

# Infanticide risk and the evolution of male–female association in primates

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## SUMMARY

Year-round association between adult males and females is common in primates, even though internal gestation and lactation predispose males to mate-desertion in the majority of mammals. Because there is little *a priori* support for alternative explanations, we hypothesized that permanent male–female association in primates serves to reduce the risk of infanticide by strange males whenever females and infants are closely associated. For a phylogenetic test of this hypothesis, we reconstructed the evolution of male–female and female–infant association among primates. The results of Maddison's concentrated changes test confirmed the prediction that mother–infant association, as opposed to infant parking, and female–male association did not evolve independently. Changes in litter size and activity, in contrast, were not significantly associated with evolutionary changes in male–female association. Thus, we demonstrate a fundamental link between primate life history and social behaviour, explain the most basic type of variation in primate social organization, and propose an additional determinant of social organization that may also operate in other mammals.

## 1. INTRODUCTION

Among mammals, internal gestation and lactation have two major consequences for sex-specific reproductive strategies. First, males are virtually always ready to mate, whereas females are not (Clutton-Brock & Parker 1992), and therefore, male reproductive success is limited by the number of females inseminated (Darwin 1871). Secondly, these constraints limit the potential for male paternal care (Clutton-Brock 1991). Therefore, in order to maximize their reproductive success, males are expected to desert females after fertilization if other mates are available and if desertion does not reduce their reproductive success (Maynard Smith 1977).

Indeed, in the majority of mammals, adult males and females are only briefly associated during the period of female receptivity. During the rest of the year they lead a solitary life or live in all-male or all-female groups. Year-round male–female associations are found in less than 15% of the genera in most orders (estimated from tables in Wilson (1975)). Among some of the better known and socially diverse orders, the proportion of genera with year-round male–female association is around 30% (table 1). In striking contrast, over two-thirds of primate genera show association between males and females throughout the year (Wrangham 1987; table 1), including all but one of the anthropoid

species. In this paper, we examine possible evolutionary causes for this unusual pattern and conclude that the risk of infanticide is ultimately responsible for the evolution of male–female association in primates.

We assume that year-round male–female association evolves whenever the costs of adding at least one male to a solitary female or a group of females are outweighed by the benefits. The main costs of the association for both sexes are those of group living in general: (i) feeding competition (Janson 1988), and (ii) incompatibility of sex-specific feeding schedules (van Schaik & van Noordwijk 1986).

For males, we envisage two potential benefits. First, permanent association with one or more females provides them with the opportunity to care for infants (Dunbar 1995). However, direct male parental investment in the form of provisioning is virtually absent in primates, and carrying of infants by males is common only among some New World primates (Wright 1990). It is also possible that males accrue important benefits through indirect parental care, but paternal certainty is generally too low for this effect to be widespread. Thus, this potential male benefit does not explain why most non-monogamous primates show year-round male–female associations.

The second potential male benefit refers to improved certainty of paternity through continuous access to mates. Zuckerman (1932) suggested that primate males are attracted to females throughout the year because the receptivity of primate females is not limited to a

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Table 1. *The proportion of genera with year-round male–female association in well-studied and speciose mammalian orders<sup>1</sup>*

order	proportion of genera
Perissodactyla	12.5% ( <i>n</i> = 8)
Marsupialia <sup>2</sup>	31.5% ( <i>n</i> = 54)
Artiodactyla	29.4% ( <i>n</i> = 68)
Carnivora	31.8% ( <i>n</i> = 66)
Chiroptera	31.0% ( <i>n</i> = 29)
Primates	73.2% ( <i>n</i> = 56)

<sup>1</sup>Based on (Grzimek 1988; Smuts *et al.* 1987; Strahan 1995). Genera showing both character states were counted twice.

<sup>2</sup>Australian taxa only.

brief breeding season. However, although many primates, such as lemurs, patas, and squirrel monkeys are seasonal breeders (Lindburg 1987), they form permanently bisexual groups (Boinski & Mitchell 1994; Hall 1965; Richard & Dewar 1991). Moreover, the aseasonal breeders are often large animals with long inter-birth intervals, in which receptivity is rare but predictable (Palombit 1994a). In all these cases, permanent association with females is not necessary for males to maintain and monopolize breeding access.

For females, the potential benefits of associating with males are either of a social or an ecological nature. Ecological benefits can refer to improved food acquisition or predation avoidance. Wrangham (1987) suggested that females benefit from being associated with males because of improved defence of feeding territories or access to high quality food sources. Males have also been suggested to be more efficient than females at detection of and defence against predators (van Schaik & van Noordwijk 1989; van Schaik & Hörstermann 1994). However, year-round male–female association is nearly ubiquitous among anthropoids, despite considerable variation in the strength of feeding competition within or between groups, or of predation risk. Although the potential roles of feeding competition and predation risk in selecting for male–female association remain to be determined, these ecological benefits are therefore unlikely to provide a sufficient explanation, and will not be examined further here.

The social advantages for females include the use of males as allies in agonistic conflicts with other females, or protection against harassment by males, either aimed at the females or their infants (van Schaik & Dunbar 1990; Watts 1989; Wrangham 1987). Males are not the preferred allies of females in most primate species (Dunbar 1988), so the use of males as agonistic allies cannot explain the ubiquity of male–female associations. Whenever female mate selection leads to potential elimination of some males from the mating process, intersexual mating conflict is expected (Hammerstein & Parker 1987; Smuts & Smuts 1993). Among mammals, this mating conflict creates conditions for sexual coercion (Smuts & Smuts 1993) whenever males are physically capable of forcing females to mate and females lack protecting allies.

Sexual coercion can be immediate (as sexual harassment in the mating context), and delayed (as in infanticide).

Sexual harassment by males should only be a problem for females who do not clearly signal oestrus because the probability of being harassed presumably increases with the duration of the mating period. Ovulation signalling has appeared and disappeared several times during the evolutionary history of primates (Sillen-Tullberg & Møller 1993). Thus, sexual harassment can principally be reduced by eliminating any ambiguity in the signalling of the female's sexual state, and long-term association with a male is not required for this.

In contrast to these other factors, the risk of infanticide is widespread among primates, and its incidence is not related to ecological conditions or social system (but see below). Infanticide by males unlikely to have sired particular infants is widely thought to reflect an adaptive male reproductive strategy, because the mother can be fertilized again sooner afterwards. It has been reported for numerous primate species (Hausfater & Hrdy 1984; Hiraiwa-Hasegawa 1988), and estimated to be responsible for 34–64% of all infant mortality in some well-studied species (Crockett & Sekulic 1984; Sommer 1994; Watts 1989). Primates may be more vulnerable to infanticide by strange males than most other mammals because primate infants develop slowly (Harvey & Clutton-Brock 1985; Lee *et al.* 1991), thereby creating long windows of vulnerability and relatively large time gains to infanticidal males. Furthermore, infants in many primates can be located easily through their association with their mother.

Several aspects of female primate sexuality, such as sexual swellings, active female preferences for mate diversity, mating during pregnancy, extra-pair mating in pair-living species, mating calls, and situation-dependent receptivity (Hrdy & Whitten 1987; O'Connell & Cowlshaw 1994; Palombit 1994b; Small 1989) are consistent with a strategy to reduce the risk of male infanticide by confusing paternity. The same is true for female behaviour: females with infants avoid new males and encounters with other groups, follow deposited males out of their natal groups, or time migration into other groups to coincide with the absence of vulnerable infants (Fairbanks & McGuire 1987; Steenbeek 1997; Sugiyama 1967).

The presence of protective males may be especially effective in reducing infanticide risk. Male infanticide is almost invariably associated with the disappearance or disabling of protective males, because of take-overs by outsiders or dominance upheavals inside groups, and can be provoked reliably by experimentally removing the dominant adult male (Angst & Thommen 1977; Hrdy *et al.* 1995; Steenbeek 1997; Sugiyama 1967). All this suggests that permanent male–female association is a strategy to prevent infanticide, which benefits males by increasing the probability of survival of their putative young, and thus their reproductive success.

While this idea is plausible (but see Sussman *et al.* 1995), it has not yet been critically tested. In this paper, we present a comparative test of a crucial

prediction of this hypothesis, using interspecific variation in male–female association found among primates. Specifically, we predict that male–female association as an adaptation to reduce the risk of infanticide is only expected where mothers and infants are associated, because only if the infant is with or near the female can the male help prevent infanticide by associating with the female. Hence, in primates where females leave infants in a nest or park them while they forage, male–female association is not expected.

## 2. MATERIALS AND METHODS

Primates show two principal modes of maternal care: infants can be left behind for the first few days or weeks postpartum during the female's period of activity, or they can be carried around by the mother from birth onwards (Kappeler 1997a; Martin 1990). Permanent association of mother and infant can arise in two ways: females can carry their infant orally wherever they go (in *Tarsius spectrum* and *Procolobus verus*), or the infants can cling to their mother's fur (in all other anthropoids and some strepsirhines).

From the perspective of vulnerability to male infanticide, the decisive criterion for mother–infant association is whether the infant is alone for a significant part of the female's activity period, i.e. whether it is parked or not. There are two complicating factors, however. First, in some species, females park the infants close to where they forage. Second, in other species, infants are both parked and carried before weaning.

The frequency with which parked infants are moved among parking sites varies from about once or twice a night (*Perodicticus*: Charles-Dominique 1977; *Lepilemur leucopus*: Russell 1977) to many times a night (galagos: Charles-Dominique 1977; *Microcebus*; Russell 1977). If the frequency of relocating infants is very high, this may according to this hypothesis, amount to female–infant association. There are no quantitative descriptions of mother–infant distances in parking species in the literature, and few studies mention close proximity of mother and infant during regular foraging. For example, among galagos, it may take up to 30 s for the mother to rush to the infant after it has emitted distress vocalizations (Charles-Dominique 1972). Thirty seconds may well be enough for an infanticidal male to strike. Hence, cases such as these are classified as 'no association'. A close association between the mother and her parked infant has only been described for *Tarsius spectrum* (MacKinnon & MacKinnon 1980), where adults and infants are rarely more than 10 m apart. In *T. bancanus*, Crompton & Andau (1987) report no female–infant association. No relevant information is available for the other *Tarsius* species.

Several strepsirhines employ a mixed infant care pattern. In *Haplemur*, young are born in nests and left there during the first few days, but are carried continuously afterwards (Steyn & Feistner 1994). Clearly, carrying is the predominant infant care pattern in *Haplemur*. In the two gracile loroid genera, *Loris* and *Arctocebus*, infants are carried most of the time during the first month, but parking increases over time, starting after about one week in *Arctocebus* and after about four weeks in *Loris* (Charles-Dominique 1977; Rasmussen 1986). Since infants are weaned at five months of age or later (Izard & Rasmussen 1985), parking time far exceeds carrying time, and we therefore classified them as having no permanent mother–infant association.

We based the classification of male–female association on overviews of primate social systems (Kappeler 1997b; Smuts

*et al.* 1987). In all diurnal species (except *Pongo*), males and females are associated year-round. In contrast, in most so-called solitary nocturnal species, males and females are not permanently associated, and their ranges overlap only partially. Although some solitary nocturnal species, such as galagos (Charles-Dominique 1977) and cheirogaleids (Kappeler 1997b), form bisexual day-time sleeping groups, we based our assignment on the active period because infanticidal males are also inactive during the day and infants are only vulnerable at night. Species living in fission–fusion societies (the genera *Pan*, *Ateles* and *Brachyteles*) were classified as having year-round male–female association, even though females spend some of their time alone (see §4). Most genera are homogeneous for this social trait. The only exception is *Tarsius*, where *T. spectrum* shows clear-cut male–female bonding (spatial proximity, duetting, alloparental care: MacKinnon & MacKinnon 1980), whereas in *T. bancanus* males and females rarely interact, and may in fact have largely separate ranges (Crompton & Andau 1987).

The phylogenetic relationships among primates are still partly unresolved (Martin 1990). For our analyses, we primarily relied on a recent composite phylogeny (Purvis 1995). Because the characters examined here are virtually invariant in haplorhines, choice of a particular haplorhine phylogeny does not affect the outcome of our analyses. On the other hand, strepsirhines, in particular Malagasy lemurs (Lemuriformes), display considerable variation in these characters (Kappeler 1997a,b). To test the robustness of our conclusions, we therefore employed alternative phylogenetic hypotheses covering the affinities among lemurs. These hypotheses were based on general morphology (Martin 1990; Tattersall 1982), chromosomal evolution (Rumpler & Dutrillaux 1986), morphological and molecular data (Yoder 1994), and on behavioural characteristics (Macedonia & Stanger 1994). Whenever these phylogenies failed to supply information about the relationships among particular genera, we relied on Purvis's tree.

Among the statistical procedures that test for the evolutionary (in)dependence of two traits, Maddison's concentrated changes test (Maddison 1990) is widely considered appropriate because it is conservative and convenient in that it does not require information on the length of branches in the phylogeny (Martins & Hansen 1996). This test was used to calculate the probability that observed evolutionary gains or losses in male–female associations are concentrated on those branches of the phylogeny with mother–infant association, given the total number of changes in male–female association in the whole clade examined. These calculations are based on parsimonious reconstructions of character evolution, also performed with the MacClade program (Maddison & Maddison 1992).

Maddison's concentrated changes test requires the absence of polytomies in the phylogeny. Several of the trees contain polytomies, but since none of these are at nodes where the two social characters were reconstructed, they were resolved randomly. The test also requires careful selection of the clade, because the inclusion of large radiations of species which are homogeneous for both traits does bias the results (Maddison & Maddison 1992). In order to reduce the resulting type II error, we restricted the test to radiations exhibiting variation in maternal style, i.e. prosimians, but repeated the analysis for all primate genera and species, respectively, to illustrate this bias.

There are currently no alternative hypotheses for the evolution of male–female association. However, mother–offspring association could be linked to other life history traits that may feature in alternative hypotheses as elements or intermediary variables. We therefore collected information

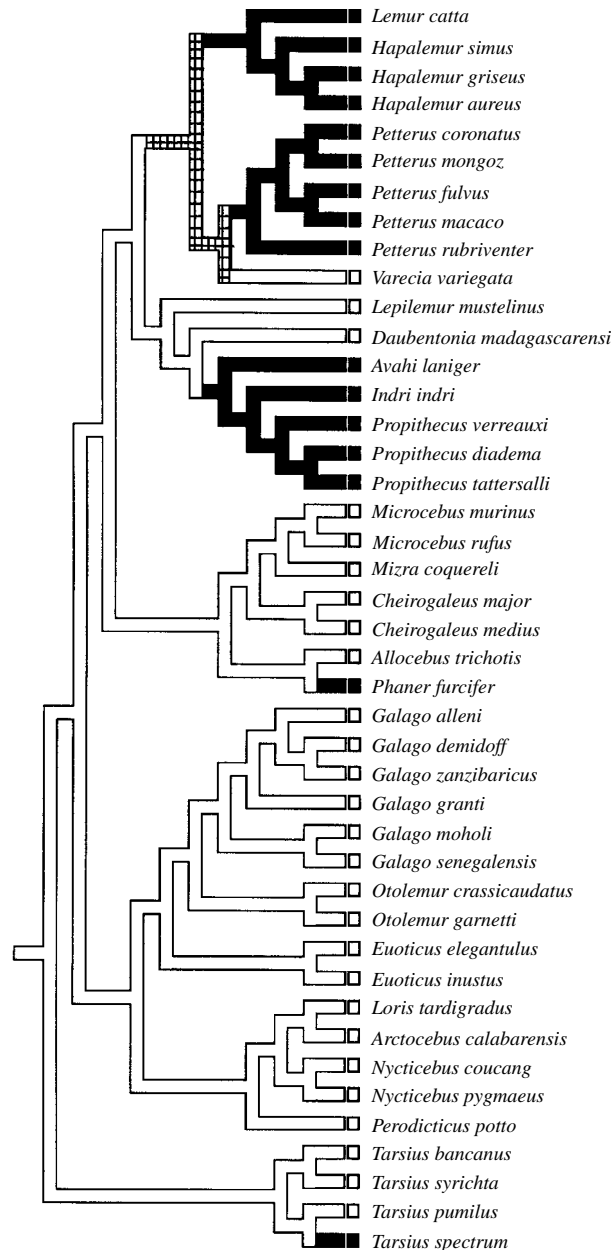


Figure 1. Mother–infant association (black) during the mother's activity period in prosimian primates. The evolution of this trait was reconstructed on a composite primate phylogeny (Purvis 1995) using a parsimony algorithm (Maddison & Maddison 1992) and data summarized previously (Kappeler 1997a).

on two obvious traits, modal litter size and activity period (Harvey & Clutton-Brock 1985; Kappeler 1996; Kappeler & Heymann 1996; van Schaik & Kappeler 1993), and conducted the same concentrated changes tests, using them as independent variables, assuming that litters (versus singletons) and nocturnality are ancestral.

### 3. RESULTS

Using the composite primate phylogeny, we reconstructed the ancestral state of infant care among primates as infant parking (figure 1). We estimate that close mother–infant association evolved five times in primates: three times in the Lemuriformes (we assume

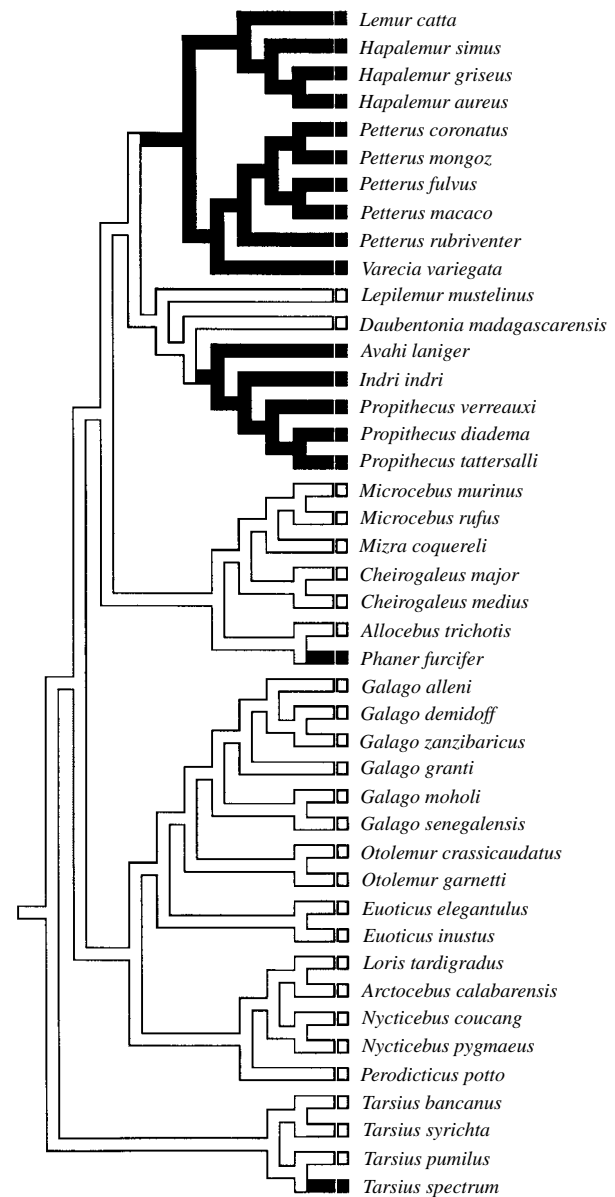


Figure 2. Year-round male–female association (black) during the activity period in prosimian primates: same phylogeny and procedure as in figure 1. The character distribution is based on previous reviews (Kappeler 1997b; Smuts *et al.* 1987; van Schaik & Kappeler 1993).

that it was lost secondarily in *Varecia* and that it represents the ancestral state for the other Lemuridae, where nine out of ten extant species and three out of four extant genera exhibit the trait), once in *Tarsius*, and once in the ancestral anthropoid. The ancestral state for male–female association was reconstructed as lack of year-round association (figure 2). In addition, all taxa in which males and females are associated year-round show mother–infant association. *Varecia* is the only taxon with male–female association in which mothers do not carry infants around, and *Pongo* is the only species with solitary females despite mother–infant associations.

The probability of male–female association and mother–infant association evolving independently among lemurs, lorises, and tarsiers (i.e. prosimians) is 0.007, supporting our prediction. By including in the

analyses many taxa that are homogeneous for both traits at the levels of primate genera and species, the probabilities increase, as expected, to 0.127 and 0.892, respectively. Because the two traits always change at the same time relative to speciation events in the predicted direction, we are unable to decide which one changed first, but the actual sequence is irrelevant for our functional hypothesis. The relationship between male–female association and mother–infant association is quite robust. If only strepsirhines (i.e. lemurs and lorises) are considered, it remains significant ( $p = 0.033$ ). If alternative phylogenies published before Purvis's (1995) composite phylogeny, and necessarily based on less exhaustive character sets, are used, all but one of the tests for prosimians remain significant ('Rumpler tree',  $p = 0.02$ ; 'Yoder tree',  $p = 0.029$ ; 'Tattersall tree',  $p = 0.047$ ; 'Macedonia & Stanger tree',  $p = 0.084$ ; 'Martin tree',  $p = 0.007$ ), but note that we had to force 'parking' and 'solitary' to be the ancestral states in the Martin and Tattersall trees. Moreover, alternative explanations for this correlated evolution are not easily provided: neither activity period ( $p = 0.169$ ) nor litter size ( $p = 0.384$ ) predict male–female association as well as mode of infant care.

#### 4. DISCUSSION

In contrast to other mammals, most primate females are permanently accompanied by at least one male. We hypothesized that this association serves to reduce the risk of infanticide by strange males. The comparative tests presented here strongly supported this hypothesis, whereas plausible alternatives, such as diet, body size, or habitat type, are less successful at predicting the observed distribution of traits among taxa because they vary greatly among anthropoids, for which male–female association is a hallmark. Predation risk may offer an alternative explanation, but it is difficult to quantify and often varies in parallel to infanticide risk. However, because nocturnal species that carry their infants invariably show male–female association, even though the effectiveness of gregariousness as a predation avoidance strategy is likely to be reduced for nocturnal species (Terborgh & Janson 1986), we conclude that infanticide and not predation risk selected for male–female association in primates.

The infanticide avoidance hypothesis did not predict the association pattern observed in two taxa, *Varecia* and *Pongo*, and these need to be discussed. In *Varecia*, a 3.5 kg diurnal lemur, pregnant females build nests for their infants, in which they leave them during the first 1–2 weeks of life, and park them outside nests for 3–4 months thereafter (Morland 1990). Nonetheless, *Varecia* shows permanent male–female association (Morland 1991; Rigamonti 1993). *Varecia* is also the only parking species in which males (and non-reproducing females) have been observed to guard the young (Morland 1990; Pereira *et al.* 1987), and is the only non-nocturnal primate known to park infants. Because visually hunting predators may detect infants easily, parking several relatively large infants during the day may necessitate active guarding. Captive and wild *Varecia* are indeed known for mobbing and attacking diurnal

predators, also away from nests (Goodman *et al.* 1993; Macedonia 1993). Thus, although the primary function of male guarding may be protection from predators, guarding males will also deter potentially infanticidal males. Indeed, captive males were recently reported to increase their guarding in the presence of potentially infanticidal males (White *et al.* 1997). We therefore conclude that the observed pattern of paternal care in this species is consistent with the core of our hypothesis.

The second exception is the orang-utan, *Pongo pygmaeus*, in which females are truly solitary most of the time, and yet carry their offspring around. In this species the lack of year-round male–female association is most likely caused by excessive feeding competition in groups because parties are only briefly formed during periods of high fruit abundance (Sugardjito *et al.* 1987). How orang-utans cope with the risk of infanticide is puzzling, especially since attempts at infanticide have never been described despite long-term studies in the wild. It is possible that a female remains in continuous, albeit long-distance, contact with an adult male with whom she has a special relationship and who is the likely father of her offspring. This contact could be maintained because the male emits individually recognizable, long calls (Mitani 1985), which may also deter strange males. We plan to test this hypothesis with playback experiments (C. P. van Schaik, in preparation).

Strong male–female bonds characterize virtually all anthropoid primates, but these are weakened in the dispersed social systems of spider monkeys, muriquis and chimpanzees, where females tend toward solitary life (Chapman *et al.* 1995; Strier *et al.* 1993). The infanticide hypothesis requires that these taxa either face reduced infanticide risk, or have evolved alternative social adaptations to reduce it. There are no indications of reduced infanticide risk in chimpanzees (Hiraiwa-Hasegawa & Hasegawa 1994) (the other taxa have been studied less intensely). However, it has been suggested that their unusual male-bonded system, in which bands of males collectively defend a territory, allows for female solitary foraging where the ecological costs of association are too high without a concomitant increase in infanticide risk (van Schaik 1996). Alternatively, perhaps also in orang-utans, the benefits of foraging alone may outweigh the costs of infanticide risk.

The risk of infanticide may also vary among primates, most likely as a result of variation in several reproductive and life history traits, such as seasonality of reproduction, weaning age, length of inter-birth intervals and lactational amenorrhoea. For example, in highly seasonal breeders, infanticidal males will still have to wait until the next breeding season to mate. However, it has been suggested that infanticide in these taxa may nevertheless occur because females may normally not reproduce every year (Wright 1995), or because females have a preference for infanticidal males (Pereira & Weiss 1991).

Furthermore, infanticide may also be less likely in taxa with post-partum matings because it does not accelerate female reproductive rates. However, when infant development is so slow that lactation is longer than gestation, post-partum conception is not an

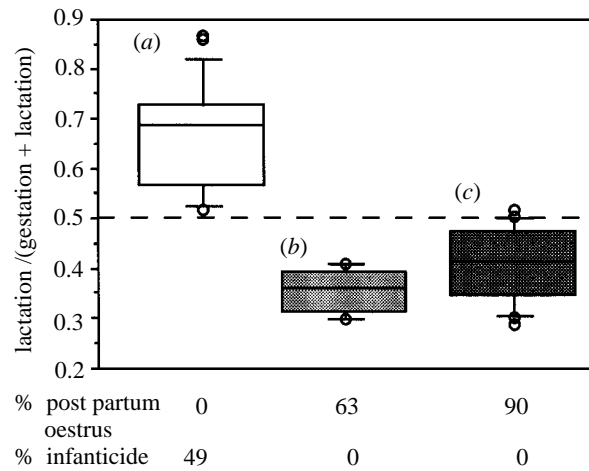


Figure 3. Relative gestation length in primates with different types of infant care. Box plots for the duration of lactation in relation to the total duration of gestation and lactation are shown for species in which (i) only females carry the young ('carriers',  $n = 23$ ); (ii) males participate in carrying young ('communal care',  $n = 7$ ); and (iii) infants are parked ('parkers',  $n = 17$ ). The difference in mean relative lactation length among groups is highly significant ( $F_{2,44} = 51.28, p < 0.001$ ). Data are from Harvey & Clutton-Brock (1985) and Roberts (1994). For each category of infant care, the proportions of species with (i) post-partum oestrus and (ii) reports of male infanticide were determined in an extensive literature search (total  $n = 88$ ; van Schaik *et al.* 1998).

option because it would result in the presence of dependent offspring with very different ages. Thus, whenever lactation is longer than gestation, we expect no post-partum mating, rather a significant risk of infanticide. A comparison of relative lactation length (in relation to total length of lactation and gestation) across primates with different types of infant care supported this prediction (figure 3). This relationship may also explain why observations of males guarding parked infants are rare, although more focused observations are needed. In addition, the distinction between taxa with maternal and communal infant care suggests that infanticide risk is highest in taxa where only mothers carry infants, an expectation fully supported by published accounts of infanticide among primates (figure 3).

Our analyses also indicate that infanticide prevention ultimately contributes to some of the most outstanding social and cognitive features of anthropoids. Social complexity is facilitated by gregariousness and by permanent male–female association. Although coalitions and alliances are mainly found within sexes (Harcourt 1992), the bonds between the sexes provide the context for negotiations and transactions that extend well beyond the direct mating context (Noë & Hammerstein 1994). Species that live in large, bisexual groups are also the ones with the largest brains and most highly developed cognitive abilities (Barton 1996).

Finally, the results of this study indicate a strong link between life history and social organization. The fundamental life history change from parking to carrying infants may have made it possible for primate

females to become nomadic and form permanent groups (Kappeler 1997a), and also favoured permanent association between the sexes. The number and sex of primates associated in individual social units, as well as their social relationships, are therefore not determined by ecological factors, such as resource distribution and predation risk, alone (Kappeler 1997b; van Schaik 1996).

At this stage, it is not clear to what extent the infanticide prevention hypothesis can account for variation in male–female association in other mammalian orders because the need or potential for male protection and unique physiological constraints also varies (e.g. Geffen *et al.* 1996; Strahan 1995), but one can speculate that the speed of life history (Promislow & Harvey 1990) should also correlate with variation in male–female association. Some studies indeed indicate that the risk of infanticide may have favoured a convergent solution in some of these taxa (Gubernick 1994; Pusey & Packer 1994).

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