

16 Socioecology of Asian Colobines

Elisabeth H. M. Sterck and Tom S. Roth

Introduction

Many diurnal non-human primates live in groups (Sterck et al. 1997), yet these groups show a wide diversity in social organization, mating systems and social structure (Schuelke and Ostner 2012). Socioecological models explain this social diversity using ecological factors (van Schaik 1983, 1989; Sterck et al. 1997; Wrangham 1980; but see Clutton-Brock and Janson 2012), where food competition among females is central. The type of food competition has been linked to female social characteristics (van Schaik 1989; Sterck et al. 1997; Wrangham 1980) and is expected to limit group size (Koenig 2002). However, how folivorous primates like Asian colobines fit in these models has been debated. Several propositions have been made, which will be discussed in detail here. First, in some models folivorous primates are expected to experience only scramble competition (see below; e.g. van Schaik 1989; Sterck et al. 1997), yet this proposition does not fit Nepal sacred langurs (*Semnopithecus schistaceus*: Koenig 2000; Koenig and Borries 2001) and Bengal sacred langurs (*S. entellus*: Borries 1993). Second, folivores are proposed to show no food competition at all (e.g. Isbell 1991; Yeager and Kirkpatrick 1998). Third, the small group sizes often found in folivores are surprising and factors other than food may limit folivores' group size. This has been called the 'Folivore Paradox' (Janson and Goldsmith 1995; Steenbeek and van Schaik 2001). These three propositions lead to different predictions concerning the relationship between female competitive regimes, social relationships and dispersal patterns in the Asian colobines.

First, socioecological models propose a link between ecological factors and female social behaviour. Primates benefit from living in groups since it reduces the risk of predation (Dunbar et al. 2018; Fichtel 2012; van Schaik 1983, 1989) and infanticide (van Schaik and Kappeler 1997; Sterck et al. 1997; Wrangham 1979), but have to balance this with the costs of competition for food. The type of competition depends on the distribution of food sources, where clumped defendable food sources can lead to monopolization within the group or between groups, resulting respectively in contest competition within (within-group contest: WGC) and between (between-group contest: BGC) groups. In addition, scramble competition is found when individuals interfere with the amount group members can eat, yet food sources are not monopolizable. This results in within-group scramble competition (WGS). It has been

This chapter includes Electronic Supplementary Material (ESM) at: www.cambridge.org/colobines

proposed that folivore diets, with their high proportion of leaves, are not monopolizable (Isbell 1991; van Schaik 1983; Wrangham 1980) and will result in WGS (van Schaik 1989; Sterck et al. 1997). The different competition types will affect female social behaviour (van Schaik 1989; Sterck et al. 1997). In folivores, due to a lack of WGC, females are expected to show individual and egalitarian dominance relationships and the ability to disperse between groups. WGC, expected in frugivores, leads to despotic, nepotistic dominance hierarchies where female kin support each other and form coalitions to maintain their rank. BGC is expected to reduce the degree of despotism, because females require their female group members in between-group conflicts. This model has been applied with positive results (e.g. squirrel monkeys, *Saimiri oerstedii* and *S. sciureus*: Mitchell et al. 1991), but has also been criticized (Clutton-Brock and Janson 2012; Koenig 2002; Thierry 2008). Important counterexamples concern the folivorous Nepal (Koenig 2002) and Bengal sacred langurs (Borries 1993), where the despotic dominance hierarchy has reproductive effects and indicates WGC, without the predicted nepotism. Moreover, female dispersal can occur in species with a despotic dominance hierarchy, contradicting the original prediction (Koenig and Borries 2001).

Second, some researchers propose that folivores have abundant food sources since leaves are omnipresent. They predict that folivores will experience no competition for food (Isbell 1991; Yeager and Kirkpatrick 1998; reviewed in Snaith and Chapman 2007). Any evidence of food competition, either scramble or contest, contrasts with the proposition that folivores lack food competition.

Third, folivores may indeed experience little or no food competition, yet this is a consequence of their relatively small group sizes (Janson and Goldsmith 1995), while the ubiquity of their folivore food would predict relatively large groups (Schuelke and Ostner 2012). This mismatch between expected and observed group sizes has been called the Folivore Paradox (Janson and Goldsmith 1995; Steenbeek and van Schaik 2001). Two solutions have been proposed for the Folivore Paradox. First, the scramble food competition may be underestimated and ecology actually does limit group size (Snaith and Chapman 2005, 2007). This, in principle, proposes that the behaviour of colobines converges with the socioecological model. Second, group size may be limited by infanticide risk since this risk is highest in larger groups (Crockett and Janson 2000; Steenbeek and van Schaik 2001). This second proposition predicts that infanticide risk, and not food competition, has the strongest link with group size effects on female fitness indicators.

Altogether, the relationship between ecology, conspecific threats and female social behaviour in Asian colobines needs further scrutiny. Koenig and Borries (2009) argue that to understand Asian colobine socioecology four questions need to be answered: (1) do Asian colobine females experience food competition and what type (WGC; WGS, BGC); (2) if there is WGC, why are dominance relationships not nepotistic and are female-female coalitions absent; (3) if there is WGC (i.e. a linear dominance hierarchy), why do females disperse and (4) what causes the Folivore Paradox, i.e. why do folivores live in such small groups.

In this chapter, we first describe patterns in female aggression, dominance and dispersal in Asian colobines. Next, we explore the type of food competition

experienced by females and link this with measures of food distribution. We contrast these with alternative factors, such as infanticide risk, that may limit group size. For only a few sites and species data are available that link female social behaviour, food competition and food distribution. Therefore, we detail these species and evaluate whether the more limited data on other species yield a general pattern. The taxonomy follows Roos (Chapter 2) and field sites have been assigned to a particular species on the basis of Rowe and Myers (2016). We consider the *Semnopithecus* spp. formerly referred to as grey langurs (formerly *S. entellus*; Brandon-Jones 2004) as one taxonomic group that we label 'sacred langurs'.

Diet and Food Distribution

Colobines are foregut fermenters (Chapter 6) and this allows them to consume considerable amounts of leaves in their diet (Chapter 8). It was expected that mature leaves would form an important part of their diet, which led to the suggestion that colobine food sources are abundant (Wrangham 1980; Yeager and Kirkpatrick 1998; Yeager and Kool 2000). However, the notion of colobines not being limited by food has been criticized (e.g. Snaith and Chapman 2007; Sayers 2013).

The first indication that food does limit colobines regards findings that colobine densities depend on the quality of their diet, measured by the ratio of protein to fibre in mature leaves. Though primarily assessed in African colobus monkeys, colobine population densities are higher when food quality is better (Davies 1994; Chapman et al. 2004; Fashing et al. 2007a). Therefore, food is limiting colobines, which may lead to food competition.

Second, it has become clear that many colobines do not depend on mature leaves but eat a varied diet that contains a large portion of young leaves and fruits (Sterck 2012; Chapter 8). Young leaves and fruits are often seasonal and their availability may be limited. Moreover, colobines can be selective feeders that prefer to consume specific food items (Grueter et al. 2009a; Kirkpatrick 2007; Sayers 2013; Snaith and Chapman 2007). In addition, folivores can deplete food patches (Grueter et al. 2009a; Snaith and Chapman 2005), indicating that WGC exists (Snaith and Chapman 2007) and suggesting that monopolization of these patches may be beneficial. Therefore, folivores may experience competition for food.

Food competition may also depend on the temporal distribution of food (van Schaik 1989), which may be more continuous for colobines than that for frugivorous species. Frugivorous species are strongly dependent on periods in which ripe fruit is available and this is often seasonal (van Schaik et al. 1993; van Schaik and Pfannes 2005). Folivorous colobines, however, may be buffered against strong seasonal variation in food availability. First, because they are more flexible in their diet, they can replace fruits with leaves (e.g. maroon langur, *Presbytis rubicunda*: Clink et al. 2017) or other food (e.g. lichens: golden snub-nosed monkey, *Rhinopithecus roxellana*: Liu et al. 2013b; Yunnan snub-nosed monkey, *R. bieti*: Huang et al. 2017b), allowing them to switch primary food sources (see Chapter 12). Second, colobines prefer unripe fruit and do not often consume ripe fruit (but see Dela 2012). Unripe

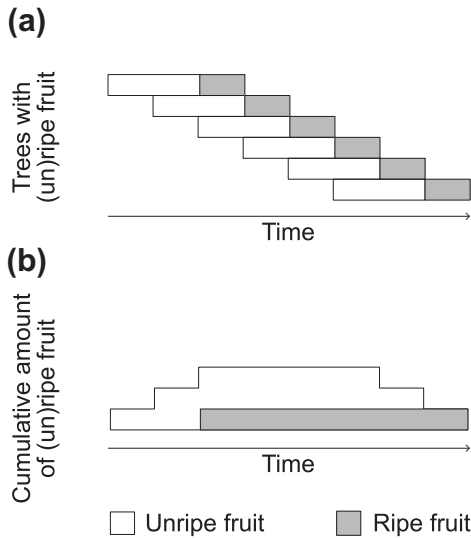


Figure 16.1 Unripe fruit will be less seasonal and be available more often than ripe fruit. Fruit will typically be longer unripe than ripe (here 2:1). (a) Six trees that fruit after one another and that contain two time periods unripe and one time period ripe fruits. (b) Cumulative amount of fruit available: the amount of time that unripe fruit is available is most often longer than when ripe fruit is available.

fruit is available for a longer period than ripe fruit (Yamagiwa et al. 2005; Janmaat et al. 2016), increasing the amount of food present at one moment of time and simultaneously reducing seasonality in food availability (Figure 16.1). Therefore, unripe fruit is more ubiquitous and less likely to incur contest competition than ripe fruit (Sterck 1995). However, some habitats are clearly seasonal, such as the habitat of naturally feeding Nepal sacred langurs (Koenig and Borries 2001) and snub-nosed monkeys in China (Grueter et al. 2009b). In such species or locations, stronger effects of food competition may be found. Indeed, in the Nepal sacred langurs of Ramnagar, a seasonal forest in the Himalayan foothills, a clear seasonal effect of food competition is found (Koenig 2000). Data on seasonality in food competition are lacking for the snub-nosed monkeys.

Altogether, the notion that the preferred foods of folivores are ubiquitous is an oversimplification. The distribution of colobine food sources shows that there is potential for food competition, especially in seasonal habitats. This may be reflected in female social behaviour.

Asian Colobine Female Social Behaviour

If female colobines lack WGC and BGC, it is expected that dominance hierarchies are egalitarian and individualistic and that female dispersal is possible (van Schaik 1989; Sterck et al. 1997). Here we explore whether this is indeed found.

Female Aggression and Dominance

Aggression among Asian colobine females has been reported in several species. A recent cross-taxon analysis indicates that published rates of overall female-female agonism do not differ much between folivore colobines and frugivore cercopithecines (Wheeler et al. 2013). This suggests that colobine females may form despotic and linear dominance hierarchies.

With the current taxonomy (Chapter 2), different species have to be distinguished within the sacred (or grey or Hanuman) langurs. In the Malabar sacred langur, no clear dominance ranks are found among females (*Semnopithecus hypoleucos*; Dharwar: Sugiyama 1965, 1967; Yoshida 1968).

Two other sacred species are well studied, the Bengal and the Nepal sacred langurs. At several sites, Bengal sacred langur females show aggressive interactions and form linear, i.e. despotic, dominance hierarchies (Abu: Hrdy and Hrdy 1976; Jodhpur: Borries et al. 1991; Lu et al. 2008). These hierarchies are unstable (Jodhpur: Lu et al. 2008). In addition, the dominance hierarchies are age-inversed, since nulliparous females become dominant without forming coalitions, and female dominance rank drops with age (Abu: Hrdy and Hrdy 1976; Jodhpur: Borries et al. 1991). In contrast, at other study sites females may form dominance categories, but dominance within a category is not well defined (Orcha and Kaukori: Jay 1965), or female dominance hierarchies are not important (Kanha Meadows: Newton, pers. comm. in Newton and Dunbar 1994) and the rate of female-female aggression is low. However, these latter studies do not provide behavioural data, hampering the comparison. Altogether, different populations seem to differ in the linearity of the dominance hierarchy.

In Nepal sacred langurs at Ramnagar, females show aggressive interactions and form linear dominance hierarchies (Koenig 2000; Koenig et al. 1998) but these hierarchies are unstable (Koenig 2000) and age-inversed (Koenig 2000; Lu et al. 2013). Notwithstanding this, Nepal sacred langur females at another site show bidirectional aggression (Junbesi: Boggess 1980) indicating that the hierarchies are non-linear. Again, different populations seem to differ in the linearity of the dominance hierarchy.

Altogether, female dominance relationships in these two species of sacred langurs differ between populations (see also Chapter 13). It is possible that populations with an age-inversed linear female dominance hierarchy may represent only some of the ecological settings where these species are found. However, data do not support this proposition. Bengal sacred langurs that live near towns in highly disturbed habitats may either form linear (Abu; Jodhpur) or non-linear (Orcha) dominance hierarchies, whereas populations at undisturbed sites form non-linear hierarchies (Kaukori; Kanha). Nepal sacred langurs that live in a relatively undisturbed but highly seasonal mountain forest (Ramnagar) have a linear dominance hierarchy, while at another site (Junbasi) dominance is not linear. Note that the reports of non-linear dominance hierarchies are based on descriptive data. Therefore, whether the suggested between-population variation in female despotism is linked to food competition remains to be established.

Indications for a linear and age-inversed female dominance hierarchy are also found in Phayre's langur (*Trachypithecus phayrei*, Koenig et al. 2004; but see Lu et al. 2016). Captive red-shanked douc (*Pygathrix nemaeus*: Kavanagh 1978) and Yunnan snub-nosed monkeys (Cui et al. 2014) also have a linear hierarchy, although the rate of aggression is low. In proboscis monkeys (*Nasalis larvatus*) aggression is rare, yet females have conflicts for sleeping sites and, while quantitative data are not available, they are suggested to be hierarchical (Abai and Sukau: Boonratana 1993).

In contrast, dominance hierarchies of other Asian colobine species that have been investigated are not linear and therefore these species may be egalitarian. Female aggression is found in Thomas's langurs (*Presbytis thomasi*), and the rate is similar to that of frugivorous long-tailed macaques (*Macaca fascicularis*: Sterck and Steenbeek 1997). Although in several dyads aggression was unidirectional, no clear dominance hierarchies were found (Sterck and Steenbeek 1997). Also, in Thomas's langurs one nulliparous female rose in rank, consistent with age-inversed dominance. In Nilgiri langurs (*Trachypithecus johnii*), the data on dominance interactions indicate a non-linear dominance hierarchy (Poirier 1970b, table II; note that this contrasts with the [mistaken] conclusion arguing for a linear hierarchy in the original text). Similarly, aggression is rare in capped langurs (*T. pileatus*; Stanford 1991a) and pale thighed langurs (*Presbytis siamensis*: Bennett 1983) and no female dominance hierarchy is discernible. In captive Yunnan snub-nosed monkeys, a linear dominance hierarchy was found (see above), but the rate of female aggression was low (0.13 interactions per hour) and directional inconsistency relatively high (Cui et al. 2014). Another study at the same institute reports that aggression rates are low, aggression is not severe, and high rates of reconciliation are seen (Grueter 2004, who uses the term 'tolerant'). Altogether, this indicates that they can be considered rather egalitarian. In golden snub-nosed monkeys, aggression is bidirectional (Zhang et al. 2008a) and there are high rates of reconciliation (Ren R et al. 1991), suggesting that they are also egalitarian (Zhang et al. 2008a, who uses the term 'relaxed'; see also Chapter 12). This suggests that in many Asian colobines the rate of female-female aggression is low, the age-inverted dominance indicates individualistic hierarchies, and dominance relationships are egalitarian.

Female nepotism is found when related females form coalitions against other females (Sterck et al. 1997). However, in Asian colobines, female coalitions against other females in their own group are not often reported. Accordingly, no indications of nepotism are found in some populations of sacred langurs (Malabar sacred langur, Dharwar: Yoshiba 1968; Nepal sacred langur, Ramnagar: Lu et al. 2013). In contrast, at Orcha and Kaukori such coalitions have been observed (Bengal sacred langur: Jay 1965), yet their effect on female dominance was not established. Nilgiri langur females rarely formed coalitions (Poirier 1970b). In other Asian colobines, female-female coalitions against other females are not reported. Therefore, dominance hierarchies in all these species appear to be individualistic. However, females do have the capacity to form coalitions, since they are formed against infanticidal males (Bengal sacred langurs: Hrdy 1977a; golden snub-nosed monkeys: Zhang et al. 1999b; review: Palombit 2012), including in species with a despotic

dominance hierarchy. Therefore, the lack of nepotism in the colobine species with linear female dominance hierarchies and where female relatives are available, such as some well-studied sacred langur populations, is puzzling.

In summary, the combined evidence on aggression for Asian colobine females indicates that rates of aggression among females may vary from low (see above) to similar to cercopithecines females (Wheeler et al. 2013). However, crucial quantitative data on the rates of aggression are especially lacking where verbal accounts indicate low aggression rates. Dominance hierarchies vary in their linearity, ranging from egalitarian to despotic. However, dominance hierarchies do not appear nepotistic, since female–female coalitions against other females are not reported in connection with despotic dominance hierarchies. Also, evidence for age-inversed dominance, meaning that nulliparous females obtain a high rank, is consistent with the proposition that dominance hierarchies are individualistic.

Notwithstanding this general pattern, for many Asian colobine species quantitative data on the rate and direction of aggression are lacking. This may be due to a lack of detailed observations, a lack of individual recognition, or potentially that low rates of female–female aggression remain unpublished. Therefore, publications should report quantified data on female aggression and dominance relationships.

Female Dispersal

The socioecological model predicts that female dispersal may be found when dominance relations are egalitarian and will be absent when they are despotic. Asian colobines show two different dispersal patterns: dispersal by both sexes or dispersal by males with female philopatry. These two dispersal patterns may actually form two ends of a graded scale, where female dispersal may vary from all females to none, while in all species males disperse. Despite this variation in female dispersal, overall colobines are characterized by a relatively high incidence of female dispersal (Sterck 2012).

There is no equivocal evidence that females disperse to avoid food competition. In Thomas's langurs, females emigrate from groups that are larger than the groups they immigrate into, but this is only due to the number of immatures and not the number of adults in the group (Sterck 1997). In addition, females do not disperse when food demands are highest, e.g. when pregnant or lactating or in lean seasons. Therefore, female dispersal as a response to food competition seems to be absent.

Female dispersal may have a function depending on the type of dispersal: primary and secondary dispersal. Primary dispersal concerns nulliparous females that leave their natal group. This is found in several species (ESM Table 16.1). Dispersal of nulliparous females may function to avoid inbreeding. Indeed, primary dispersal is found when male tenure exceeds female age at menarche (Sterck and Korstjens 2000). In Thomas's langurs, nulliparous females disperse when the father of the nulliparous female still remained in the group (Sterck et al. 2005). Also, in golden snub-nosed monkeys, nulliparous females disperse to avoid inbreeding (Qi et al. 2009).

In addition, parous females may disperse after their natal dispersal, which is called secondary dispersal. Secondary dispersal may concern female mate choice. Indeed, in Thomas's langurs parous females disperse to better mating partners, because they often immigrate to new, young males who provide better protection against infanticide after dispersal (Sterck 1997; Sterck et al. 2005). In addition, Nilgiri langur females may disperse after losing an infant to infanticide (1 case: Kavana et al. 2014). In golden snub-nosed monkeys, parous females may also disperse to acquire a better mate (Qi et al. 2009). Additionally, in white-headed langurs (*Trachypithecus leucocephalus*), females with young infants may temporarily disperse together with the old male after a group takeover, likely to avoid infanticide (Zhao Q et al. 2011a).

Overall, female dispersal in Asian colobines fits the pattern predicted by the dominance hierarchy. For instance, in several Asian colobine species (ESM Table 16.1), including one Bengal sacred langur population (at Kanha), the dominance hierarchy is egalitarian and female dispersal is found. In addition, female dispersal is rare or absent in several sacred langur populations with despotic dominance hierarchies (ESM Table 16.1). Therefore, the interaction between female dispersal and linear dominance hierarchies fits the expected pattern (see also Koenig and Borries 2001). One exception is the Phayre's langur, where the dominance hierarchy is despotic yet females regularly disperse. However, the kinship pattern in a group, irrespective of female dispersal, may explain this exception (see below).

The socioecological model (van Schaik 1989; Sterck et al. 1997) proposes that females in species with a nepotistic dominance hierarchy cannot disperse, because dispersal without (related) coalition partners would lead to a low dominance position in the new group where females are not related to the immigrant. This will be especially detrimental when the dominance hierarchy is nepotistic. The setting may be different in Asian colobines, since female dispersal may not disrupt female kinships patterns. Data on Thomas's langurs indicate that females disperse to a new protector male, but females tend to choose the same male as the other females of their group. Therefore, although females may range separately for several months to a year, they know the females in the group of immigration and the kinship patterns in groups are stable in the long run (Figure 16.2; Sterck 1997; Wich and Sterck 2010). Similarly, recent evidence shows that golden snub-nosed monkey females tend to disperse into groups with female kin, or disperse to a new group together (Guo et al. 2015). Unfortunately, no such information is available for other colobine species with female dispersal. However, if this pattern is also present in the Phayre's langur, it may explain their unexpected combination of female dispersal and a linear dominance hierarchy.

Altogether, most data support that notion that female dispersal is found when the dominance hierarchy is egalitarian and it is absent when it is despotic. Therefore, this fits with the patterns proposed by the socioecological model.

Asian Colobine Competition for Food

The proposition that colobine food is ubiquitous (Isbell 1991; Yeager and Kirkpatrick 1998; Yeager and Kool 2000) has led to the suggestion that these primates do not

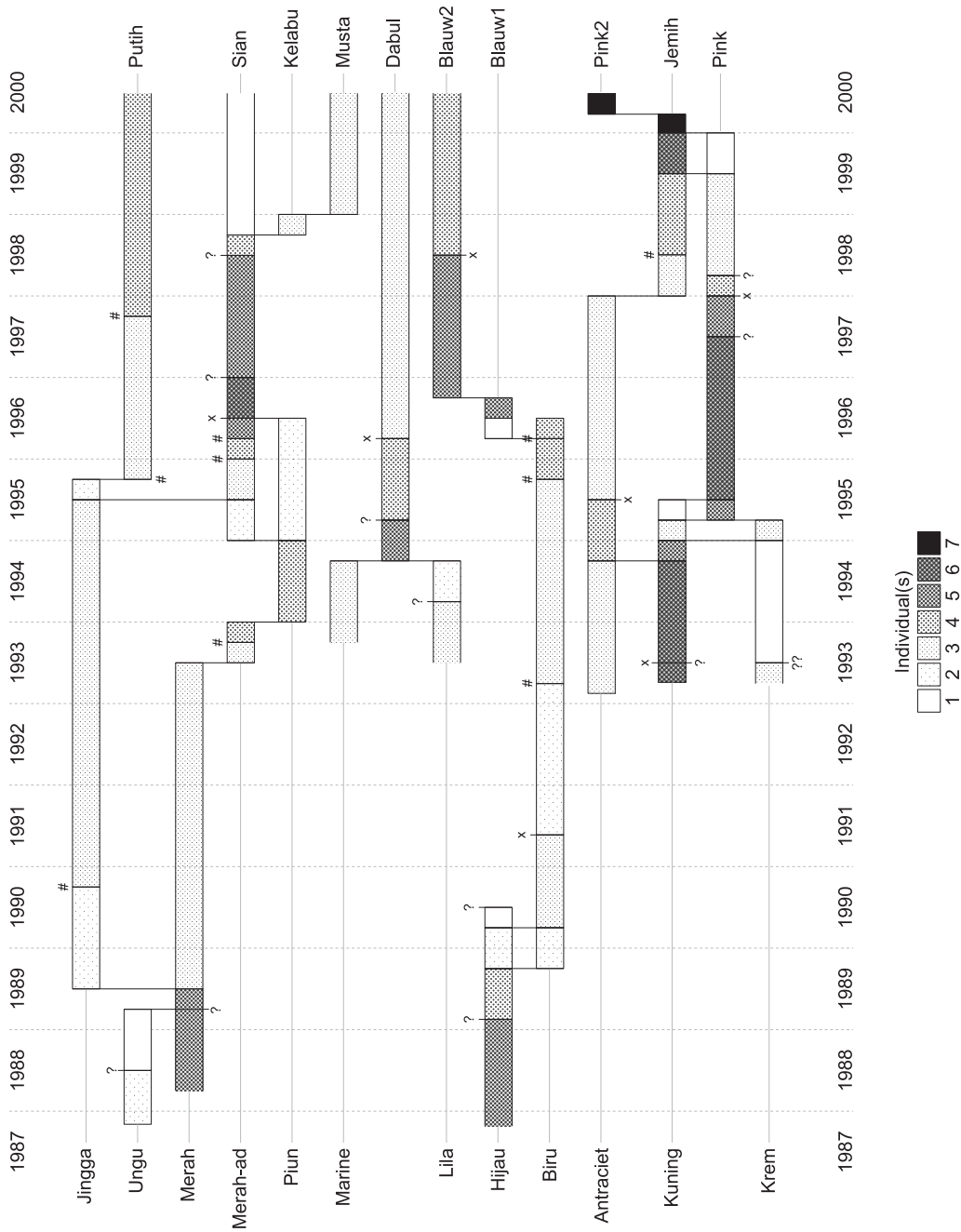


Figure 16.2 Female group membership (depicted in $N = 1-7$ females per group) and female dispersal in the Thomas langurs from Ketambe, Indonesia (after Wich and Sterck 2010, figure 17.9). Each horizontal bar represents a group; the name of the group is shown to the left or right. Vertical lines indicate dispersal events (of one or more females). When a female matures (i.e. 65 months after her birth date) is indicated with #, and this is when she is counted as a new adult female; ? concerns females that immigrate from or possibly emigrate to an unknown group; X concerns a female that died. Events are rounded to quarter-year periods.

experience food competition. Similarly, the Folivore Paradox, the phenomenon that folivore primate group sizes are smaller than expected (Janson and Goldsmith 1995), has been interpreted to mean that colobines do not experience competition for food. This may concern a lack of within-group scramble (WGS) or contest competition (WGC). Alternatively, no (net) competition is found because between-group contest competition (BGC) compensates for WGS. WGS and BGC are both group size effects that respectively increase or decrease the amount of food available for the whole group, so success in BGC may increase the availability of food for larger groups, compensating for the costs of WGS. No competition for food implies that colobine monkeys are not food limited. However, population densities depend on the productivity of the habitat (Chapman et al. 2004; Korstjens and Dunbar 2007; Wasserman and Chapman 2003), indicating that food is limiting for colobines. Below, we explore evidence for the different types of food competition on foraging effort or fitness indicators.

Within-Group Contest

WGC is expected when food may be acquired through aggression, measured as aggression, submission and displacements. It is known that rates of female-female agonism do not differ much between colobines and cercopithecines (Wheeler et al. 2013), indicating that colobine foods may also be contestable. Indeed, consistent with the notion that contest competition for food exists, Asian colobine females can be aggressive over food (Thomas's langur: Sterck and Steenbeek 1997; Bengal sacred langur: Borries et al. 1991; Nepal sacred langur: Koenig 2000; capped langurs: Stanford 1991a; Phayre's langur: Koenig et al. 2004). Such aggressive competition can be found for both fruit and leaf sources (Sterck and Steenbeek 1997). Therefore, all types of food may cause aggression (Sterck and Steenbeek 1997; Koenig et al. 1998) and colobine species have the potential to experience WGC.

However, while the potential for food competition is present, in several species it is relatively rarely expressed. Indeed, the rate of aggression is low in capped langurs (Stanford 1991a) and Phayre's langurs (Koenig et al. 2004). In contrast, Thomas's langur females have similar rates of aggression inside food patches as long-tailed macaques (Sterck and Steenbeek 1997), a species with WGC (van Schaik and van Noordwijk 1988; van Noordwijk and van Schaik 1999). Yet they show more aggressive interactions in small food patches that only represent a minor part of their diet (Sterck and Steenbeek 1997). In addition, female dominance does not affect feeding time (Sterck 1995). This contrasts with sacred langurs, where high-ranking females feed in larger feeding parties (Nepal sacred langur, Ramnagar: Koenig et al. 1998) and have a higher food intake (Bengal sacred langur, Jodhpur: Borries 1993).

For an effect of WGC, a differential effect of female dominance on foraging effort should be reflected in female fitness parameters. Accordingly, in Ramnagar Nepal sacred langurs, high-ranking females have better body condition (Koenig 2000) and females in better condition are more likely to conceive (Koenig et al. 1997). In addition, low-ranking females have a lower birth rate than middle- or high-ranking

females and infants of low-ranking females have a lower survival rate (but these results may be confounded by age; de Vries et al. 2016). Similarly, in Jodhpur Bengal sacred langurs, low-ranking females have lower birth rates than other females (Borries et al. 1991). In contrast, in Thomas's langurs no rank effects on female reproductive rate are found (Sterck 1995; Sterck et al. 1997). This suggests that for the three best studied species, WGC does occur in the Bengal and Nepal sacred langurs, while it is absent in Thomas's langurs. Unfortunately, for most colobine species no data on female dominance rank or its effect on foraging effort or fitness indicators exist. Therefore, it is not possible to propose what a general Asian colobine pattern of WGC may be. However, the opposing evidence from sacred and Thomas's langurs suggests that variation in the strength of WGC exists.

The effect of female dominance on fitness in sacred langurs has been attributed to WGC, but alternatively may be explained by the age-inversed dominance hierarchy where high-ranking individuals are relatively young. When young females have relatively good body condition, this may cause them to be both high-ranking and have a relatively high reproductive output (Borries et al. 1991; Hrdy and Hrdy 1976; de Vries et al. 2016). However, the suggestion that young females have more offspring is contradicted in another colobine species, where the inter-birth interval of primiparous females is relatively long (silvered langur, *Trachypitecus cristatus*: Shelmidine et al. 2009; primates: Pusey 2012). This suggests that in Bengal sacred langurs it may not be the young age, but rather high dominance that explains high female reproductive output.

Within-Group Scramble

It has been hypothesized by the socioecological model that colobines experience WGS (van Schaik 1989; Sterck et al. 1997), while others suggested that colobines do not experience any form of feeding competition due to the ubiquity of leaves (Isbell 1991; Yeager and Kirkpatrick 1998). This can be tested by determining the relationship of group size with indicators of WGS (ESM Table 16.2). These indicators are either related to foraging effort (e.g. day range, home range size) or fitness indicators (e.g. reproductive rate, inter-birth interval: Snaith and Chapman 2007).

WGS is present when foraging costs increase with group size (ESM Table 16.2). Accordingly, colobines living in larger groups have larger home range sizes (Phayre's langurs: Koenig et al. 2013; capped langurs: Stanford 1991a; Chamba sacred langur, *Semnopithecus ajax*: Minhas et al. 2013; Yunnan snub-nosed monkey: Grueter et al. 2008) and a longer day range (Thomas's langurs: Steenbeek and van Schaik 2001; Yunnan snub-nosed monkey: Grueter and van Schaik 2010; Chamba sacred langur: Minhas et al. 2013). In addition, in larger groups animals spend more time moving and less time resting than in smaller groups (golden snub-nosed monkeys: Liu et al. 2013a). In another species, the diet was lower quality in larger groups, containing more leaves and less fruit (Thomas's langurs: Sterck 1995). In some species, group size becomes smaller in periods with less food (red-shanked doucs: Phiapalath et al. 2011; black-shanked doucs, *Pygathrix nigripes*: Rawson 2009, but see Hoang Minh

Duc 2007). Therefore, the limited evidence indicates that all Asian colobines species with data on the relationship between group size and foraging effort show effects of WGS. This supports the socioecological model and counters that colobines do not experience food competition.

The effect of group size should also be measured on female fitness indicators (ESM Table 16.2). Consistent with WGS, Phayre's langur females in larger groups have lower reproductive rates and infant development is slower (Borries et al. 2008). In Bengal sacred langurs, the inter-birth interval is longer in larger groups (Jodhpur: Sommer and Rajpurohit 1989). In these species a larger group size leads to lower female reproductive output. In contrast, the birth rate is not lower in Thomas's langurs, while infant survival is higher in larger groups (Steenbeek and van Schaik 2001). Nepal sacred langurs in intermediate-sized groups have the best bodily condition and the highest reproductive output (Ramnagar: Koenig 2000), although in the lean season, females in small groups have the best body condition. In Kanha's Bengal sacred langurs, the number of infants per female is higher in larger groups, indicating a higher reproductive rate (Newton and Dunbar 1994). Therefore, the evidence for WGS on female fitness is mixed and effects of BGC may be found.

In the golden snub-nosed monkeys, living in layered societies, a lower birth rate was found in larger one-male units (OMU's), yet no unit size effect on inter-birth intervals and infant survival was present (Zhao D et al. 2011b). However, in species with a layered society, not the measured OMU size, but band size may determine WGS. Since no data on the effect of band size on female fitness are available, we cannot judge fitness effects of WGS.

Altogether, living in a larger group results in a larger foraging effort in all studied species of Asian colobines, indicating that all studied species experience scramble food competition. This greater foraging effort seems to result in a WGS effect on female fitness in several species (Phayre's langurs; Jodhpur's Bengal sacred langurs; possibly golden snub-nosed monkeys), consistent with the socioecological model. However, no negative effect is found in some other species (Thomas's langurs; Ramnagar's Nepal sacred langurs; Kanha's Bengal sacred langurs). Clearly, in these latter species scramble food competition does not limit group size and fitness. This may be due to BGC, which favours larger groups, or to the influence of other limiting factors, such as infanticide risk.

Between-Group Contest

BGC can be expressed in female between-group aggression (ESM Table 16.1). Female between-group aggression has been reported for sacred langurs (Nepal sacred langur; Ramnagar: Koenig 2000; Bengal sacred langur; Abu: Hrdy 1977b; Jodhpur: Borries 1993; Kanha: Newton 1987; Malabar sacred langur; Dharwar: Yoshida 1968). It is rare in Nilgiri langurs (Poirier 1970b) and golden snub-nosed monkeys (Zhao D et al. 2013), and absent in many other Asian colobine species (reviewed in van Schaik et al. 1992; Sterck 1998).

Female between-group aggression may result in benefits for larger groups. In Ramnagar's Nepal sacred langurs, females in the intermediate-sized group fared better than females in the small and in the large group, indicating a trade-off between BGC and WGS. However, whether this is linked to female between-group aggression is not clear (Koenig 2000). In golden snub-nosed monkeys, female participation in between-group conflicts is highest during the winter, when food availability is relatively low, indicating that females defended access to food during lean periods (Zhao D et al. 2013). The number of participating individuals, and not group size, determines who wins a between-group conflict (Zhao Q and Tan 2010). In addition, in this species larger OMU's have a higher rank and the benefits of this higher rank may explain why OMU's merge (Zhang et al. 2008b). However, it is not clear whether this translates in effects of BGC on female fitness. Therefore, while in several species, female between-group aggression is lacking and no signs of BGC are found, in other species, females aggress females of other groups and in Ramnagar's Nepal sacred langurs indications of BGC are present in reproductive output (Koenig 2000).

In Asian colobines, male between-group aggression is often found and reflects male defence of females (Sterck 2012). Still, when males defend locations with food this may also provide ecological benefits to females. When the sexes are sexually dimorphic and males are larger and/or have long canines, only males and not females may take part in between-group aggressive encounters (Willems et al. 2013). Indeed, many colobines are characterized by sexual dimorphism (Grueter and van Schaik 2009). Moreover, when only one individual of a sex is present, collective action problems between individuals over who should bear the costs of between-group aggression and who derives benefits without participating are absent (Nunn 2000). Therefore, males in one-male groups may be important resource defenders (Willems et al. 2015). Indeed, Asian colobine groups often contain only one male (Sterck 2012) and such a male may perform the defender role. In short, it is possible that BGC takes place in the form of aggressive interactions between males, an effect that has been seen in two species of African colobus monkeys (Chapter 17), but this proposition remains to be tested.

Other Limitations of Group Size

The Folivore Paradox – that in folivores food competition seems absent yet group size is small – may apply when factors other than food competition limit group size. Infanticide has been proposed as an alternative factor limiting group size (Crockett and Janson 2000). In addition, time constraints may provide an alternative explanation (Korstjens and Dunbar 2007).

The sacred langurs are the classic example of a taxon experiencing male infanticide. The Malabar sacred langur was the first species where male infanticide was systematically observed and studied (Sugiyama 1965, 1966). The proposal that male infanticide is a male sexual strategy (Bengal sacred langur: Hrdy 1977a) that has selected for female counterstrategies (cf. Hrdy 1979) has yielded wide support

(Nepal sacred langur: Borries et al. 1999a; primates: Palombit 2012; van Schaik and Janson 2000). The risk of infanticide is pervasive in primates because infant care lasts longer than a pregnancy (van Schaik 2000a) and males are present in bisexual groups to protect their offspring against infanticidal males (van Schaik and Kappeler 1997; Wrangham 1979). Infanticide has been reported in several Asian colobine species (Palombit 2012; van Schaik 2000a; Sterck 1998).

Female anti-infanticidal strategies depend on the number of males in the group. When groups contain one male, females may associate with a male protector as a female counterstrategy against infanticide (Sterck et al. 1997; Wrangham 1979). This counterstrategy is associated with small group size, since only groups with relatively few females will have one resident male (Nunn 1999; Schuelke and Ostner 2012; Srivastava and Dunbar 1996; Treves and Chapman 1996). In addition, females should have the option to change males, which has been confirmed in Asian colobines with female dispersal (see above). Indeed, the adult male protects against infanticide, since the disappearance of the resident male (experimental: Sugiyama 1966; natural: reviewed in Steenbeek 1996; reviewed by Palombit 2012) leads to infanticidal attacks by extra-group males. When groups contain several males, females will mate promiscuously (Hrdy 1979) and female dispersal is not required. Indeed, in Nepal sacred langurs living in multi-male groups, males defend infants against male attacks (Borries et al. 1999b). Therefore, males in both single and multi-male groups provide safety against infanticide by conspecific males.

The risk of infanticide can limit group size when the risk of infanticide increases with group size (Crockett and Janson 2000). Indeed, in a comparison of sacred langur populations, those with a high risk of male takeover, measured as the number of extra-group males, also had larger groups containing more females (Treves and Chapman 1996). However, this evidence is indirect and may be spurious, since populations with more females per group will also result in a larger number of extra-group males. More direct evidence for a higher risk of infanticide is found in Thomas's langurs, where infanticidal attacks tended to occur more often at larger group sizes (Steenbeek and van Schaik 2001). Additionally, in Nepal sacred langurs male immigration was more common in the larger group, and consequently infant mortality as result of infanticide was higher than in the intermediate-sized group (Borries 1997). Unfortunately, no data of infanticide risk are available for other species. However, in Thomas's langurs and possibly in sacred langurs infanticide risk may limit group size.

Alternatively, group size may also be limited by time constraints (baboons: Dunbar 1992; African colobines: Korstjens and Dunbar 2007; Asian colobines: Kavana et al. 2015b). Diurnal primates have about 12 hours per day to obtain sufficient food. In baboons, resting time is considered exchangeable for feeding and travelling time. This adjustment of time budget may be less flexible in colobines, since fore-stomach fermentation may require resting time (Dunbar 1988). Accordingly, the amount of resting time in Malabar sacred langurs and Nilgiri langurs is linked to the proportion of leaves in their diet (Kavana et al. 2015b) and group sizes of Nilgiri langurs are smaller than of Malabar sacred langurs, because their diet requires more resting time.

This would predict that food competition is present and that WGS is expected (cf. Snaith and Chapman 2005, 2007), even though group sizes are relatively small. This converges with the socioecological model.

Evidence for Colobine Food Competition/Folivore Paradox

Altogether, the data clearly show that colobines can experience food competition. Different species, and possibly different populations of the same species, can experience different combinations of costs and benefits of group living. In three different species this has been studied in multiple aspects, in the Ramnagar Nepal sacred langur, the Jodhpur Bengal sacred langur and the Ketambe Thomas's langurs.

Three Well-Studied Species

Nepal sacred langurs at Ramnagar experience WGS, WGC and BGC (Koenig 2000). Groups of intermediate size had the highest female body condition (Koenig 2000), which was linked to female reproductive output (Koenig et al. 1997). Group size effects show that females in the intermediate-sized group fared better than females in the small and large group. The females in the small group have a lower bodily condition than females in the intermediate-sized group because they cannot exert sufficient BGC, while the large group females have a lower bodily condition than females in the intermediate-sized group because of WGS. This indicates that WGS and BGC food competition balance group size. On top of group size effects, female dominance rank is despotic (Lu et al. 2008) and effects of female dominance rank on body condition and reproductive success are found, indicating WGC. As predicted with WGC, female dispersal is rare (Borries 1997; Borries and Koenig 2000). However, nepotism and alliance formation are absent and this is inconsistent with the predictions of the socioecological model (Koenig 2000). Moreover, there is some evidence that infanticide risk, as predicted by the Folivore Paradox, may limit group size at Ramnagar since the infanticide rate in the large group was higher than in the intermediate-sized group (Borries 1997). Simultaneously, the evidence indicates that in the Ramnagar Nepal sacred langurs food competition limits group size (Koenig 2000), and although an additional cost to a large group size may be a high infanticide rate, this seemingly does not lead to relatively small groups. So, it seems that the Folivore Paradox does not apply to this population.

While the findings of the Ramnagar population indicate that all three types of food competition are important (Koenig 2000), it is not clear whether this is a taxon-specific pattern. At Jodhpur, Bengal sacred langur females also experience WGS (Borries 1993; Sommer and Rajpurohit 1989), have a despotic dominance hierarchy suggesting WGC (Borries et al. 1991) and experience female aggression between groups suggesting the potential for BGC (Borries 1993). Therefore, also at Jodhpur all three types of competition may be present. In contrast, other sacred langur populations may show patterns consistent with the Folivore Paradox. A comparative analysis of sacred langur populations indicated that populations with high infanticide risk

also have larger groups (Treves and Chapman 1996). However, for the Folivore Paradox to operate, the relation between infanticide risk and group size should be established within a population. Only descriptive data on two groups of Nepal sacred langurs have been reported (Borries 1997). Moreover, group sizes in sacred langurs are not always small and regularly multiple males are present. Therefore, direct evidence for a larger risk of infanticide for females in the larger groups of a population is largely lacking. Thus far, the only convincing evidence suggests that, in this taxon, group size is limited by food competition.

Thomas's langurs at Ketambe experience WGS in foraging effort, but no WGC or BGC (Steenbeek and van Schaik 2001; Sterck 1995; Sterck et al. 1997). The birth rate of females is not affected by group size, indicating that group size effects on foraging (WGS) are not large enough to limit the birth rate. In larger groups immature survival tended to be higher, similarly suggesting that group size effects on foraging (WGS) do not limit immature survival. Larger groups may more effectively protect infants against outside threats, such as predators or infanticidal males. This contrasts with the finding that male takeovers are more prevalent in larger groups, which has been interpreted as a higher risk of infanticide (Steenbeek and van Schaik 2001). Thus, although food competition is present, it does not limit group size since female fitness is not reduced. This finding is consistent with the idea that other factors, e.g. infanticide risk, can limit groups size. However, evidence for a higher risk of infanticide in large groups is mixed: while larger groups may be taken over more often, immature survival is higher (Steenbeek and van Schaik 2001). Altogether, Thomas's langurs fit the Folivore Paradox, but evidence that infanticide risk is the limiting factor is mixed.

Thus, while Ramnagar Nepal sacred langurs experience three types food competition (WGS, BGC and WGC) and Jodhpur Bengal sacred langurs experience WGC that affects female fitness, in Thomas's langurs the WGS effect on foraging effort does not translate into an impact on female reproductive success. This indicates that, with the available data, no general Asian colobine pattern exists. Simultaneously, this variation within Asian colobines opens the possibility of investigating female socioecology.

General Asian Colobine Pattern

For other Asian colobine species a less complete picture exists and few data are available. In all investigated species, indications for a WGS effect on foraging effort are found. However, data of its effect on female reproductive success indicate that living in a large group is in some species disadvantageous, while in others it is advantageous. This suggests that some species may be limited by food competition and the socioecological model may apply, while other species may be limited by other factors, such as infanticide.

Much less attention has been given to BGC and, especially, WGC. Given that females can be aggressive over food sources, it remains surprising that this is often neglected. The characteristics of female relationships, i.e. low intensities of

aggression and lacking female-female coalitions, suggests WGC may often be unimportant, but why Asian colobines do not experience WGC more often remains to be determined. Altogether, a lack of data is the main reason we do not fully understand the socioecology of Asian colobines.

The Folivore Paradox Revisited

The few available data indicate that while some Asian colobines are limited by food competition, others are limited by an alternative factor. The best candidate for this alternative factor is that infanticide risk increases with group size (Crockett and Janson 2000). This implies that this male sexual strategy is crucial to understanding female social organization. Still, it begs the question of why there is a Folivore Paradox but not a Frugivore Paradox. In other words, why are frugivorous primates not found in unexpectedly small groups? We propose that an explanation should be sought in the causes and consequences of living in one-male groups, as often found in Asian colobines.

The number of males in a group depends on the number of females and on the seasonality of their fertility (general: Emlen and Oring 1977; primates: Nunn 1999; Srivastava and Dunbar 1996). In species that are relatively a-seasonal, one male can monopolize more females than in highly seasonal species (Figure 16.3a). Folivores are relatively a-seasonal in their food intake (see above), consequently they also have relatively a-seasonal births (Nunn 1999: ESM Table 16.2) and relatively many females associate with one male. Living in one-male groups has consequences for female anti-infanticidal strategies (cf. Palombit 2012). While in multi-male groups females reduce the risk of infanticide by promiscuous mating and spreading the chance of paternity, in one-male groups females depend on the resident male's defending capacities. In multi-male groups the infanticide risk will be higher after a new male has become dominant, but he may be less likely to kill infants of females that he mated with, reducing the overall infanticide risk. In one-male groups, the new dominant male will always be an outsider and pose a risk for all females with infants. Therefore, in one-male groups the infanticide risk will usually be higher than in multi-male groups (but see Teichroeb et al. 2012). This argues that ecology, i.e. low seasonality in food, resulting low birth seasonality is translated into one male groups with many females and a high risk of infanticide.

The relatively skewed sex ratio in these groups, with one male and quite a large number of females, also results in many extra-group males (Figure 16.3b; cf. Treves and Chapman 1996). These extra-group males will aim to take over groups. Since only one male is present, whether a takeover attempt is successful will crucially depend on the relative strengths of the resident and extra-group male(s). The number of females in a group will not determine whether an extra-group male or all-male band succeeds in replacing the resident male. Extra-group males may therefore target in particular groups with many females, since this will maximize their fitness. Therefore, the risk of takeover and infanticide will increase with the number of females in a group. Females may reduce their risk of infanticide by shifting group

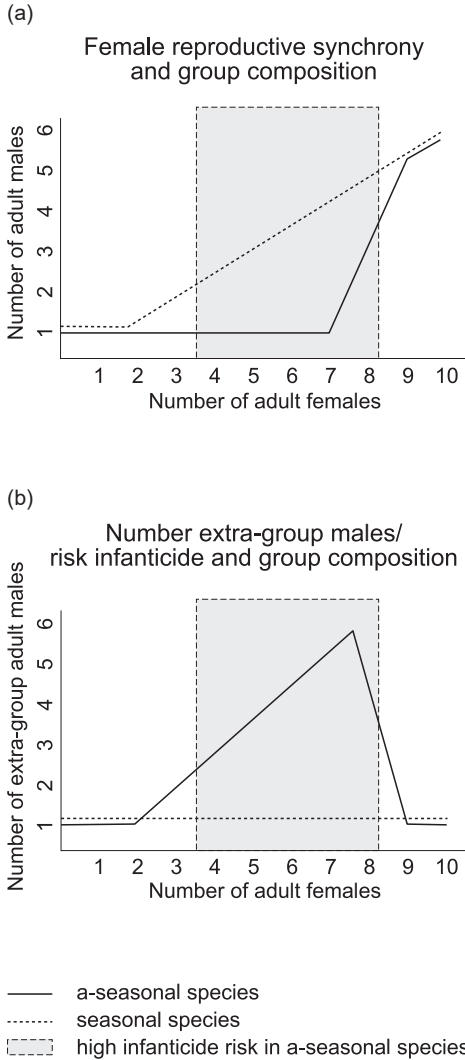


Figure 16.3 The seasonality of food and female reproduction will affect the number of males in a group and as a result determine the risk of infanticide. (a) In seasonal species, one-male groups are replaced by multi-male groups at a lower number of females than in a-seasonal species. (b) A-seasonal populations with one-male groups that contain relatively many females will have relatively more extra-group males. In seasonal species, the number of extra-group males will be low. Extra-group males may form a risk of infanticide (grey box). A high number of extra-group males will lead to more frequent takeovers and a higher risk of infanticide (cf. Treves and Chapman 1996). Note that we aim to illustrate the relationship between the number of females and males. The depicted number of females and males is not based on actual calculations.

membership, either by migration or the group may be temporarily split between some females that reside with the old male and others that reside with a new male (cf. Zhao Q et al. 2011a). In this scenario, the risk of infanticide will be especially strong in large groups with only one male. Since such one-male groups are found in many folivores, this may explain the Folivore Paradox. However, some frugivorous primates that live in one-male groups, e.g. guenons, may also fit the 'Folivore Paradox' and be limited in their group sizes by infanticide risk. Although guenons may breed seasonally, the number of simultaneously fertile females seems relatively low (Nunn 1999). In addition, while groups can temporarily experience multi-male influxes, especially when multiple fertile females are present (Mugatha et al. 2007), they typically contain one adult male (Cords 2000) and experience infanticide (Cords and Fuller 2010). Accordingly, the assertion that guenon populations are limited by food quality, but that group sizes are smaller than expected on the basis of food competition (Korstjens et al. 2018) hints that there may also be a thus far unnoticed 'Frugivore Paradox'.

This proposition also indicates that the Folivore Paradox will not be found in clearly seasonal species, with high reproductive overlap. Indeed, in the Ramnagar Nepal and Jodhpur Bengal sacred langurs not infanticide risk, but food competition is limiting group size. In contrast, infanticide risk is limiting (Steenbeek and van Schaik 2001) for the a-seasonal Thomas's langurs (Sterck and van Hooff 2000).

Discussion

We tested three hypotheses proposed to explain Asian colobine socioecology: (1) the socioecological model that proposes mainly WGS; (2) no food competition due to abundant food and (3) the Folivore Paradox, i.e. infanticide limits group size. When testing these proposals, Koenig and Borries (2009) argued that four questions need to be answered: (1) do Asian colobine females experience food competition and what type (WGC; WGS, BGC); (2) if there is WGC, why are dominance relationships not nepotistic and are female-female coalitions absent; (3) if there is WGC (i.e. a linear dominance hierarchy), why do females disperse and (4) what causes the Folivore Paradox, i.e. why do folivores live in unexpectedly small groups. After our review, we can partially answer these questions.

First, it should be mentioned that very few relevant data are available. Therefore, the answers are based on often scant data from a few species. However, it is clear that all species with relevant data experience WGS effects on their foraging effort (ESM Table 16.2; part of question 1), thereby rejecting proposal 2: Asian colobines do experience food competition. This is consistent with general evidence indicating that folivores actually do experience competition for food (e.g. Majolo et al. 2008; Snaith and Chapman 2007), and that the notion of their preferred foods being ubiquitous is an oversimplification (e.g. Sayers 2013).

Whether food competition is expressed in female reproductive output differs between species, in some it seems limiting, in others not. In the species where no group size effects on female reproductive output is found, either infanticide risk may

limit group size, or BGC may counter WGS, consistent with the socioecological model. The Thomas's langurs may be an example of the first scenario (Steenbeek and van Schaik 2001), the Ramnagar Nepal sacred langur of the latter (Koenig 2000). Therefore (part of question 1), BGC is evident in one population, in others it has not been conclusively established.

The presence of WGC has been measured in three species (part of question 1); it is absent in Thomas's langurs and present in Nepal and Bengal sacred langurs (Ramnagar and Jodhpur). In other Bengal sacred langurs (at Abu), the Phayre's langur (Koenig et al. 2004) and the red-shanked douc langurs (Kavanagh 1978) the despotic female dominance hierarchy indicates WGC, yet female rank effects on foraging effort and fitness indicators have not been tested. However, the behaviour of these langurs does not fit the socioecological model in one important aspect: females do not form coalitions and are not nepotistic (Koenig 2000; Koenig et al. 2004). We found no answer to this discrepancy (question 2). One solution may be to argue that despotism need not be accompanied by nepotism. This still leaves open the question of when selection pressures result in nepotism. Alternatively, Asian colobines may only have experienced WGC recently, due to human changes of the environment (cf. Koenig 2000; Sterck 1998, 1999), and may not have yet evolved the optimal evolutionary strategy. To summarize, WGC can be present or absent, females may form despotic dominance hierarchies, yet nepotism is not found. Altogether, Asian langurs can experience different forms of food competition (question 1), yet what species and populations experience which type of food competition and whether food competition limits group size remains to be established for most species.

We offer an explanation for the presence of female dispersal in despotic species (question 3): female dispersal may be easy and not costly when females disperse to a group with previously known female group members, and not to a group with unknown females. The Thomas's langur dispersal pattern (Figure 16.2) suggests that in the long run females stay together with their female group members, even when some have already migrated to a new male while others still remain with the previous one. Similar patterns have been found for female golden snub-nosed monkeys (Guo et al. 2015). The temporary group splitting in other species indicate that this relative flexibility in female grouping may be a general pattern (Sterck and Korstjens 2000; Zhao Q et al. 2011a). However, whether indeed females typically immigrate into groups with previous female associates remains to be tested.

The Folivore Paradox begs for an explanation for why colobines live in relatively small groups. This may result from strong WGS (Snaith and Chapman 2005) of from infanticide risk (Janson and Goldsmith 1995; Steenbeek and van Schaik 2001). In some Asian colobine species, females in larger group have a greater foraging effort and suffer reduced fitness. In these species, group size may be limited by food competition. Also, the suggestion that diet limits the time budget, predicts an effect of food competition. Both of these explanations converge with the socioecological model (Sterck et al. 1997). Alternatively, not food competition but infanticide risk may limit group size. This would be a truly alternative scenario, where a social factor,

i.e. a male sexual strategy, limits female group size. There is evidence, albeit mixed, for infanticide limiting group size in Thomas's langurs (Steenbeek and van Schaik 2001). Unfortunately, the relationship between infanticide risk and group size has received little attention in other Asian colobine species. Therefore, it is not clear whether this can explain in general the relatively small group sizes often found.

We also offer a related explanation for the Folivore Paradox (Question 4). Due to their diet folivores may experience relatively little seasonality in food availability. This translates into one male groups with relatively many females, thereby increasing the risk of takeover and/or infanticide by extra-group males. When these males preferentially target groups with many females, group size may be limited by infanticide risk, not by food competition. Thus, the low seasonality in fertility is pivotal for the Folivore Paradox. This suggests that infanticide could limit group size in a-seasonal frugivores as well. In addition, this would predict that the Folivore Paradox does not apply to seasonal folivores. This is consistent with the findings for the Ramnagar Nepal sacred langurs, but whether this also applies to seasonal odd-nosed monkeys remains to be tested.

Conclusion

In conclusion, the selection pressures on female Asian langurs are diverse and they may experience strong selection from food competition and/or from male sexual strategies, in particular infanticide. These patterns are also evident when the socioecology of African colobus monkeys is examined (Chapter 17). The balance between these forces will determine whether the enhanced foraging effort with group size is translated in an effect of food competition on female reproductive success. We propose that in more seasonal species, food competition will play a more important role, while in a-seasonal ones this will be male infanticide. How this applies to the seasonal odd-nosed colobines living in layered societies remains to be established (Chapter 18). One puzzling pattern in female social behaviour may have been solved: females in despotic species may disperse when they enter a group with previous female group members. However, the other puzzle, namely the lack of nepotism in species with despotic dominance hierarchy, remains unsolved.

Altogether, the predictions of the socioecological model and the Folivore Paradox can be brought together when the consequences of the low seasonality in folivores are taken into account. This indicates that Asian colobines are not exempt from an effect of ecology on female social organization, but that male sexual strategies can have an exceptionally large impact of female group size and grouping patterns in specific Asian colobine species.

Acknowledgements

We thank the editors Ikki Matsuda, Julie Teichroeb and Cyril Grueter for inviting us to contribute to this volume. Furthermore, we thank Cyril Grueter and Julie Teichroeb for their constructive comments on an earlier version of this chapter.