairie dogs (*Cynomys gunnisoni*) social monogamy was associated with an even resource distribution, whereas social polygyny and polygynyandry prevailed with increasing environmental patchiness (Travis et al., 1995, 1996).

² Female optimum varies with status: paired females' optimum is social monogamy, whereas yet unpaired females' optimum is social polygyny

³ Dunnocks (*Prunella modularis*), have a flexible mating system and only some pairs of the study population were socially monogamous (Davies, 1992)

⁴ Male optimum varies with status: paired males' optimum is social monogamy, whereas yet unpaired males' optimum is social polyandry

⁵ Female optimum is variable and depends on intrinsic female quality and/or environmental condition

⁶ Male optimum varies with status: paired males' optimum is social monogamy, whereas yet unpaired males' optimum is social polyandry

because males could just as well adopt spatio-reproductive strategies other than social monogamy (Sandell & Liberg, 1992). Males could aim to realise socioreproductive polygyny by defending an area large enough to encompass several separate female ranges (e.g., Ferron & Oullet, 1989; Green et al., 1998; Berteaux et al., 1999; Fisher & Owens, 2000). Alternatively, they could try to defend two separate ranges and become polyterritorial (Temrin & Arak, 1989), although, polyterritoriality may be a risky strategy in terms of lost matings with the primary female (Alatalo et al., 1987). Finally, males could rove around to successively visit females living in different areas as these become fertile, as found in primates like the orangutan (*Pongo pygmaeus*; van Schaik & van Hooff, 1996) or the aye-aye, (*Daubentonia madagascariensis*; Sterling & Richard, 1995).

Pathways to social monogamy: when females live apart from each other

Given the different options males have when females live in separate ranges, social monogamy is expected to evolve under only one of the following three conditions: First, when males are physically or otherwise unable to realise any of the above mentioned polygynous strategies (Parker, 1974; Emlen & Oring, 1977; Barlow, 1988). Second, when the chance to find another breeding partner is low so that staying with and guarding a current partner becomes a male's best option (cf. van Rhijn, 1991; Brotherton & Rhodes, 1996). Third, when staying with one female provides reproductive benefits to males not otherwise accessible under alternative mating strategies.

The first condition for social monogamy is straightforward and depends largely on intrinsic male capacities. The second condition addresses difficulties for males to find another breeding partner, which may result from different situations. It may arise when a single brood or young is produced during a short breeding season and nearly all adults start reproduction at about the same time leaving negligible polygyny potential for males (Ligon, 1999). Finding another partner may also become difficult where breeding space is highly limited (Freed, 1987), for example, in circumstances imposed by ecological constraints, and in populations with a male-biased sex ratio. Male-biased adult sex ratios may result, e.g., in birds, from female-biased adult mortality due to migration or predation during

incubation (McKinney, 1986; Møller, 1994). Although alternatively, a male-biased sex ratio may lead to an increase of socially polyandrous units due to changing cost-benefit equations when male-male competition for breeding positions increases, as noticed by Davies (1992) in a dunnoek (*Prunella modularis*) population after harsh winters.

Under the third condition, males are theoretically able to achieve socioreproductive polygyny but they live socially monogamously (e.g., Brotherton & Manser, 1997; Reichard, chapter 13), suggesting that social monogamy conveys higher fitness returns to males than, e.g., roving and searching for additional females (cf. Parker, 1974; Wickler & Seibt, 1981). Reproductive benefits to males from staying with a single female may exceed reproductive success from alternative strategies when the continuous male presence with a female and her offspring significantly increases offspring survival and/or female reproductive rate (Clutton-Brock, 1989, 1991; van Schaik & Dunbar, 1990).

Territorial behaviour of mammalian males has been interpreted as increasing offspring survival and female reproductive rate sufficiently to make social monogamy beneficial to males (Rutberg, 1983). However, although access to an exclusive food supply benefits a female and her offspring and may influence a female's partner choice, a prime function of male territoriality is probably to attract reproductive partners (Baker, 1983; Gosling, 1986; Carranza et al., 1990), and only secondarily to provide food resources. Territorial defence by socially monogamous males may therefore have become important for the maintenance of social monogamy, but this defence perhaps evolved secondarily after social monogamy was already in place for other reasons (cf. Brotherton & Rhodes, 1996).

Male protection from predation is another form of indirect male care that has been proposed as a positive influence on offspring survival and female reproductive rate (Dunbar & Dunbar, 1980). This pathway to social monogamy assumes that for nongregarious females the permanent company of a male relieves them from predator vigilance, allows them optimised feeding, and leads to an increased female reproductive rate. Such reasoning is supported by the observation that, e.g., primate males are particularly effective in detecting and deterring predators (van Schaik & van Noordwijk, 1989; van Schaik & Hörstermann, 1994). However, empirical

evidence for the predicted causal link between predation pressure and social monogamy is scarce. Moreover, the predation-hypothesis for the evolution of social monogamy makes a contradicting assumption: on one hand, predation pressure is assumed to be so strong that predator protection increases offspring survival and hence socially monogamous males' reproductive success beyond what could be achieved by alternative strategies. On the other hand, however, the belief is that in order for females to be able to live a nongregarious lifestyle in the first place, predation pressure must be almost negligible. If predation pressure is important, social polygyny, perhaps with small female group size, seems more likely to have evolved than social monogamy (Isbell, 1994), and under conditions of moderate predation pressure it seems questionable to assume that male predator protection could sufficiently compensate for lost mating opportunities. The contradiction can only be resolved if social monogamy was assumed to have evolved at a very specific predation pressure magnitude where predation pressure is just low enough to allow females to live nongregariously, but at the same time high enough to adequately compensate protecting males for lost matings. Alternatively, and similar to the resource defence function of male territoriality, perhaps a special male role in predator vigilance, detection, and deterrence evolved after social monogamy already existed because the male was close to the female anyway. Even if male predator protection did not cause social monogamy to evolve it may have become important thereafter because it may have further increased reproductive benefits derived from social monogamy.

Van Schaik and Kappeler (1993; 1997; chapter 4) suggested another pathway to social monogamy via a specific male role. They proposed that in infant-carrying primates the risk of infanticide by strange males was the selective advantage for males to stay with a female. The hypothesis predicts that when males protect females and infants from infanticide through their continuous presence, then they achieve higher fitness than males that leave a female after impregnation to search for another mate. The risk and occurrence of male infanticide is widespread among mammals (Hausfater & Hrdy, 1984; van Schaik, 2000b) and also occurs in some birds (Møller, 1988a; Veiga, 2000). Infanticide by immigrating males has been interpreted as part of a male reproductive strategy whereby males stop females from

from investing in an offspring of another male to speed up the females return to receptivity (Hrdy, 1979). Male infanticide will be an adaptive strategy under specific conditions: (1) the probability must be zero or close to zero that the infanticidal male sired the infant(s); (2) the mother returns to menstrual cycling earlier than if the infant(s) had lived; and (3) the infanticidal male has an increased probability of siring the female's next infant(s) (Hrdy et al., 1995; van Schaik, 2000a). Empirical support for a direct link between male infanticide and the evolution of social monogamy is still lacking for primates as well as rodents (Blumstein, 2000) and birds (Veiga, 2000). Nonetheless, the concept of male infanticide appears as valid for socially monogamous as for other one-male social mating systems in which infanticide has been documented (e.g., Hanuman langur *Semnopithecus entellus*: Sommer, 1994). Since male changes do occur in some socially monogamous species (e.g., gibbons: Treesucon & Raemaekers, 1984; Brockelman et al., 1998; Reichard, chapter 13), a potential for male infanticide does exist. Therefore, social monogamy may have evolved as an infanticide prevention strategy in some lineages (van Schaik & Kappeler, chapter 4).

Finally, when females live in separate territories and males join them the evolution of social monogamy - instead of social polyandry - may depend on intrinsic female qualities. This hypothesis resembles the reversed version of the polygyny-threshold hypothesis for females (see below) and suggests a reversed polyandry-threshold model for the evolution of social monogamy. It assumes that males would only accept cooperative polyandry if the loss from shared mating is compensated by the increased quality of offspring. Otherwise, males would opt for a socially monogamous strategy. Two pathways to social monogamy appear plausible: First, where variation in female quality is low, males pair with yet unpaired females to avoid potential costs of shared mating and reproduction. Second, even where the polyandry-threshold is exceeded, and females vary sufficiently in quality to make social polyandry a beneficial strategy for some males, already paired males may prevent other males from joining and forming socially polyandrous units in order to avoid the reproductive costs of shared matings. Studies of cooperatively polyandrous species indicate that indeed males often share matings (Heymann, 2000) and paternity (Hartley et al., 1995),

suggesting that cooperative polyandry may be costly to a dominant male, who may then, therefore, enforce social monogamy.

Pathways to social monogamy: when males defend a territory

So far, the focus has been on situations where resource access strategies of females would lead to females living apart from each other and males pairing with single females. This situation seems more common in mammals than in birds. However, another important starting point for pathways to social monogamy exists. Social monogamy may evolve when males defend a territory to attract a precious resource female(s) (e.g., Alatalo et al., 1986). And this male strategy seems more common in birds than in mammals.

When males live in separate territories, and females join them, social monogamy evolves if males, or the resources they hold, vary little in quality and an individual female gains most from pairing with an unmated male (cf. Orians, 1969; Slagsvold & Drevon, 1999). This hypothesis reverses the logic of the polygyny-threshold hypothesis originally proposed to explain the evolution of social polygyny in birds in relation to different habitat qualities (Verner, 1964; Verner & Willson, 1966). The polygyny-threshold hypothesis predicted that: if males, or the resources they defend, vary sufficiently in quality, some females would breed more successfully as the second female with a high quality male or in a high quality territory than as the sole female with a low quality male or in a poor quality territory (cf. Orians, 1969; Slagsvold & Drevon, 1999). Consequently, when the polygyny-threshold is exceeded, social polygyny is expected, whereas below the threshold, females would pair monogamously. This hypothesis also assumes that females generally profit from social monogamy by avoiding the costs associated with sharing either paternal care or territorial resources.

The final pathway to social monogamy proposed here predicts that social monogamy evolves even when males and/or the resources they hold vary sufficiently in quality to allow some females to successfully become socially polygynous. Under such conditions, social monogamy evolves when adding a second female to a pair or a home range would considerably decrease the paired female's reproductive success due to the costs of sharing territorial resources and/or male care. Hence, a paired female may aggressively enforce

social monogamy (Rutberg, 1983; Slagsvold & Lifjeld, 1994; Kokita, 2002).

Empirical support for pathways to social monogamy

Paternal care is important

The most convincing examples of the selective importance of biparental/ male care come from species where loss of male care results in complete breeding failure. Such examples fit the classical approach in which paternal care cannot be shared, i.e., is 'essential', and only if this condition is met will the evolution of social monogamy be triggered (cf. Wittenberger & Tilson, 1980). However, as outlined above in the discussion of pathways to social monogamy, even when male care is not directly essential for offspring survival, paternal care may still exert an important influence on social monogamy's evolution.

In birds, males can perform most parental duties equally well as females, and biparental care is the norm (Clutton-Brock, 1991; Gowaty, 1996c). Evidence of one of the benefits of direct paternal care is provided by the observation that reduction in female reproductive success due to the absence of a male mate was positively correlated with a male's provisioning contribution (Møller, 2000): The less the male was present, and therefore not providing food, the lower the female's reproductive success. There is little doubt that in species where biparental care occurs, removing the male has a negative effect on offspring survival (Mock & Fujioka, 1990; Ligon, 1999). An essential role of male helping behaviour is, however, not always evident (Clutton-Brock, 1991; Gowaty, 1996a). Perhaps a male's contribution to incubation qualifies as critical male assistance and hence a strong selective pressure for biparental care and social monogamy in some birds (Ligon, 1999). In the socially monogamous, biparental western sandpiper (*Calidris mauri*), removal of the female parent during incubation led to males abandoning the nest before the eggs hatched (Erckmann, 1983). Møller (2000) determined the importance of male parental care (feeding) across birds by measuring the reduction in female reproductive success in the absence of male care, and providing several examples in which male absence would lead to complete breeding failure. In addition to the importance of shared incubation, Bart and Tornes (1989) identified other stages of the nesting cycle where male loss would considerably decrease reproductive success,

including laying, nestling, and post-nestling, and which were supported by additional studies (Wolf et al., 1988; Rees et al., 1996).

Because of gestation and lactation, female mammals are particularly well adapted to care for young without male help. This is reflected in the sparse distribution of paternal care in mammals, with only about 5 % of species showing a measurable amount of direct male care (Clutton-Brock, 1991). Paternal behaviour occurs primarily in rodents, carnivores, and primates (Kleiman & Malcolm, 1981; Wright, 1990; Woodroffe & Vincent, 1994), and despite its general rarity seems essential in some species (Moehlman, 1989). In an experimental laboratory study of the Djungarian hamster (*Phodopus campbelli*), Wynne-Edwards (1987) showed that the presence of a pair-male significantly affected offspring survival. Females raised almost all young (95 %) when males were present, whereas solitary females lost more than half of their offspring (53 %). Even assistance from a littermate sister could only marginally compensate for the loss of male assistance (61 % surviving young), verifying that male care was essential. In an experimental study under natural conditions, Gubernick and Teferi (2000) also confirmed an essential role for the male California mouse (*Peromyscus californicus*). Significantly fewer offspring emerged from the burrows where a female's male partner was captured compared to controls (81 % emerging offspring father-present; 26 % emerging offspring father-absent). This effect was not due to different female reproductive performance because those females whose males were captured subsequently raised a second litter with a new male and achieved significantly greater reproductive success than for the litter without male assistance. Ribble (chapter 5) also concluded that male warming of offspring was essential in the California mouse (*Peromyscus californicus*): A relatively smaller litter size and greater relative litter mass compared to other small rodents resulted in comparatively greater heat loss of offspring. Male presence appeared essential for offspring survival during the first days after birth when the female is away from the nest. Finally, in a mark-recapture study of the nocturnal, tree-hole nesting fat-tailed dwarf lemur (*Cheirogaleus medius*), females also failed to raise young without male help (Fietz, 1999a, b). An interesting parallel emerges from a bird-mammal comparison. In birds, male presence appeared important when incubation needed to be shared during early infancy. And similarly, in the mammalian

examples, shared attendance of a burrow or nest-hole directly after birth appeared to be the strongest selective force for paternal investment. Biparental care may ultimately be linked to those species in which offspring are sensitive to heat loss early in their development, so that while one parent forages, the other must remain with the offspring in order to mitigate the thermal disadvantages connected to small litter size (cf. van Rhijn, 1991; Ribble, chapter 5).

In general, biparental care has a positive effect on offspring survival (but see Royle et al., 2002), although, it is also highly variable within and between species as well as across mating systems. Therefore, it is unlikely to provide a universal explanation for the evolution of social monogamy (Mock, 1985; Bart & Tornes, 1989; Gowaty, 1996a; Møller, 2000). Because of its general positive effect on offspring survival, paternal care may also reflect the maintenance of social monogamy rather than its ultimate function (Gowaty 1996c; Komers & Brotherton, 1997; Tullberg et al., 2002).

Males defend a resource important to females

The reversed polygyny-threshold hypothesis

Despite some criticism (Davies, 1989; Ligon, 1999), examples exist for birds, which support the logic of the reversed polygyny-threshold hypothesis for the occurrence of social monogamy, because females vary their socioreproductive strategy in response to varying resource availability. When males or the resources they hold do not vary significantly in quality, females prefer to pair with an unmated male.

In the well-studied red-winged blackbird (*Agelaius phoeniceus*) females generally preferred to settle in the territories of unpaired males because socioreproductive polygyny decreased female reproductive success (Pribil & Picman, 1996). However, if territory quality was manipulated experimentally, with some territories providing better nesting opportunities than others, female mate choice could be reversed and females preferred to settle with an already paired male (Pribil & Searcy, 2001), suggesting that indeed social monogamy was usually resource dependent. Similarly, in an extended version of the polygyny-threshold theory Slagsvold and Drevon (1999) directly manipulated male quality (phenotypic degree of bright coloration) and demonstrated that females would mate monogamously when male quality did not vary but changed their choice when male quality did vary.

The polygyny-threshold hypothesis was particularly suited to situations where males occupied their territories first, e.g., as found in some migratory birds. In these species, newly-arrived females may be able to fly around to inspect and assess different males and/or the territories those males are defending, freely basing their eventual choice of male and territory on male and/or territorial quality (e.g., Møller, 1994). These results suggest that females' choice of mating strategy (polygynous versus monogamous) may be based either on the resources a male can provide or directly on a male's quality. This situation rarely emerges in mammals because females are often philopatric (Greenwood, 1980) and do not migrate between seasons, staying in the same social groups for long periods. Furthermore, even dispersing females often remain close to their natal area (e.g., Sterck & Korstjens, 2000), which limits their opportunities to visit and inspect a variety (or any) groups in which they might take-up future residence. Finally, dispersing females may encounter hostile conspecifics and may be able to neither evaluate several territories/groups prior to emigration nor freely choose which group or male to join (e.g., Dietz & Baker, 1993).

The limitations on female decision making in choosing a particular male and/or territory make it difficult to test when a female would do better by choosing an unpaired male compared to an already paired male. In humans, however, Borgerhoff Mulder (1990) found some indirect evidence supporting the idea that a low resource holding potential results in socially monogamous marriage: Among the Kipsigis of Kenya, wealth was a strong, although not the only predictor of socioreproductive polygyny. Hence, when this logic is reversed, a low resource holding potential may explain why some Kipsigi men had to remain socially monogamous. Another example of resource dependent development of social monogamy is Gunnison's prairie dog (*Cyanomys gunnisoni*): Social monogamy was associated with an even resource distribution, whereas social polygyny and polygynandry prevailed with increasing environmental patchiness (Travis et al., 1995, 1996).

Overall, the polygyny-threshold model appears of limited value in studies of mammalian mating systems because socioecological conditions of mammals rarely meet the models' various assumptions (see Clutton-Brock, 1989; Borgerhoff Mulder, 1990). These limitations make it difficult to further explore whether environmental

and/or male quality may be important pathways leading to socioreproductive monogamy in mammals. In contrast, the reversed polygyny-threshold hypothesis may explain social monogamy in some birds (but see Davies, 1989).

When a paired female does not share resources

This hypothesis assumes that the polygyny-threshold is exceeded because either environmental quality or male quality varies (or both vary) sufficiently to allow socioreproductive polygyny to become an optional reproductive strategy for some females. However, the presence of a second breeding female would be costly for an already paired female, who would thus aggressively enforce social monogamy (Arcese, 1989; Slagsvold et al., 1992; Ahnesjö et al., 1993). Female-female aggression is the suggested mechanism that maintains social monogamy. The suggested potential costs to a resident female bird from an additional female are, e.g., loss or decrease of parental care, loss of food or nest sites, egg destruction, egg dumping, displacement from the territory, and increased predation risk (Slagsvold, 1983; Slagsvold & Lifjeld, 1994).

Female-female aggression: birds

An example from the bird literature is Veiga's (1992) study of the predominantly monogamous house sparrow (*Passer domesticus*). Male reproductive success increased with the number of females acquired. Nonetheless, many males remained socially monogamous despite the abundance of unpaired females, suggesting that the polygyny threshold should have been exceeded for many females of the population. Even when reproductive options were manipulated by giving males more nest boxes, experimental males could not attract additional females any more frequently than control males. The prevalence of social monogamy was explained by the observation that females already present on a male's territory prevented other females from settling, presumably to avoid costs associated with resource sharing (Veiga, 1992). In cases where two females did breed on one male's territory, Veiga (1992) proposed that the costs of expelling female competitors were higher than benefits derived from maintaining social monogamy. Another example is the song sparrow (*Melospiza melodia*), in which settled females would also try to prevent unpaired females from settling, and where unpaired females could only successfully join an established pair if the resident

female was already incubating and could not defend her monogamous status (Arcese, 1989). In the European starling (*Sturnus vulgaris*), Sandell and Smith (1996) experimentally manipulated the distance between nest boxes, thereby artificially increasing the chance for additional females to settle. Most males remained socially monogamous as long as nest boxes were close to one another because primary females would prevent secondary females from settling. Only when nest boxes were sufficiently far apart that costs of defending two boxes presumably exceeded the benefits of social monogamy could two females breed on one male home range. Finally, aggression between females, presumably to prevent male socioreproductive polygyny, may be intense even when males are polyterritorial (Slagsvold et al., 1992).

Female-female aggression:mammals

Aggression between females has also been suggested as an important mechanism for maintaining social monogamy in pair-living mammals. Gibbons (*Hylobates lar*), small apes of the tropical forests of Asia, e.g., show mainly intrasexual territorial aggression in preventing male social polygyny (Brockelman & Srikosamatara, 1984; Mitani, 1984). In golden lion tamarins (*Leontopithecus rosalia*), a small Neotropical primate in which sociosexual monogamous as well as sociosexual polyandrous units occur, resident breeding females always vigorously chased nongroup females away (Baker & Dietz, 1996) and no female was recorded as having ever successfully joined a group that already contained a breeding female (Dietz & Baker, 1993). However, social polygyny via a familial route was found in a few cases where group habitats appeared rich enough to allow mature daughters to share their mothers' ranges, suggesting that a resident, paired female would only accept an increase in female group size if the cost of sharing resources would be compensated by an exceptionally rich territory.

The above examples of female-female aggression are suggestive of the hypothesis stated earlier, i.e., that adding a second female to a pair or home range significantly decreases the paired female's reproductive success as a result of sharing territorial resources and/or male care, and they do not contradict the evolution of social monogamy via this route. However, most studies do not provide the data and quantitative tests that would document the reproductive consequences of both

Socially monogamous and socially polygynous females, evidence necessary to evaluate the potential costs to a paired female when a second female settles in her range. Specific studies are needed to address the link between social monogamy and the interests of a paired female since female-female aggression could occur for reasons other than maintaining this form of monogamy (Wittenberger & Tilson, 1980).

Females live separate from each other

When females fail to attract several males

Social or cooperative polyandry is relatively rare in birds and mammals but regularly occurs in, e.g., shorebirds, pukekos, saddle-back tamarins, and some other species (Goldizen, 1987; Ligon, 1999). Under conditions that would generally favour the evolution of social polyandry (cf. Erckmann, 1983), social monogamy may evolve when females vary little in quality because males may then prefer to pair with a yet unpaired female.

Examples where social monogamy may have developed because females failed to attract more than one male are rare. Perhaps this pathway was relevant for some dunnocks (*Prunella modularis*) of the Cambridge University Botanic Garden population studied by Davies (1992). Dunnocks have a variable socioreproductive mating system, with individuals being either socially monogamous, socially polyandrous, socially polygynous, or socially polygynandrous (Davies & Lundberg, 1984). Socially monogamous pairs comprised between 25–63% of the population's social units during 11 years (Davies, 1992). Among the different socioreproductive units, socially polyandrous females achieved the greatest reproductive success and also defended the largest ranges (Davies, 1992). In contrast, females that occupied small areas were mostly socially monogamous. This observation is in line with the hypothesis that the strongest females of the highest quality could perhaps defend the largest ranges and also attract more males than lower quality females inhabiting smaller ranges. Males would thus only accept social polyandry if the potential loss of shared matings would be compensated by high female quality, as expressed in these females' occupancy of a large territory. Perhaps variation in female quality could also explain the occurrence of social monogamy in the Otika pukeko (*Porphyrio porphyrio*) study population (Jamieson, 1997). Pukekos usually live in socially polyandrous units, but at the Otika site, social

monogamy was relatively common, perhaps in relation to a low quality of certain females.

The few examples mentioned here to point towards a causal relationship between individual female quality and the evolution of social monogamy lack the required quantitative measures of individual quality. Currently, therefore, it can only be stated that the observations do not contradict to the expectations derived from the hypothesis. Examples for mammals are even more sparse than for birds. However, studies focusing on individual quality variation in female primates with a variable sociosexual mating system, such as the Callitrichines (Goldizen, 1987; Heymann, 2000) appear potentially rewarding.

When males fail to become socially polygynous

The basic condition for this pathway to social monogamy is that females live dispersed in separate ranges. When males fail to establish ranges large enough to encompass several female ranges, social monogamy may be the resulting compromise between the sexes.

An example of this pathway to social monogamy in birds is the willow ptarmigan (*Lagopus lagopus*), most of whom live in pairs. Hannon and Martin (1992) found no difference in the reproductive success of socially monogamous compared to socially polygynous females, indicating that female reproduction was independent of the two alternative male strategies. In contrast, reproductive profit for males came most from social polygyny. However, because females were largely aggressive towards each other, which resulted in spatial separation (Hannon, 1983), only a small fraction of males (5–20% per year) could establish a territory large enough for two females (Hannon & Martin, 1992). Socioreproductive polygynous males achieved higher 'scores' on a relative scale indexing male quality based on physiological parameters than did socioreproductive monogamous males, suggesting that because those males were only able to defend ranges large enough for one female physical limitations indeed restricted most males to socioreproductive monogamy, (Hannon & Dobush, 1997). Another interesting example where male physical condition may also limit males to social monogamy is the tree swallow (*Tachycineta bicolor*), studied by Kempenaers and colleagues (2001). Males of the study population were divided into two main categories: (i) resident breeders who formed socioparental monogamous relationships with a female, and (ii) floating males who

were considered nonbreeders because they did not establish a recognisable partnership with any female. Surprisingly, the floating males achieved high reproductive success in the population through extra-pair copulations. In addition to considerable reproductive success, floater males also appeared to be in better physical shape (heavier) than breeding residents. It was suggested (Kempenaers et al., 2001), that males in good physical condition could afford to float, avoid the burden of paternal duties, and possibly breed polygynously, whereas males in worse body condition would become socially monogamous, accepting the duty of paternal care and the additional cost of a potentially high frequency of extra-pair young in the broods they fed.

In mammals, physical strength seems to limit most Japanese serow males (*Capricornis crispus*) from becoming socially polygynous with two females. Males only achieved social polygyny when one of the female ranges with which the male's overlapped was considerably smaller than the average female home range (Kishimoto & Kawamichi, 1996; Kishimoto, chapter 10). Male home ranges were on average only about 10% larger than average female home ranges, thus allowing only males who happened to overlap with a female inhabiting an average size home range and a female with a particularly small range to become socially polygynous. Therefore, males generally appeared physically unable to defend sufficiently large areas to realise socioreproductive polygyny. Otherwise, at least the strongest males in the population would have defended two average size female ranges.

Considering that males can usually maximise their reproductive success with a socioreproductive polygynous strategy, it seems plausible that social monogamy may occasionally occur as a consequence of males being unable to gain or defend access to several females.

When guarding a single female becomes a male's best option

Maintaining breeding status may be a critical factor influencing partner fidelity and continuous male-female association. Where loss of a breeding position is very costly, individuals may employ strategies to control their partner's activities in order to forestall mate change, thus leading to social monogamy.

In Macaroni penguins (*Eudyptes chrysolophus*), breeding success following mate change was not associated with reproductive disadvantages, and as many newly formed pairs as reunited pairs raised one offspring

to fledging (Williams, 1996). However, more than a third of the males that had divorced a female remained without a partner the following breeding season and did not breed again for from two to four years, although they retained their old nest site (Williams, 1996). The long period after divorce without a breeding partner, despite retention of the nest site, indicates how important it is for these penguins to stay with their current mates. Similarly, in Tropical house wrens (*Troglodytes aedon*), a limited number of suitable breeding territories coupled with a low number of available partners probably resulted in social monogamy. Already breeding males were forced to continuously mate guard their female partners to maintain their breeding positions (Freed, 1987). An important guarding role of a male has also been suggested for barnacle geese (*Branta leucopsis*), where male presence significantly affected female and offspring survival (Black & Owen, 1989).

A mammalian example of the evolution of social monogamy via mate guarding is the prairie vole (*Microtus ochrogaster*). Females lived dispersed and males were assumed to optimise their reproductive success by staying with one female because of the high probability of again successfully mating with the female when she entered her postpartum oestrous (Getz et al., 1987). Intensive mate guarding was also suggested as the key male strategy and the origin of socioreproductive monogamy in Africa's small Kirk's dik-dik antelope (*Madoqua kirkii*; Brotherton & Komers, chapter 3). Females experienced short fertility periods of only one day, which made male roving in search of fertile females a risky and probably inferior male strategy compared to social monogamy. Moreover, male-male competition for territory ownership was intense, which promoted year-round maintenance of existing pair relationships (Brotherton & Rhodes, 1996; Brotherton & Komers, chapter 3). Females probably also preferred the constant presence of only one male who could protect them from the harassment of other males (Brotherton et al., 1997). Another mammalian example of the mate-guarding route to social monogamy is the mara (*Dolichotis patagonum*), a large rodent that relies on a swiftly depleted, slowly replenished, and patchily dispersed food supply during the wet season. Like dik-dik females, mara females experienced a short fertility period of only a few hours that lead to male mate guarding as a male's most successful reproductive strategy (Taber & Macdonald, 1992).

When males protect a female and offspring from predators

Protecting offspring and females from predator attacks, and remaining vigilant while the female forages, has been offered as an explanation for the evolution of social monogamy in klipspringer (*Oreotragus oreotragus*; Dunbar & Dunbar, 1980; Roberts & Dunbar, 2000). The predation rate is high in this species, and both sexes alternate in watching for predators. However, males were more vigilant and they also detected predators earlier, thus allowing females to forage more efficiently (Dunbar & Dunbar, 1980). A second example is the Malagasy giant jumping rat (*Hypogeomys antimena*), a large rodent endemic to Madagascar. During a period of annual peak predation, male but not female rats showed behaviours leading to an increase in predator contacts, indicating that males played an important role in trying to protect offspring from predators (Sommer, 2000). The influence of predation on the evolution of social monogamy in birds remained difficult to assess because no specific evidence was found in support of this route to social monogamy.

Few examples supported the predicted causal link between predation pressure and the evolution of social monogamy. Nonetheless, predation represents a strong selective force in the lives of animals (Alexander, 1974) and it is possible, for example, that predation protection evolved secondarily after socially monogamous pair relationships were already in place (cf. Roberts & Dunbar, 2000; Brotherton & Komers, chapter 3). Further studies are needed that test whether male predation protection was a selective force for the evolution of social monogamy in some species or if it evolved as a consequence of pair living.

When males defend an exclusive food resource

Although this hypothesis is commonly included among those proposed for the evolution of socioreproductive monogamy (Wittenberger & Tilson, 1980; Rutberg, 1983), convincing empirical support is largely absent. The resource-defence hypothesis predicts that all intruders in a territory are evicted by the male, irrespective of whether the intruders are male or female. Without this level of intervention, a resident female would lose the benefit of her pair-mate's territorial defence. Territorial male defence was suggested as the origin for social monogamy in gibbons (Rutberg, 1983; Leighton, 1987); however, contrary to the prediction, territorial

aggression was found to be mainly sex-specific (Mitani, 1984; Cowlshaw, 1992; Reichard & Sommer, 1997; Reichard, chapter 13).

This hypothesis is questionable because it assumes that socially monogamous males were unable to defend an area large enough to encompass two or more separate female ranges. Because otherwise, males would be expected to become socioreproductively polygynous. Socioreproductive polygyny would also benefit female interests since it further reduces male feeding competition. Furthermore, Komers and Brotherton (1997) showed that at least mammalian socially monogamous female home range sizes were smaller compared to home range sizes of individual socially polygynous females, which would also facilitate the evolution of socioreproductive polygyny instead of social monogamy.

The only possible examples where resource exploitation and perhaps male defence of a feeding territory may have played an important role in the evolution of social monogamy were found in Blanford's foxes (*Vulpes cana*) and the beaver (*Castor fiber*). Blanford's foxes are small, nocturnal canids that live in marginally overlapping territories. Their specialised, insectivorous diet is mainly found in dry creekbeds (Geffen & Macdonald, 1992), and this dependence on such a specific insect prey usually does not permit them to forage in groups of more than two adult individuals. Adding a breeding female to a group would require a considerable increase in territory size and would probably result in higher territorial defence costs for the male than benefits he would derive from socioreproductive polygyny (Geffen & Macdonald, 1992). Beavers (*Castor fiber*) consume a specialised diet comprised of deciduous tree species with comparatively low nutritional value and a slow re-growth rate. Providing enough food for offspring during winter months requires collecting plant material from a large territory. Maintaining a large-size territory is an important male task, although females also engage in territorial behaviour, both of which probably limit beaver males to social monogamy (Sun, chapter 9).

The hypothesis that males defend a feeding territory for females and offspring, a strategy that increases male reproductive success beyond that of alternative strategies, due to an increased female reproductive rate, still awaits convincing empirical support. Although under specific conditions male territorial defence provides females and offspring with access to an exclusive resource, the causal link to social monogamy still must be

quantitatively validated. Similar to some other explanations, it appears possible that male territorial defence in socially monogamous animals evolved secondarily.

When males protect females and offspring from harassment and infanticide

The hypothesis suggests that the threat of male harassment, and particularly the risk of infanticide in infant-carrying species, may have selected for the evolution of social monogamy (van Schaik & Kappeler, 1993, 1997, chapter 4).

Support for the hypothesis comes from observations of waterfowl, where paired males tried to protect and shield females from harassment by other males (McKinney et al., 1984). Male harassment is potentially costly. In ducks, for example, forced copulation can lead to female death (McKinney & Stolen, 1982). For mammals, van Schaik and Dunbar (1990) and recently van Schaik and Kappeler (1993, 1997, chapter 4) suggested that year-round male-female association (including social monogamy) evolved in infant-carrying species in response to the risk of infanticide. There are examples of male infanticide in birds and mammals (Crook & Shields, 1985; Freed, 1986; Møller, 1994; van Schaik & Janson, 2000). However, a convincing example for the causal link between infanticide and social monogamy is still missing. On the other hand, that the suggested evolutionary step to uniform socially monogamous male-female pairs was caused by the threat of infanticide cannot yet be excluded (van Schaik & Kappeler, chapter 4). So far, only indirect circumstantial evidence supports the hypothesis (see Reichard, chapter 13) and further tests are necessary to evaluate the importance of male infanticide risk for the evolution of monogamy.

SEXUAL CONFLICT AND SOCIAL MONOGAMY

Under social monogamy, it is more likely to be assumed that the sexes have identical interests, perhaps because pair partners usually maintain close spatial association and often perform spectacular, well co-ordinated, pair-specific display behaviour before, during, and after pairing (e.g., duetting, Haimoff, 1986; tail-twining, Anzenberger, 1988; pair dancing, Vincent, 1995). Where male care is considered essential for females to achieve any reproductive success, male and female

interests are probably closest and both sexes may benefit equally from socioreproductive monogamy (cf. Birkhead & Møller, 1996; Figure 1.1). Outside this scenario, however, adopting an idealised view of harmonious, monogamous pair relationships where partners share mutual socioreproductive interests is probably misleading (cf. Parker, 1984; Davies, 1989; Gowaty, 1996a) for at least two reasons. First, assuming shared interests that lead to social monogamy is just one possible evolutionary pathway to social monogamy, as shown above (see also Wittenberger & Tilson, 1980; Wickler & Seibt, 1981). Second, pair formation is not equivalent to an absence of sexual conflict, and the costs and benefits of mating may be asymmetric for males and females (Parker, 1979, 1984). Conflict of interests between pair partners may arise over the duration and intensity of sociosexual relationship(s), particularly the frequency of mating, as well as parental duties. Also, in socially monogamous relationships individuals are expected to take advantage of their social partner's contributions whenever possible (Trivers, 1972; Davies, 1989; Lessells, 1999; Johnstone & Keller, 2000; Royle et al., 2002).

An especially informative example that demonstrates the dynamics of sexual conflict and its resolution is given by Davies' (1992) study of the dunnock (*Prunella modularis*). Dunnocks show a variable mating system in which social monogamy, social polygyny, social polygynandry and social polyandry occur (Davies & Lundberg, 1984). Davies (1989, 1992) could show that females achieve highest reproductive success with cooperative social polyandry and least with social polygyny, whereas the opposite held for males, which achieved highest success with social polygyny and lowest with cooperative polyandry. Depending on varying ecological conditions and power symmetries, individuals were able to achieve their preferred option, despite the conflicting preferences of others, resulting in various social compositions (Davies, 1989).

Potential sexual conflict also characterises most pathways to social monogamy in Figure 1.1. Expected optima, representing the socioreproductive strategy with the theoretically greatest payoff for male and female, were presented below each pathway to social monogamy and shaded grey boxes were put around optima to visualise where the compromise (social monogamy) potentially conflicted with preferred options. 'Optimal social strategies' were derived from sexual

selection theory and adapted, where necessary, to particular conditions (e.g., assumed optimal strategies for paired versus unpaired individuals varied). Sociosexual polygyny was principally assumed to be an optimal male strategy whereas sociosexual monogamy or sociosexual polyandry were the assumed optimal female strategies (cf. Parker, 1984).

Most pathways to the social-monogamy-compromise conflicted with the 'optimal strategies' of one or both sexes. Only where biparental care and infanticide protection were important factors did social monogamy coincide with the greatest payoff for both sexes (Figure 1.1). Hence, these appear as the clearest pathways along which social monogamy is expected to correspond to genetic monogamy given the sexes' shared interests. In contrast, when optimal reproductive interests of one or both partners do not overlap with social monogamy, further conflict between the sexes on the sexual and genetic level is expected. Different pathways contain the potential for different conflicts along the evolutionary routes to social monogamy, and may explain the variations between the social and the genetic system of socially monogamous species that were identified in the 1990s and early 2000s (cf. Petrie & Kempenaers, 1998; Petrie et al., 1998; Hasselquist & Sherman, 2001).

CONCLUSIONS

Social monogamy does not evolve from a common, single origin but arises independently through different evolutionary pressures and along different pathways in different lineages. Social monogamy in birds and mammals, including humans, represents just one possible outcome of the compromise between the reproductive interests and strategies of the sexes under specific conditions. The three components that influence the occurrence of social monogamy are: the magnitude of paternal care, the mode of resource access, and mate choice. These components interact with each other and produce ten distinct pathways to social monogamy, most of which are supported by empirical studies. The evolution of social monogamy in different animal groups is the focus of the first part of this book (chapters 2 -5).

Parts II and III focus on the reproductive strategies of males and females. With the exception of chapters 11 and 16, the authors focus on a particular species or taxon (chapter 15) to identify the specific conditions and

evolutionary pressure(s) responsible for social monogamy and corresponding genetic mating systems, as well as how those systems are maintained.

The influence of paternal care on the evolution of social monogamy has always been an important focus (cf. Kleimann, 1977; Wittenberger & Tilson, 1980). Where paternal care becomes highly important it may directly lead to social monogamy. But, paternal care often plays a more subtle role along the routes to social monogamy and depends largely on the balance between the amount of care provided by males and how much is needed or wanted by females. Whenever direct or indirect paternal investment in offspring is important for female reproductive success it will influence whether or not females are willing to share a male with another female. Similarly, under certain conditions, males may avoid sharing a female, and in both cases, if either of two prime preconditions are met, social monogamy is expected to evolve. Females must live nongregariously in separate ranges, or males must defend resources that are important to females, which are often territories. The conditions of females living apart from each other and males defending a territory represent basic male and female strategies to maximise access to the resources relevant for their respective reproduction and to lay the foundation of the pathways to social monogamy. Part of the dialogue presented here is an interesting difference that emerged between birds and mammals. Males defending resources necessary for females appears to be a more frequent starting point for the evolution of bird social monogamy, whereas females living in separate ranges appears to be a more common starting point for the evolution of social monogamy in mammals. If this assumption holds, it may explain why more socially monogamous mammals are also genetically monogamous (Foltz, 1981; Ribble, 1991; Heller et al., 1993; Brotherton et al., 1997; Sommer & Tichy, 1999) than are socially monogamous birds because a greater potential for the sexes to share a monogamous reproductive interest exists when females live apart than when males occupy territories as a way to attract a mating partner (see Figure 1.1). The hypothesis, that the discrepancy between social and genetic mating system may be predicted by evolutionary pathways to social monogamy and the intensity of sexual conflict will have to be scrutinised with further studies.

This volume's approach to social monogamy builds on and extends earlier concepts of the evolution of

monogamy (cf. Emlen & Oring, 1977; Wittenberger, & Tilson, 1980) because it integrates pathways rarely considered in a comprehensive framework. In the classical approach of Emlen and Oring (1977), the evolution of social monogamy was reduced to two elements: (1) neither sex has the opportunity to monopolise additional members of the opposite sex, and (2) the absence of an environmental potential for polygamy. It has since become clear that additional avenues to social monogamy do exist. As shown by Davies (1992), the outcome of social conflict may be just as important as ecological factors in shaping social monogamy and other social arrangements. Even when the polygyny-threshold is exceeded, social monogamy may evolve because payoff expectations for involved individuals vary, influencing their mate choice and reproductive decisions accordingly. The classical four or five explanations for the evolution of social monogamy (cf. Wittenberger & Tilson, 1980; Clutton-Brock, 1989) were refined to incorporate specific conditions favouring the evolution of social monogamy, like the threat of infanticide (van Schaik & Dunbar, 1990) or the influence of individual quality variation.

Because models of the mating system's evolution still appear to be biased by a single-sex perspective, additional research is needed. Identifying ecological factors and tracing individual decisions that may lead to social monogamy is difficult enough in one sex. However, to fully understand what shapes social monogamy, male and female perspectives must be combined. Furthermore, the interplay between the sexes' interests, on the social, sexual, and reproductive levels, as well as resolutions of the conflicts between them, must be examined in more detail. These studies should test for what the optimal strategies for each sex would look like and what constraints may exist, and should then analyse how these aspects correspond to compromises between partners. Furthermore, it will be important to look at the interplay between factors like paternal care and individual quality, which may produce varying affects along the steps to social monogamy, in order to better understand individual behavioural variation on the levels of social-, sexual- and genetic partnerships. For example, in male care, at what cut-off point in relation to a female's needs does a female resist the arrival of a second female on her breeding ground, and how does this influence (additional?) male parental behaviour? Or, what are the necessary female quality characters that allow for social variation within

a population? The answers to questions like these will be critical if the fine structure of social monogamy is to be clearly understood.

Since the 1980s, the gross settings in which social monogamy can evolve have been identified. However, information on the finely-tuned evaluations of individual decisions about whether or not to establish socially monogamous relationships, with whom, and for how long are still relevant lines to pursue. An interesting area for continued research on social monogamy and its corresponding genetic systems is the variation in individual female quality (cf. Hoi-Leitner et al., 1999; Forstmeier et al., 2001). Because the opportunity to increase reproductive success via the number of breeding partners is limited when individuals live predominantly in socially monogamous units, variation in individual quality may become an increasingly important factor (Anderson, 1994). The present model has begun to recognise and integrate individual quality variation on a theoretical level, and future research will evaluate how important this aspect is for the origin and maintenance of social monogamy.

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References

- Ahnesjö, I., Vincent, A., Alatalo, R. V., Halliday, T. & Sutherland, W. J. (1993). The role of females in influencing mating patterns. *Behavioral Ecology*, **4**, 187-9.
- Alatalo, R. V., Gottlander, K. & Lundberg, A. (1987). Extra-pair copulations and mate guarding in the polyterritorial pied flycatcher, *Ficedula hypoleuca*. *Behaviour*, **101**, 139-55.
- Alatalo, R. V., Lundberg, A. & Glynn, C. (1986). Female pied flycatchers choose territory quality and not male characteristics. *Nature*, **323**, 152-3.
- Alexander, R. D. (1974). The evolution of social behaviour. *Annual Review of Ecology and Systematics*, **5**, 325-83.
- Altmann, J. (1990). Primate males go where the females are. *Animal Behaviour*, **39**, 193-5.
- Andelman, S. J. (1986). Ecological and social determinants of cercopithecine mating patterns. In *Ecological Aspects of Social Evolution: Birds and Mammals*, ed. D. Rubenstein & R. Wrangham, pp. 201-16. Princeton: Princeton University Press.
- Anderson, M. (1994). *Sexual Selection*. Princeton: Princeton University Press.
- Anzenberger, G. (1988). The pair bond in the titi monkey (*Callicebus moloch*): intrinsic versus extrinsic contributions of the pairmates. *Folia Primatologica*, **50**, 188-203.
- Arceese, P. (1989). Intrasexual competition and the mating system in primarily monogamous birds: the case of the song sparrow. *Animal Behaviour*, **38**, 96-111.
- Baker, R. R. (1983). Insect territoriality. *Annual Review of Entomology*, **28**, 65-89.
- Baker, A. J. & Dietz, J. M. (1996). Immigration in wild groups of golden lion tamarins (*Leontopithecus rosalia*). *American Journal of Primatology*, **38**, 47-56.
- Barlow, G. W. (1988). Monogamy in relation to resources. In *The Ecology of Social Behaviour*, ed. C. N. Slobodchikoff, ed., pp. 55-79. London: Academic Press.
- Bart, J. & Tornes, A. (1989). Importance of monogamous birds in determining reproductive success. *Behavioral Ecology and Sociobiology*, **24**, 109-16.
- Bateman, A. J. (1948). Intra-sexual selection in *Drosophila*. *Heredity*, **2**, 349-68.
- Beecher, M. D. & Beecher, I. M. (1979). Sociobiology of bank swallows: reproductive strategy of the male. *Science*, **205**, 1282-85.
- Berteaux, D., Bêty, J., Regifo, E. & Bergeron, J.-M. (1999). Multiple paternity in meadow voles (*Microtus pennsylvanicus*) investigating the role of the female. *Behavioral Ecology and Sociobiology*, **45**, 283-91.
- Birkhead, T. R. & Møller, A. P. (1992). *Sperm Competition in Birds: Evolutionary Causes and Consequences*. London: Academic Press.
- Birkhead, T. R. & Møller, A. P. (1993). Female control of paternity. *Trends in Ecology and Evolution*, **8**, 100-4.
- Birkhead, T. R. & Møller, A. P. (1995). Extra-pair copulations and extra-pair paternity in birds. *Animal Behaviour*, **49**, 843-48.
- Birkhead, T. R. & Møller, A. P. (1996). Monogamy and sperm competition in birds. In *Partnerships in Birds: The Study of Monogamy*, ed. J. M. Black, pp. 323-43. Oxford: Oxford University Press.
- Birkhead, T. R. & Møller, A. P. (1998). *Sperm Competition and Sexual Selection*. London: Academic Press.
- Birkhead, T. R., Atkin, L. & Møller, A. P. (1987). Copulation behaviour of birds. *Behaviour*, **101**, 101-38.
- Black, J. M. (1996). Pair bonds and partnerships. In *Partnerships in Birds: The Study of Monogamy*, ed. J. M. Black, pp. 3-20. Oxford: Oxford University Press.
- Black, J. M. & Owen, M. (1989). Parent-offspring relationships in wintering barnacle geese. *Animal Behaviour*, **37**, 187-98.

- Black, J. M., Choudhury, S. & Owen, M. (1996). Do Barnacle Geese benefit from lifelong monogamy? In *Partnerships in Birds: The Study of Monogamy*, ed. J. M. Black, pp. 91-117. Oxford: Oxford University Press.
- Blumstein, D. T. (2000). The evolution of infanticide in rodents: a comparative analysis. In *Infanticide by Males and its Implications*, ed. C. P. van Schaik & C. H. Janson, pp. 178-197. Cambridge: Cambridge University Press.
- Blurton Jones, N. G., Marlowe, F. W., Hawkes, K. & O'Connell, J. F. (2000). Paternal investment and hunter-gatherer divorce rates. In *Adaptation and Human Behavior*, ed. L. Cronk, N. Chagnon & W. Irons, pp. 69-90. New York: Aldine de Gruyter.
- Borgerhoff Mulder, M. (1990). Kipsigis women's preferences for wealthy men: evidence for female choice in mammals? *Behavioral Ecology and Sociobiology*, **27**, 255-64.
- Bray, O. E., Kennely, J. K. & Guareno, J. K. (1975). Fertility of eggs produced on territories of vasectomized re-winged blackbirds. *Wilson Bulletin*, **87**, 187-95.
- Brockelman, W. Y. & Srikosamatara, S. (1984). Maintenance and evolution of social structure in gibbons. In *The Lesser Apes: Evolutionary and Behavioural Biology*, ed. H. Preuschoft, D. J. Chivers, W. Y. Brockelman & N. Creel, pp. 298-323. Edinburgh: Edinburgh University Press.
- Brockelman, W. Y., Reichard, U., Treesucon, U. & Raemaekers, J. J. (1998). Dispersal, pair formation and social structure in gibbons (*Hylobates lar*). *Behavioral Ecology and Sociobiology*, **42**, 329-39.
- Brotherton, P. N. M. & Manser, M. B. (1997). Female dispersion and the evolution of monogamy in the dik-dik. *Animal Behaviour*, **54**, 1413-24.
- Brotherton, P. N. M. & Rhodes, A. (1996). Monogamy without biparental care in a dwarf antelope. *Proceedings of the Royal Society of London, Series B: Biological Sciences*, **263**, 23-9.
- Brotherton, P. N. M., Pemberton, J. M., Komers, P. E. & Malarkey, G. (1997). Genetic and behavioural evidence of monogamy in a mammal, Kirk's dik-dik (*Madoqua kirkii*). *Proceedings of the Royal Society of London, Series B: Biological Sciences*, **264**, 675-81.
- Bull, C. M., Cooper, S. J. B. & Baghurst, B. C. (1998). Social monogamy and extra-pair fertilization in an Australian lizard, *Tiliqua rugosa*. *Behavioral Ecology and Sociobiology*, **44**, 63-72.
- Burley, N. T. & Johnson, K. (2002). The evolution of avian parental care. *Philosophical Transactions of the Royal Society of London, Series B: Biological Sciences*, **357**, 241-50.
- Carranza, J., Alvarez, F. & Redondo, T. (1990). Territoriality as a mating strategy in red deer. *Animal Behaviour*, **40**, 79-88.
- Catry, P., Ratcliff, N. & Furness, R. W. (1997). Partnerships and mechanisms of divorce in the great skua. *Animal Behaviour*, **54**, 1475-82.
- Chapman, T. & Partridge, L. (1996). Sexual conflict as fuel for evolution. *Nature*, **381**, 189-90.
- Clutton-Brock, T. H. (1989). Mammalian mating systems. *Proceedings of the Royal Society of London, Series B: Biological Sciences*, **236**, 339-72.
- Clutton-Brock, T. H. (1991). *The Evolution of Parental Care*. Princeton: Princeton University Press.
- Clutton-Brock, T. H. & Harvey, P. H. (1977). Primate ecology and social organization. *Journal of Zoology*, **183**, 1-39.
- Clutton-Brock, T. H. & Parker, G. A. (1992). Potential reproductive rates and the operation of sexual selection. *Quarterly Reviews in Biology*, **67**, 437-56.
- Cowlshaw, G. (1992). Song function in Gibbons. *Behaviour*, **121**, 131-53.
- Crook, J. R. & Shields, W. M. (1985). Sexually selected infanticide by adult male barn swallows. *Animal Behaviour*, **33**, 754-61.
- Davies, N. B. (1989). Sexual conflict and the polygamy threshold. *Animal Behaviour*, **38**, 226-34.
- Davies, N. B. (1991). Mating systems. In *Behavioural Ecology: an Evolutionary Approach*, ed. J. R. Krebs & N. B. Davies, pp. 263-94. Oxford: Blackwell Science Publications.
- Davies, N. B. (1992). *Dunnock Behaviour and Social Evolution*. Oxford: Oxford University Press.
- Davies, N. B. & Lundberg, A. (1984). Food distribution and a variable mating system in the dunnock, *Prunella modularis*. *Journal of Animal Ecology*, **53**, 895-912.
- Desrochers, A. & Magrath, R. D. (1996). Divorce in the European Blackbird: seeking greener pastures? In *Partnerships in Birds: The Study of Monogamy*, ed. J. M. Black, pp. 344-401, Oxford: Oxford University Press.
- Dewsbury, D. A. (1988). The comparative psychology of monogamy. In *Nebraska Symposium on Motivation 1987: Comparative Perspectives in Modern Psychology*, Volume 35, ed. R. A. Dienstbier & D. W. Leger, pp. 1-50. Lincoln: University of Nebraska Press.
- Dietz, J. M. & Baker, A. J. (1993). Polygyny and female reproductive success in golden lion tamarins, *Leontopithecus rosalia*. *Animal Behaviour*, **46**, 1067-78.
- Dunbar, R. I. M. (1995). The mating system of callitrichid primates: I. Conditions for the coevolution of pair bonding and twinning. *Animal Behaviour*, **50**, 1057-70.
- Dunbar, R. I. M. & Dunbar, E. P. (1980). The pairbond in klipspringer. *Animal Behaviour*, **28**, 219-29.
- Emlen, S. T. & Oring, L. W. (1977). Ecology, sexual

- selection and the evolution of mating systems. *Science*, **197**, 215-23.
- Ens, B., Choudhury, S. & Black, J. M. (1996). Mate fidelity and divorce in monogamous birds. In *Partnerships in Birds: The Study of Monogamy*, ed. J. M. Black, pp. 344-401, Oxford: Oxford University Press.
- Eckmann, W. J. (1983). The evolution of polyandry in shorebirds: an evaluation of hypotheses. In *Social Behavior of Female Vertebrates*, ed. S. K. Wasser, pp. 113-68. New York: Academic Press.
- Ferron, J. & Ouellet, J. P. (1989). Temporal and intrasexual variations in the use of space with regards to social organization in the woodchuck (*Marmota monax*). *Canadian Journal of Zoology*, **67**, 1642-9.
- Fietz, J. (1999a). Monogamy as a rule rather than exception in nocturnal lemurs: The case of the fat-tailed dwarf lemur, *Cheirogaleus medius*. *Ethology*, **105**, 259-72.
- Fietz, J. (1999b). Demography and floating males in a population of *Cheirogaleus medius*. In *New Directions in Lemur Studies*, ed. B. Rakotosamimanana, H. Rasaminanana & J. U. Ganzhorn, pp. 159-72. New York: Kluwer Academic/Plenum Public.
- Fietz, J., Zischler, H., Schwiegg, C., Tomiuk, J., Danzman, K. H. & Ganzhorn, J. U. (2000). High rates of extra-pair young in the pair-living fat-tailed dwarf lemur, *Cheirogaleus medius*. *Behavioral Ecology and Sociobiology*, **49**, 8-17.
- Fisher, D. O. & Owens, I. P. F. (2000). Female home range size and the evolution of social organization in macropod marsupials. *Journal of Animal Ecology*, **69**, 1083-98.
- Foltz, D. W. (1981). Genetic evidence for long-term monogamy in a small rodent, *Peromyscus polionotus*. *American Naturalist*, **117**, 665-75.
- Forstmeier, W., Leisler, B. & Kempnaers, B. (2001). Bill morphology reflects female independence from male parental help. *Proceedings of the Royal Society of London, Series B: Biological Sciences*, **268**, 1583-8.
- Freed, L. A. (1986). Territory takeover and sexually selected infanticide in tropical house wrens. *Behavioral Ecology and Sociobiology*, **19**, 197-206.
- Freed, L. A. (1987). The long-term pair bond of tropical house wrens: advantage or constraint? *American Naturalist*, **130**, 507-25.
- Geffen, E. & Macdonald, D. W. (1992). Small size and monogamy: spatial organization of Blanford's foxes, *Vulpes cana*. *Animal Behaviour*, **44**, 1123-30.
- Getz, L. L., Hofmann, J. E. & Carter, C. S. (1987). Mating systems and fluctuations of the prairie vole, *Microtus ochrogaster*. *American Journal of Zoology*, **27**, 909-20.
- Gladstone, D. E. (1979). Promiscuity in monogamous colonial birds. *American Naturalist*, **114**, 545-57.
- Goldizen, A. W. (1987). Facultative polyandry and the role of infant-carrying in wild saddle-back tamarins (*Saguinus fuscicollis*). *Behavioral Ecology and Sociobiology*, **20**, 99-109.
- Goossens, B., Graziani, L., Waits, E. F., Magnolon, S., Coulon, J., Bel, M.-C., Taberlet, P. & Allainé, D. (1998). Extra-pair paternity in the monogamous Alpine marmot revealed by nuclear DNA microsatellite analysis. *Behavioral Ecology and Sociobiology*, **43**, 281-8.
- Gosling, L. M. (1986). The evolution of mating strategies in male antelopes. In *Ecological Aspects of Social Evolution: Birds and Mammals*, ed. D. Rubenstein & R. Wrangham, pp. 244-81. Princeton: Princeton University Press.
- Gowaty, P. A. (1996a). Battles of the sexes and origins of monogamy. In *Partnerships in Birds: The Study of Monogamy*, ed. J. M. Black, pp. 21-52. Oxford: Oxford University Press.
- Gowaty, P. A. (1996b). Multiple mating by females selects for males that stay: another hypothesis for social monogamy in passerine birds. *Animal Behaviour*, **51**, 482-4.
- Gowaty, P. A. (1996c). Field studies of parental care in birds: new data focus questions on variation in females. In *Advances in the Study of Behavior*, Volume 25, ed. C. T. Snowdon & J. S. Rosenblatt, pp. 476-531. New York: Academic Press.
- Green, K., Mitchell, A. T. & Tennant, P. (1998). Home range and microhabitat use by the long-footed potoroo, *Potorous longipes*. *Wildlife Research*, **25**, 357-72.
- Greenwood, P. J. (1980). Mating systems, philopatry and dispersal in birds and mammals. *Animal Behaviour*, **28**, 1140-1162.
- Gubernick, D. J. (1994). Biparental care and male-female relations in mammals. In *Infanticide and Parental Care*, ed. S. Parmigiani & F. vom Saal, pp. 427-63. London: Harwood Academic Press.
- Gubernick, D. J. & Teferi, T. (2000). Adaptive significance of male parental care in a monogamous mammal. *Proceedings of the Royal Society of London, Series B: Biological Sciences*, **267**, 147-50.
- Haimoff, E. H. (1986). Convergence in the duetting of monogamous Old World primates. *Journal of Human Evolution*, **15**, 51-9.
- Hannon, S. J. (1983). Spacing and breeding density of willow ptarmigan in response to an experimental alteration of sex ratio. *Journal of Animal Ecology*, **52**, 807-20.
- Hannon, S. J. & Dobush, G. (1997). Pairing status of male willow ptarmigan: is polygyny costly to males? *Animal*

- Behaviour*, **53**, 369-80.
- Hannon, S. J. & Martin, K. (1992). Monogamy in willow ptarmigan: is male vigilance important for reproductive success and survival of females? *Animal Behaviour*, **43**, 747-57.
- Hartley, I. R., Davies, N. B., Hatchwell, B. J., Desrouchers, A., Nebel, D. & Burke, T. A. (1995). The polyandrous mating system of the alpine accentor, *Prunella collaris*. II. Multiple paternity and parental effort. *Animal Behaviour*, **49**, 789-803.
- Hasselquist, D. S. & Sherman, P. W. (2001). Social mating systems and extrapair fertilizations in passerine birds. *Behavioral Ecology*, **12**, 457-66.
- Hatchwell, B. J., Russell, A. F. & Ross, D. J. (2000). Divorce in cooperatively breeding long-tailed tits: a consequence of inbreeding avoidance? *Proceedings of the Royal Society of London, Series B: Biological Science*, **267**, 813-9.
- Hausfater, G. & Hrdy, S. B. (1984). *Infanticide. Comparative and Evolutionary Perspectives*. New York: Aldine.
- Heller, K.-G., Achmann, R. & Witt, K. (1993). Monogamy in the bat *Rinolophus sedulus*? *Zeitschrift für Säugetierkunde*, **58**, 376-7.
- Hendrichs, H. (1975). Changes in a population of Dikdik, *Madoqua (Rhynchotragus) kirki* (Gunther 1880). *Zeitschrift für Tierpsychologie*, **38**, 55-69.
- Heymann, E. W. (2000). The number of adult males in callitrichine groups and its implications for callitrichine social evolution. In *Primate Males. Causes and Consequences of Variation in Group Composition*, ed. P. M. Kappeler, pp. 159-68. Cambridge, Cambridge University Press.
- Hoi-Leitner, M. H., Hoi, H., Romero-Pujante, M & Valera, F. (1999). Female extra-pair behaviour and environmental quality in the serin (*Serinus serinus*): a test of the 'constrained female hypothesis'. *Proceedings of the Royal Society of London, Series B: Biological Sciences*, **266**, 1021-6.
- Hrdy, S. B. (1979). Infanticide among animals: a review, classification, and examination of the implications for the reproductive strategies of females. *Ethology and Sociobiology*, **1**, 13-40.
- Hrdy, S. B. (1986). Empathy, polyandry, and the myth of the coy female. In *Feminist Approaches to Science*, ed. R. Bleier, pp. 119-46. New York: Pergamon Press.
- Hrdy, S. B., Janson, C. & van Schaik, C. P. (1995). Infanticide: let's not throw out the baby with the bath water. *Evolutionary Anthropology*, **3**, 151-4.
- Hughes, C. (1998). Integrating molecular techniques with field methods in studies of social behavior: a revolution results. *Ecology*, **79**, 383-99.
- Isbell, L. A. (1994). Predation on primates: ecological patterns and evolutionary consequences. *Evolutionary Anthropology*, **3**, 61-71.
- Jamieson, I. G. (1997). Testing reproductive skew models in a communally breeding bird, the pukeko, *Porphyrio porphyrio*. *Proceedings of the Royal Society of London, Series B: Biological Sciences*, **264**, 335-40.
- Janson, C. H. (1992). Evolutionary ecology of primate social structure. In *Evolutionary Ecology and Human Behavior*, ed. E. A. Smith & B. Winterhalder, pp. 95-130. New York: Aldine de Gruyter.
- Jeffreys, A. J., Wilson, V. & Thein, S. L. (1985). Hypervariable "minisatellite" regions in human DNA. *Nature*, **314**, 67-73.
- Johnstone, R. A. & Keller, L. (2000). How males can gain by harming their mates: sexual conflict, seminal toxins, and the cost of mating. *American Naturalist*, **156**, 368-77.
- Keane, B., Waser, P. M., Creel, S. R., Creel, N. M., Elliott, L. F. & Minchella, D. J. (1994). Subordinate reproduction in dwarf mongooses. *Animal Behaviour*, **47**, 65-75.
- Kempnaers, B. (1997). Does reproductive synchrony limit male opportunities or enhance female choice for extra-pair paternity. *Animal Behaviour*, **134**, 551-62.
- Kempnaers, B., Everding, S., Bishop, C., Boag, P. & Robertson, R. J. (2001). Extra-pair paternity and the role of male floaters in the tree swallow (*Tachycineta bicolor*). *Behavioral Ecology and Sociobiology*, **49**, 251-9.
- Kempnaers, B., Verheyen, G. R., van den Broeck, M., Burke, T., van Broeckhoven, C. & Dhondt, A. A. (1992). Extra-pair paternity results from female preferences for high-quality males in the blue tit. *Nature*, **357**, 494-6.
- Kishimoto, R. & Kawamichi, T. (1996). Territoriality and monogamous pairs in a solitary ungulate, the Japanese serow, *Capricornis crispus*. *Animal Behaviour*, **52**, 673-682.
- Kleiman, D. G. (1977). Monogamy in mammals. *Quarterly Review of Biology*, **52**, 39-69.
- Kleiman, D. G. & Malcolm, J. R. (1981). The evolution of male paternal investment in mammals. In *Paternal Care in Mammals*, ed. D. J. Gubernick & P. H. Klopfer, pp. 347-87. New York: Plenum Press.
- Kokita, T. (2002). The role of the female behavior in maintaining monogamy of a coral-reef fish. *Ethology*, **108**, 157-68.
- Komers, P. E. & Brotherton, P. N. M. (1997). Female space use is the best predictor of monogamy in mammals. *Proceedings of the Royal Society of London, Series B: Biological Sciences*, **264**, 1261-70.
- Lack, D. (1968). *Ecological Adaptations for Breeding in Birds*. London: Methuen Press.
- Leighton, D. R. (1987). Gibbons: territoriality and monogamy. In *Primate Societies*, ed. B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham & T. T. Struhsaker, pp. 135-45. Chicago: University of Chicago Press.
- Lessells, C. M. (1999). Sexual conflict in animals. In *Levels*

- of *Selection in Evolution*, ed. L. Keller, pp. 75-99. Princeton: Princeton University Press.
- Ligon, J. D. (1999). *The Evolution of Avian Breeding Systems*. Oxford: Oxford University Press.
- Malcolm, J. R. (1985). Paternal care in canids. *American Zoologist*, **25**, 853-9.
- Marlowe, F. (2000). Paternal investment and the human mating system. *Behavioural Processes*, **51**, 45-61.
- McKinney, F. (1986). Ecological factors influencing the social systems of migratory dabbling ducks. In *Ecological Aspects of Social Evolution: Birds and Mammals*, ed. D. Rubenstein & R. Wrangham, pp. 153-71. Princeton: Princeton University Press.
- McKinney, F. & Stolen, P. (1982). Extra-pair-bond courtship and forced copulation among captive green-winged teal (*Anas crecca caolinensis*). *Animal Behaviour*, **30**, 461-74.
- McKinney, F., Cheng, K. M. & Bruggers, D. J. (1984). Sperm competition in apparently monogamous birds. In *Sperm Competition and the Evolution of Animal Mating Systems*, ed. R. L. Smith, pp. 523-45. London: Academic Press.
- Mitani, J. C. (1984). The behavioural regulation of monogamy in gibbons (*Hylobates muelleri*). *Behavioral Ecology and Sociobiology*, **15**, 225-9.
- Mitani, J., Gros-Louis, J. & Manson, J. H. (1996). Number of males in primate groups: comparative tests of competing hypotheses. *American Journal of Primatology*, **38**, 315-32.
- Mock, D. W. (1985). An introduction to the neglected mating system. In *Avian Monogamy. Ornithological Monographs*, Volume 37, ed. P. A. Gowaty & D. W. Mock, pp. 1-10.
- Mock, D. W. & Fujioka, M. (1990). Monogamy and long-term pair bonding in vertebrates. *Trends in Ecology and Evolution*, **5**, 39-43.
- Moehlman, P. D. (1989). Intraspecific variation in canid social systems. In *Carnivore Behavior, Ecology, and Evolution*, ed. J. L. Gittleman, pp. 143-63. New Jersey: Cornell University Press.
- Møller, A. P. (1988a). Infanticidal and anti-infanticidal strategies in the swallow *Hirundo rustica*. *Behavioral Ecology and Sociobiology*, **22**, 365-71.
- Møller, A. P. (1988b). Female choice selects for male sexual tail ornaments in the monogamous swallow. *Nature*, **332**, 640-2.
- Møller, A. P. (1994). *Sexual Selection and the Barn Swallow*. Oxford: Oxford University Press.
- Møller, A. P. (1998). Sperm competition and sexual selection. In *Sperm Competition and Sexual Selection*, ed. T. R. Birkhead & A. P. Møller, pp. 55-90. San Diego: Academic Press.
- Møller, A. P. (2000). Male parental care, female reproductive success and extra-pair paternity. *Behavioral Ecology*, **11**, 161-8.
- Murray, B. G. Jr. (1984). A demographic theory on the evolution of mating systems as exemplified by birds. In *Evolutionary Biology*, Volume 18, ed. M. K. Hecht; B. Wallace & G. T. Prance, pp. 71-140. New York: Plenum Press.
- Orians, G. H. (1969). On the evolution of mating systems in birds and mammals. *American Naturalist*, **103**, 589-603.
- Otter, K., Ratcliffe, L., Michaud, D. & Boag, P. T. (1998). Do female black-capped chickadees prefer high-ranking males as extra-pair partners. *Behavioral Ecology and Sociobiology*, **43**, 25-36.
- Parker, G. A. (1974). Courtship persistence and female-guarding as male time investment strategies. *Behaviour*, **48**, 157-84.
- Parker, G. A. (1979). Sexual selection and sexual conflict. In *Sexual Selection and Reproductive Competition in Insects*, ed. M. S. Blum & N. A. Blum, pp. 123-66. New York: Academic Press.
- Parker, G. A. (1984). Sperm competition and the evolution of animal mating strategies. In *Sperm Competition and the Evolution of Animal Mating Systems*, ed. R. L. Smith, pp. 1-59. London: Academic Press.
- Parker, G. A., Baker, R. R. & Smith, V. G. F. (1972). The origin and evolution of gamet dimorphism and the male-female phenomenon. *Journal of Theoretical Biology*, **36**, 529-33.
- Petrie, M. & Kempenaers, B. (1998). Why does the proportion of extra-pair paternity in birds vary between species and between populations? *Trends in Ecology and Evolution*, **13**, 52-8.
- Petrie, M., Doums, C. & Møller, A. P. (1998). The degree of extra-pair paternity increases with genetic variability. *Proceedings of the National Academy of Sciences USA*, **95**, 9390-5.
- Pizzari, T. & Birkhead, T. R. (2000). Female feral fowl eject sperm of subdominant males. *Nature*, **405**, 787-9.
- Pribil, S. & Picman, J. (1996). Polygyny in the red-winged blackbird: do females prefer monogamy or polygamy? *Behavioral Ecology and Sociobiology*, **38**, 183-90.
- Pribil, S. & Searcy, W. A. (2001). Experimental confirmation of the polygyny threshold model for red-winged blackbirds. *Proceedings of the Royal Society of London, Series B: Biological Sciences*, **268**, 1643-6.
- Rees, E. C., Lievesley P., Pettifor, R. A. & Perrins, C. (1996). Mate fidelity in swans: an interspecific comparison. In *Partnerships in Birds: The Study of Monogamy*, ed. J. M. Black, pp. 118-37. Oxford: Oxford University Press.
- Reichard, U. (1995). Extra-pair copulations in a monogamous gibbon (*Hylobates lar*). *Ethology*, **100**, 99-112.
- Reichard, U. & Sommer, V. (1997). Group encounters in wild gibbons (*Hylobates lar*): agonism, affiliation, and the concept of infanticide. *Behaviour*, **134**, 1135-74.

- Ribble, D. O. (1991). The monogamous mating system of *Peromyscus californicus* as revealed by DNS fingerprinting. *Behavioral Ecology and Sociobiology*, **29**, 161-6.
- Roberts, S. C. & Dunbar, R. I. M. (2000). Female territoriality and the function of scent-marking in a monogamous antelope (*Oreotragus oreotragus*). *Behavioral Ecology and Sociobiology*, **47**, 417-23.
- Royle, N. J., Hartley, I. R. & Parker, G. A. (2002). Sexual conflict reduces offspring fitness in zebra finches. *Nature*, **416**, 733-6.
- Rutberg, A. T. (1983). The evolution of monogamy in primates. *Journal of Theoretical Biology*, **104**, 93-112.
- Sandell, M. & Liberg, O. (1992). Roamers and stayers: a model on male mating tactics and mating systems. *American Naturalist*, **139**, 177-89.
- Sandell, M. & Smith, H. G. (1996). Already mated females constrain male mating success in the European starling. *Proceedings of the Royal Society of London, Series B: Biological Sciences*, **263**, 743-7.
- Sheldon, B. C. (1994). Male phenotype, fertility, and the pursuit of extra-pair copulations by female birds. *Proceedings of the Royal Society of London, Series B: Biological Sciences*, **257**, 25-30.
- Shellman-Reeve, J. S. & Reeve, H. K. (2000). Extra-pair paternity as the result of reproductive transactions between paired mates. *Proceedings of the Royal Society of London, Series B: Biological Sciences*, **267**, 2543-6.
- Sillero-Zubiri, C., Gottelli, D. & Macdonald, D. W. (1996). Male philopatry, extra-pack copulations and inbreeding avoidance in Ethiopian wolves (*Canis simensis*). *Behavioral Ecology and Sociobiology*, **38**, 331-40.
- Slagsvold, T. (1983). Female-female aggression and monogamy in great tits *Parus major*. *Ornis Scandinavica*, **24**, 155-8.
- Slagsvold, T. & Drevon, T. (1999). Female pied flycatchers trade between male quality and mating status in mate choice. *Proceedings of the Royal Society of London, Series B: Biological Sciences*, **266**, 917-21.
- Slagsvold, T. & Lifjeld, J. T. (1994). Polygyny in birds: the role of competition between females for male parental care. *American Naturalist*, **143**, 59-94.
- Slagsvold, T., Amundsen, S., Dale, S. & Lampe, H. (1992). Female-female aggression explains polyterritoriality in male pied flycatchers. *Animal Behaviour*, **43**, 397-407.
- Smiseth, P. T. & Amundsen, T. (1995). Female bluethroats (*Luscinia svecica*) regularly visit territories of extrapair males before egg laying. *Auk*, **112**, 1049-53.
- Snowdon, C. T. (1997). The "nature" of sex differences: myths of male and female. In *Feminism and Evolutionary Biology. Boundaries, Intersections, and Frontiers*, ed. P. A. Gowaty, pp. 276-93. New York: Chapman and Hall.
- Sommer, S. (2000). Sex-specific predation on a monogamous rat, *Hypogeomys antimena* (Muridae: Nesomyinae). *Animal Behaviour*, **59**, 1087-94.
- Sommer, S. & Tichy, H. (1999). Major histocompatibility complex (MHC) class II polymorphism and paternity in the monogamous *Hypogeomys antimena*, the endangered, largest endemic Malagasy rodent. *Molecular Ecology*, **8**, 1259-72.
- Sommer, V. (1994). Infanticide among the langurs of Joghpur - testing the sexual selection hypothesis with a long-term record. In *Infanticide and Parental Care*, ed. S. Parmigiani & F. vom Saal, pp. 155-93. London: Harwood Academic Press.
- Sommer, V. & Reichard, U. (2000). Rethinking monogamy: the gibbon case. In *Primate Males. Causes and Consequences of Variation in Group Composition*, ed. P. M. Kappeler, pp. 159-68. Cambridge: Cambridge University Press.
- Southgate, V. R., Jourdan, J. & Tchuemtchuenté, L. A. (1998). Recent studies on the reproductive biology of the schistosomes and their relevance to speciation in the Digenea. *International Journal of Parasitology*, **28**, 1159-72.
- Spencer, P., Horsup, A. & Marsh, H. (1998). Enhancement of reproductive success through mate choice in a social rock-wallaby, *Pterogale assimilis* (Macropodidae) as revealed by microsatellite markers. *Behavioral Ecology and Sociobiology*, **43**, 1-9.
- Sterck, E. H. M. & Korstjens, A. H. (2000). Female dispersal and infanticide avoidance in primates. In *Infanticide by Males and its Implications*, ed. C. P. van Schaik & C. H. Janson, pp. 293-321.
- Sterling, E. J. & Richard, A. F. (1995). Social organization in the aye-aye (*Daubentonia madagascariensis*) and the perceived distinctiveness of nocturnal primates. In *Creatures of the Dark. The Nocturnal Prosimians*, ed. L. Alterman, G. A. Doyle & M. K. Izard, pp. 439-51. New York: Plenum Press.
- Taber, A. B. & Macdonald, D. W. (1992). Spatial organization and monogamy in the mara, *Dolichotis patagonum*. *Journal of Zoology*, **227**, 417-38.
- Tardif, S. D. (1994). Relative energetic costs of infant care in small bodied Neotropical primates and its relation to infant-care patterns. *American Journal of Primatology*, **34**, 133-43.
- Temrin, H. & Arak, A. (1989). Polyterritoriality and deception in passerine birds. *Trends in Ecology and Evolution*, **4**, 106-9.
- Travis, S. E., Slobodchikoff, C. N. & Keim, P. (1995). Ecological and demographic effects on intraspecific variation in the social system of prairie dogs. *Ecology*, **76**, 1794-1803.
- Travis, S. E., Slobodchikoff, C. N. & Keim, P. (1996). Social assemblages and mating relationships in prairie dogs: a DNA fingerprint analysis. *Behavioral Ecology*, **7**, 95-100.

- Treesucon, U. & Raemaekers, J. J. (1984). Group formation in gibbon through displacement of an adult. *International Journal of Primatology*, **5**, 387.
- Trivers, R. L. (1972). Parental investment and sexual selection. In *Sexual Selection and the Descent of Man 1871-1971*, ed. B. Campbell, pp. 136-79. Chicago: Aldine Press.
- Tullberg, B. S., Ah-King, M. & Temrin, H. (2002). Phylogenetic reconstruction of parental-care systems in the ancestors of birds. *Philosophical Transactions of the Royal Society of London, Series B: Biological Sciences*, **357**, 251-7.
- van Rhijn, J. G. (1991). Mate guarding as a key factor in the evolution of parental care in birds. *Animal Behaviour*, **41**, 963-70.
- van Schaik, C. P. (1983). Why are diurnal primates living in groups. *Behaviour*, **87**, 120-44.
- van Schaik, C. P. (2000a). Infanticide by male primates: the sexual selection hypothesis revisited. In *Infanticide by Males and its Implications*, ed. C. P. van Schaik & C. H. Janson, pp. 27-60. Cambridge: Cambridge University Press.
- van Schaik, C. P. (2000b). Vulnerability to infanticide by males: patterns among mammals. In *Infanticide by Males and its Implications*, ed. C. P. van Schaik & C. H. Janson, pp. 61-72. Cambridge: Cambridge University Press.
- van Schaik, C. P. & Dunbar, R. I. M. (1990). The evolution of monogamy in large primates: a new hypothesis and some crucial tests. *Behaviour*, **115**, 30-62.
- van Schaik, C. P. & Hörstermann, M. (1994). Predation risk and the number of adult males in a primate group: A comparative test. *Behavioral Ecology and Sociobiology*, **35**, 261-72.
- van Schaik, C. P. & Janson, C. H. (2000). *Infanticide by Males and its Implications*. Cambridge: Cambridge University Press.
- van Schaik, C. P. & Kappeler, P. M. (1993). Life history, activity period and lemur social systems. In *Lemur Social Systems and their Ecological Basis*, ed. P. M. Kappeler & J. Ganzhorn, pp. 241-60. New York & London: Plenum Press.
- van Schaik, C. P. & Kappeler, P. M. (1997). Infanticide risk and the evolution of male-female association in primates. *Proceedings of the Royal Society of London, Series B: Biological Sciences*, **264**, 1687-94.
- van Schaik, C. P. & van Hooff, J. A. R. A. M. (1996). Toward an understanding of the orangutan's social system. In *Great Ape Societies*, ed. W. C. McGrew, L. Marchand & T. Nishida, pp. 3-15. Cambridge: Cambridge University Press.
- van Schaik, C. P. & van Noordwijk, M. A. (1989). The special role of male *Cebus* monkeys in predation avoidance and its effect on group composition. *Behavioral Ecology and Sociobiology*, **24**, 265-76.
- Veiga, J. P. (1992). Why are house sparrows predominantly monogamous: a test of hypotheses. *Animal Behaviour*, **43**, 361-70.
- Veiga, J. P. (2000). Infanticide by male birds. In *Infanticide by Males and its Implications*, ed. C. P. van Schaik & C. H. Janson, pp. 189-220. Cambridge: Cambridge University Press.
- Verner, J. (1964). Evolution of polygyny in the long-billed marsh wren. *Evolution*, **18**, 252-61.
- Verner, J. & Willson, M. L. (1966). The influence of habitats on mating systems of North American passerine birds. *Ecology*, **47**, 143-7.
- Vincent, A. C. J. (1995). A role for daily greetings in maintaining seahorse pair bonds. *Animal Behaviour*, **49**, 258-60.
- Wagner, R. H. 1992. The pursuit of extra-pair copulations by monogamous female razorbills: how do females benefit? *Behavioral Ecology and Sociobiology*, **29**, 455-64.
- Wickler, W. & Seibt, U. (1981). Monogamy in Crustacea and Man. *Zeitschrift für Tierpsychologie*, **57**, 215-234.
- Wickler, W. & Seibt, U. (1983). Monogamy: an ambiguous concept. In *Mate Choice*, ed. P. Bateson, pp. 33-50. Cambridge: Cambridge University Press.
- Williams, M. & McKinney, F. (1996). Long-term monogamy in a river specialist the Blue duck. In *Partnerships in Birds: The Study of Monogamy*, ed. J. M Black, pp. 73-90. Oxford: Oxford University Press.
- Williams, T. D. (1996). Mate fidelity in penguins. In *Partnerships in Birds: The Study of Monogamy*, ed. J. M Black, pp. 268-85. Oxford: Oxford University Press.
- Wittenberger, J. F. & Tilson, R. L. (1980). The evolution of monogamy: hypothesis and evidence. *Annual Review of Ecology and Systematics*, **11**, 197-232.
- Wolf, L., Ketterson, E. D. & Nolan, V. Jr. (1988). Paternal influence on growth and survival of dark-eyed junco young: do parental males benefit? *Animal Behaviour*, **36**, 1601-18.
- Woodroffe, R. & Vincent, A. (1994). Mother's little helpers: patterns of male care in mammals. *Trends in Ecology and Evolution*, **9**, 294-7.
- Wrangham, R. W. (1980). An ecological model of female-bonded primate groups. *Behaviour*, **75**, 262-300.
- Wright, P. C. (1990). Patterns of paternal care in primates. *International Journal of Primatology*, **11**, 89-102.
- Wundt, W. (1894). *Lectures on Human and Animal Psychology*. London: Swan Sonnenschein.
- Wynne-Edwards, K. E. (1987). Evidence for obligate monogamy in the Djungarian hamster, *Phodopus campbelli*: pup survival under different parenting conditions. *Behavioral Ecology and Sociobiology*, **20**, 427-37.