
GROWING UP IN A FLEXIBLE FAMILY:
BEHAVIOURAL DEVELOPMENT AND
FAMILY SOCIAL DYNAMICS IN CAPTIVE
GIBBONS AND SIAMANGS
(PRIMATES: HYLOBATIDAE)

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ABSTRACT

The gibbons and siamangs (family Hylobatidae) are renowned for their unusual social organisation (social monogamy) and were once thought to be inflexible in their social behaviour; however, hylobatids share many characteristics with their cousins (the great apes) that increase the benefits of, and capacity for, social flexibility. These include: large brains relative to body size, long developmental periods and long lifespans. Moreover, recent research on other family-living species reveals a complexity in social dynamics that reflects the importance of cooperation in coordinating group activities and maintaining group cohesion. Variation in social behaviour among families of hylobatids should be investigated, but detailed observation of intra-group social behaviour is difficult in wild groups. Captive family groups provide a valuable resource for investigating variation in social behaviour in this taxon. Despite the relative abundance of hylobatids in zoos, little is known about their social development and capacity for flexible behaviour. This thesis provides the first quantitative analysis of behavioural development in hylobatid families (*Hylobates moloch*, *Nomascus leucogenys* and *Symphalangus syndactylus*), and explores variation in behaviour both within and among individuals, relative to the age of individuals and the reproductive and social context within the group. The behaviour of 36 individuals in 13 groups (residing in Australasian Zoos) was recorded over a 5 year period from 2008 to 2012, including over 1137 focal observation hours. For some families, data from a previous study in 2005/2006 was also included, such that the data set for some groups spanned a 7 year period.

I focus on family social dynamics and address adult pair behaviour, parental roles, immature development and patterns of aggression and affiliation within the family. The

presence of offspring and the reproductive status of the breeding female produce differences in the activity budgets of both males and females in captivity, but sex differences in behaviour are greater when offspring are present, and/or when mothers are pregnant or lactating. Activity budgets of group members differ in complementary ways, such that males contribute more to parental care when females contribute less, and when no siblings are present. In addition, maturity of offspring is both age-related and conditional on the social environment; developmental timing depends on whether offspring remain in their natal group and whether younger siblings are present in the group. Contrary to expectation, the expression of bonding behaviour between adult males and females does not depend on the length of time together or the female's reproductive status. Similarly, the birth of new offspring and greater family size does not increase conflict within family groups. The flexible social roles displayed by these captive individuals indicate that cooperation may be an important driver of social behaviour in hylobatids, as in other family-living species. In combination with other sociodemographic characteristics (e.g. production of overlapping offspring and delayed dispersal), flexible coordinated social roles may allow hylobatids to pool individual efforts in territorial defence and parental care across a small, highly related social group. In this way, the social behaviour and life history of the small apes bears a remarkable resemblance to that of humans, and some family-living birds.

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STATEMENT OF CANDIDATE CONTRIBUTION

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I hereby declare that all work presented in this thesis is entirely my own, except where the contributions of other persons are acknowledged. I have obtained permission to include some data collected by Helen M Dooley and acknowledge its inclusion where appropriate. This thesis also incorporates raw data collected by me for a BSc Honours thesis at The University of Western Australia in 2008. All analyses incorporating this data were undertaken during the doctoral candidature period outlined above. Chapter 4 of this thesis has been prepared for publication with my primary supervisor, Debra S Judge, as a co-author, but is presented here in a format consistent with the rest of the thesis. The majority of the work contained in Chapter 4 is my own.

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*We shall not cease from exploration
And the end of all our exploring
Will be to arrive where we started
And know the place for the first time*

T. S. Eliot

CHAPTER 1 INTRODUCTION

CHAPTER 1 INTRODUCTION

BACKGROUND

The small apes (family Hylobatidae) are arboreal, rainforest-dwelling primates distributed across South-East Asia. The family includes at least 16 species within four genera that are distinguishable both karyotypically and morphologically: *Nomascus*, *Symphalangus*, *Hoolock* and *Hylobates* (Thin et al. 2010). The phylogenetic relationships among genera are still disputed (Chatterjee 2009), possibly because of a very short rate of divergence (Takacs et al. 2005). The most commonly accepted order of divergence is *Nomascus*, *Symphalangus*, *Hoolock* then *Hylobates* (Roos & Geissmann 2001; Chatterjee 2006; but see Muller et al. 2003). Hylobatid research has, so far, focused heavily on socioecology, singing behaviour, genetics, and locomotion. The limited available research on hylobatid social behaviour consists of detailed descriptive data on behaviour from natural history and ecological studies, as well as more quantitative research on specific subsets of behaviour, including: mating patterns, pair bonding, infant development, and paternal care of infants (in the siamang, *Symphalangus syndactylus*).

Hylobatid socioecology has been thoroughly researched across their geographic range, including studies on representative species from all four genera. Previous research suggested differences in the diet and ecological niche between the *Hylobates* spp. and *S. syndactylus* based on body size (Chivers 1972; Gittins & Raemaekers 1980). Female body mass in *S. syndactylus* averages 10.7kg, compared to the 5.3 – 7.8kg reported for species in the other three genera (Smith & Jungers 1997). In addition, preliminary comparisons between the sympatric siamangs (*S. syndactylus*) and both *H. lar* and *H. agilis* suggested subtle differences in behaviour, including participation in infant

transport by some *S. syndactylus* males, impressions of greater social cohesion in *S. syndactylus*, and shorter daily travel lengths in *S. syndactylus* (Chivers 1972; Gittins & Raemaekers 1980; but see Fox 1972). However, the latest evidence indicates significant overlap in diets and many other aspects of social behaviour among all hylobatid species (Elder 2009; Brockelman 2009; but see Palombit 1996). Species- or generic-level differences in ecology and behaviour must therefore be interpreted cautiously, particularly when they are extrapolated from small samples (but see Lappan 2010).

Many overarching aspects of hylobatid socioecology are uniform across species; as so aptly stated by Brockelman (2009, p. 212), "...no gibbon has so far been found to be nonterritorial, predominantly polygynous, or living in large groups". Hylobatids most commonly inhabit lowland tropical or subtropical evergreen rainforest (Malone & Fuentes 2009), but also mixed-evergreen/deciduous and montane forests up to ~3800m above sea level (Jiang et al. 2006; Malone & Fuentes 2009). All species are omnivores with a heavy focus on ripe fruits (Elder 2009). Local resource exploitation is flexible, but there is usually a preferential order favouring ripe fruits before figs, and a fall-back on leaves when ripe fruit and insects are not available (Elder 2009; Vogel et al. 2009). The rainforest habitat and the heavily frugivorous diet establish some common aspects of the ecological niche across species. The distribution of fruit varies temporally, making it an unpredictable resource (Bartlett 2009b). In addition, resources like fruiting trees provide limited quantities of food, such that the amount of food available at any point in time varies and quantities differ between forest patches (Lappan 2010).

The impact of this ecological context on hylobatid social behaviour can be seen in their small average group size and low population density (Brockelman 2009; Brockelman et al. 2014). Ecological limitations constrain the evolution of behaviour and select for adaptive (but not necessarily optimal) tendencies towards particular social groupings (Clutton-Brock & Harvey 1977; Malone & Fuentes 2009). Optimal group sizes and life

history patterns (the timing of life events) are a result of food quality and distribution (van Schaik & van Hooff 1983), predation pressure (van Schaik & van Hooff 1983; van Schaik et al. 1983) and possibly parasite pressure (Freeland 1976). However, resource distribution probably has the largest influence on group living in primates (Wrangham 1980). Hylobatid social groups usually consist of a mated pair and one to three offspring with females producing a single offspring every 2 – 5 years (Palombit 1995).

Although there are many exceptions to this nuclear family model (Bleisch & Chen 1991; Jiang et al. 1999; Lappan 2007b; Barelli et al. 2008), group sizes very rarely exceed more than 10 individuals (including immatures). Reproduction is generally limited to a single female, even when additional adult-sized females are present in a group. The notable exceptions are the *Nomascus* spp. in which two females may reproduce simultaneously (Fan et al. 2006; Fan & Jiang 2010; Fan et al. 2010; Fan et al. 2015). Regardless, no hylobatid groups have been observed with more than two reproductive females. Adult pairs of all species are highly territorial and interactions between neighbouring groups can have lethal consequences (Palombit 1993). Small group size may be, in part, related to the characteristics of Asian equatorial evergreen rainforests (Fuentes 2000a). Fuentes (2000a) hypothesised that increasing resource pressure during their evolutionary history led first to fission-fusion groupings (i.e. large social groups that split up under resource pressure and re-form during seasons of abundant resource availability), then to the current territorial family pattern most commonly seen in extant hylobatids.

Despite more than 80 years of research on both wild and captive populations, which has established these underlying similarities in social organisation, knowledge of intra-group social behaviour is limited. In part, the lack of detailed research is due to the logistical difficulties researchers face in the hylobatids' rainforest habitat. However, hylobatids are also portrayed as less complex in their behaviour compared to the other

apes (Palombit 1994a; Fuentes 1998; Begun 2004; Reichard & Barelli 2008). This assumption partially stems from the types of behaviour investigated thus far in comparative studies. For example, hylobatids perform poorly in cognitive object-related tasks compared to hominids (Gossette 1973; Parker 1973; Abordo 1976; Cunningham 2006). In many cases this may be a result of the design of such experiments involving objects placed on a flat surface, which is more difficult for hylobatids to interact with due to their morphological adaptations for arboreality (Beck 1967).

Some of the apparent reduced complexity in hylobatid behaviour may also arise from their family-living social organisation (Whiten & Byrne 1988, p. 242). Early studies considered hylobatids relatively inflexible in their social behaviour, and related this to their 'simple' social structure (Chivers 1980, p.293; Kinzey 1987; Kamilar & Baden 2014). Other primates with a similar social organisation are less complex than large-group-living species in domains such as deceptive behaviour (e.g. Callitrichidae, Whiten & Byrne 1988). But family-living species display substantial cognitive function in other domains, including conflict resolution and cooperation (Shultz & Dunbar 2007; Burkart et al. 2009; Burkart & van Schaik 2010). More recent work on hylobatids reveals greater complexity in social behaviour than previously recognised, including: facial expressions (Waller et al. 2012), communicative gestures (Liebal et al. 2004), and intra-group vocalisations (Clarke et al. 2015). This mirrors paradigm shifts in understanding of other family-living primates (e.g. in the Callitrichidae, Morino 2009).

Behavioural variation within *and* between species may be explained by differences in ecological and sociodemographic variables among the observed social groups (Malone & Fuentes 2009; Wikberg et al. 2015). Differences in behaviour among individuals and social groups can arise from variation in individual behaviour or morphology in response to different socioecological contexts (phenotypic plasticity, Stearns 1989a; West-Eberhard 1989). Although long-term studies are still lacking for many hylobatid

species, data from the most commonly studied *H. lar* and *S. syndactylus*, as well as population-level comparisons of some species, indicate greater within-species variation in ecology and social behaviour than previously assumed (Brockelman 2009; Malone & Fuentes 2009; Lappan 2010; Dooley 2015). For example, while commonly labelled as socially monogamous, polygynous and polyandrous groups occur frequently in some populations, and these variations may be linked to ecological variables (E.g. *Nomascus concolor*, Bleisch & Chen 1991; Jiang et al. 1999; *Symphalangus syndactylus*, Lappan 2007b; *Hylobates lar*, Barelli et al. 2008). In addition, field research *within species* in the last two decades reveals greater deviation from the model nuclear family than was previously appreciated (Oka & Takenaka 2001); reports of mate desertion, take-overs, and re-mating following mate loss (Palombit 1994a; Brockelman et al. 1998) suggest that social organisations are flexible, and many groups are blended families. Relatively little is known about the reasons for such variability in social organisation; current research recognises the importance of this variability and of trying to gain a new perspective on hylobatid socioecology (Whittaker & Lappan 2009; Malone et al. 2012).

Despite these recent developments, few studies on hylobatids to date have explored the development of social behaviour beyond infancy, and the potential for plasticity in behaviour associated with the reproductive and socioecological context within groups. This is partially because research on the development of, and variation in, social behaviour is constrained by slow growth and long life spans. Hylobatids take at least 6 years to reach maturity (at least 8 years in the wild, Reichard et al. 2012), with some individuals exhibiting an age at first reproduction as late as 14 years of age (Brockelman et al. 1998). In contrast, the average duration of a study is usually less than six years (Reichard 2009). In addition, small group sizes (mean: 3.9 individuals, Malone & Fuentes 2009) limit the number of individuals that can be observed at any one time. In the wild, observations of intra-group social behaviour are made more difficult by the

hylobatids' tree canopy habitat. These limiting factors make it difficult to assess whether variation between social groups, populations and/or species stem from individual plasticity in hylobatids. This is unfortunate, because hylobatids have the potential to serve as a model case for investigating physiological and behavioural plasticity, for several reasons.

Phenotypic plasticity is more common in species that live in heterogeneous, unpredictable environments (Komers 1997; Snell-Rood 2013). In addition, behavioural plasticity is associated with larger brain size, since a larger neural network allows a greater capacity to respond instantaneously to various environments (Snell-Rood 2013). The benefits of phenotypic plasticity are also closely associated with a species' life history strategy. Life history theory is concerned with the allocation of an organism's limited time and energy to necessary functions, notably: growth, maintenance and reproduction (Gadgil & Bossert 1970; Stearns 1992). In mammals, the pattern of energy allocation across the lifespan is divided into a growth period in which no reproduction occurs, and a reproductive lifespan in which the energy put towards growth is reduced (and usually ceases). The timing of these transitions tends to be tightly conserved within a species due to their impact on reproductive success in a given environment (Hawkes 2006). However, because the timing of life history transitions relies broadly on physiological processes, selection for plasticity in physiological processes allows changes in life history in response to variable environments. Individual variation in the timing of life events certainly occurs in primates (Hawkes 2006; Strier 2008); the extent of these 'reaction norms' within a species are therefore of interest in measuring their potential for plasticity (Stearns 1989a).

Across species, the timing of life history transitions (e.g. age at weaning, age at sexual maturity, age at first birth, lifespan) are highly correlated, such that species that have a late age at weaning also have a late age at maturity, late age at first birth and long

lifespans (a 'slow' life history strategy, Harvey & Clutton-Brock 1985; Promislow & Harvey 1990). Importantly, a 'slow' life history strategy is associated with the expression of phenotypic plasticity because environmental change within an individual's lifetime is statistically more likely when life spans and developmental periods are long relative to the rate of change (Snell-Rood 2013). 'Slow' life histories thus create a more heterogeneous, unpredictable environment, which favours plasticity. Hylobatids, like the other apes, have large brains and 'slow' life histories relative to their body size (Judge & Carey 2000; Reichard & Barelli 2008). The small apes are therefore a particularly appropriate taxon for investigating individual flexibility in physiology and behaviour.

Observing the behaviour of captive individuals can fill some of the gaps in hylobatid research; hylobatids are common inhabitants of zoos the world over, and the structure of groups in captivity reflects the majority of wild groups. While the behaviour of captive individuals may not be wholly applicable to wild groups, captive groups provide an excellent opportunity to observe intra-group social behaviour, in the context of known variables (e.g. age and relatedness of individuals and reproductive status of females). In captivity, social interaction is limited by zoo management protocols and mature offspring cannot disperse. However, individuals in the same enclosure can completely avoid and ignore each other if necessary. The occurrence and degree of social interaction in captivity therefore reflects intentional behaviour, and allows detailed observation of changes in social relationships. Captivity also constrains the range of variation in behaviour associated with ecological variables such as resource availability. Thus, variations in social behaviour associated with variables other than food (such as the social context) can be better addressed.

WHAT THIS STUDY CONTRIBUTES

In this thesis, I explore the plasticity in behaviour and developmental timing in 3 species of hylobatids (silvery gibbons, *Hylobates moloch*, northern white-cheeked gibbons, *Nomascus leucogenys*, and siamangs, *Symphalangus syndactylus*). This is achieved by 1) describing the variation in behaviour among captive individuals and 2) quantitatively mapping differences in behaviour to group composition and female reproductive status. I also contribute the most comprehensive data on development of behaviour to date across the entire immature period using a combination of cross-sectional and longitudinal data. The result is a social family-level analysis of development and social dynamics, incorporating the behaviour of both parents and offspring.

The specific aims are to:

1. Describe social pair bonds and examine sex differences in the maintenance of the pair bond in captive gibbons and siamangs (Chapter 2),
2. Investigate the roles of captive hylobatid parents by looking at sex differences in activity and parental care and how these differ depending on the social and reproductive context (Chapter 3),
3. Collate and evaluate the available data in the literature on the timing of physiological and behavioural development in captive and wild individuals of known age (Chapter 4),
4. Describe and quantify behavioural development of captive immatures, relative to adults (Chapter 5),
5. Relate the timing and nature of behavioural development and family social dynamics, to a major event (birth of a sibling) and to sibship composition (Chapter 6),

6. Discuss how greater overlap in dependent offspring is facilitated by flexible social roles and life history adaptations in hylobatids (Chapter 7).

To address these aims, I observed and recorded the behaviour of 36 captive individuals in 13 social groups over a 5 year period from 2008 to 2012, including longitudinal sampling of 6 groups. These data were combined with previously recorded data for some families collected by Helen M Dooley in 2005/2006, such that some groups were observed multiple times over a 7 year time period. The hylobatid groups were housed at 6 Australasian Zoo and Aquarium Association (ZAA) accredited institutions in Australia and New Zealand (see Appendix A for details of research and ethics approvals). The observation of all of the individuals within each social group within a single study allows a family-level focus on the expression of social behaviour in the natal group. This produces detailed samples of behaviour that facilitate investigation of pair bonding, parental behaviour, immature development and family social dynamics.

STRUCTURE OF THE THESIS

This thesis is organised as a series of independent scientific papers with the aim of publishing in scientific journals. As such, each chapter includes specific introduction, methods, results and discussion sections, and there is some repetition of methodological details among chapters. To avoid redundancy in the thesis, methodological details that apply to all chapters are outlined only in the first experimental chapter (Chapter 2), and not repeated thereafter. I direct the reader back to Chapter 2 where necessary. The rationale behind each chapter is outlined below.

CHAPTER 2: THE SOCIAL PAIR BOND

Although hylobatids are demonstrably more flexible in their social organisation than previously thought, they are still most accurately described as being ‘monogamous’. Strong social bonds, or ‘pair bonds’ between male and female vertebrates have

previously been associated with social monogamy (Palombit 1999; Kleiman 1981). Hylobatids are commonly referred to as being 'pair bonded' (Palombit 1996); mated pairs occupy the same territory and synchronise their activities. The spatial proximity of a pair and synchrony of activity relies on investment by one or both partners into monitoring the movement of the mate and adjusting behaviour to maintain close proximity. The establishment and endurance of strong social bonds is suggested to involve emotional attachment with a hormonal basis (Dunbar & Shultz 2010). Furthermore, activities such as grooming or duetting are suggested to maintain social bonds between individuals (Dunbar 1991; Geissmann & Orgeldinger 2000; Hall 2004; Méndez-Cárdenas & Zimmermann 2009; Dunbar & Shultz 2010). Theoretical discussions of pair bonds predict that sex-biased investment (either overall or in different social contexts) reveals the ultimate adaptive explanations for the evolution of these social relationships (Fuentes 2000b; Fuentes 2002). Although some research has focused on the nature of pair bonds in hylobatids (Palombit 1992; Palombit 1994a; Palombit 1996; Geissmann 1999; Fuentes 2000a; Geissmann & Orgeldinger 2000; Poyas 2008), very little has explored variation in pair bonds in different contexts. In Chapter 2, I investigate the possible causes of variation in social relationships between captive hylobatid pairs, including sex differences in pair bonding behaviour. I predict that the expression of bonding behaviour between mates differs according to the social and reproductive context. The behaviour of 13 pairs is quantified, with the aim of comparing the social investment of each sex and whether this differs according to the presence of offspring, how long the pair have been together, and the reproductive status of the female (cycling, pregnant or lactating).

CHAPTER 3: PARENTAL BEHAVIOUR

The contribution of males and females to parenting effort varies across, and within, primate species. Females invest more energy into parenting effort than mating effort

and vice versa for males; although, some behaviours in males serve simultaneously as parenting and mating effort (van Schaik & Paul 1996). The social organisation of hylobatids ('obligate' social monogamy) not only predicts strong social pair bonds, but also predicts substantial male involvement in parental care duties. However, in hylobatids, maternal care of offspring is the default, and male care varies. This division of labour may be related to the importance of territorial defence to ensuring access to resources, and the energy and time costs associated with balancing resource defence with parental care. In Chapter 3, I explore whether sex differences in activity budgets are related to offspring presence and female reproductive status by comparing the behaviour of 7 pairs with offspring and 6 pairs without offspring. In addition, I describe parental roles within the 7 families, and investigate how male and female participation in parental care differs with the reproductive status of the female and the number of offspring.

CHAPTER 4: THE TIMING OF DEVELOPMENT

Given the importance of developmental timing to life history strategies, a more comprehensive understanding of hylobatid development is worthwhile. Accurate description of the timing of life events (particularly behavioural development at puberty) relative to chronological age is lacking for hylobatids. Quantifying the individual variation in developmental timing is of interest considering the potential for plasticity favoured by the overall 'slow' life history pattern for this taxon. In Chapter 4, I describe the chronological timing of behavioural measures of puberty and sexual maturity in 12 immatures of known age and compare this to the limited data in the literature. This provides a preliminary outline of the developmental pattern as well as a comparison with other primates. Furthermore, because hylobatid research commonly utilises only small sample sizes, reviewing the body of data allows identification of sources of variation in developmental timing within species. I discuss the overall pattern

of development and the degree of variation in captive and wild populations using these preliminary data.

CHAPTER 5: THE BENEFITS OF SLOW MATURATION

Although developmental variability in hylobatids is understudied, the slow pace of development is well established (Barrickman et al. 2008; Reichard & Barelli 2008). White-handed gibbons (*H. lar*) have the lowest production coefficient (a measure of growth velocity) of all the apes (Mumby & Vinicius 2008), with the largest hylobatid species (*S. syndactylus*) growing as slowly as humans (Mumby & Vinicius 2008). Long juvenile periods are inherently interesting to life history theorists because of their impact on the age at reproduction, but the benefits of delaying reproduction have so far been difficult to decipher for primates in general (Janson et al. 1993). Since the selective pressures favouring slow growth and delayed maturation vary among species, it is important to explore development within a taxon in the context of their socioecological niche. In Chapter 5, I quantify the activity budgets and social behaviour of 14 immature hylobatids across the entire developmental period and compare each measure of behaviour to a sample of adults. Comparing the behaviour of juvenile and adult primates can indicate the relative importance of different hypotheses for slow maturation (Schuppli et al. 2012). For example, juvenile engagement in particular activities (such as foraging or social activity) may reflect the importance of learning particular skills during development (Watts & Pusey 1993). Furthermore, an important contribution to the age at first reproduction in hylobatids is the availability of mates and vacant territories. Delayed dispersal is an important demographic characteristic commonly observed in other family-living species (Emlen 1995; Kokko & Ekman 2002) and has been discussed for some hylobatids by Brockelman et al (1998) and Huang et al (2013). Thus, in Chapter 5, I also describe the behaviour and social relationships of grown offspring resident in their natal groups.

CHAPTER 6: SIBSHIP COMPOSITION AND SOCIAL RELATIONSHIPS

Despite a relatively long juvenile period (8+ years), hylobatids produce overlapping dependent offspring every 2 – 5 years. Considering the importance of resource availability on hylobatid group size and population density, the impact of supporting multiple dependent offspring could potentially increase resource stress within the family group. This potential for increased conflict with sibling births or sibling presence has been mentioned in passing by some researchers (Aldrich-Blake & Chivers 1973; Chivers 1974, p. 231; Geissmann 1993, p. 147), but has never been investigated quantitatively. Chapter 6 assesses the impact of increasing family size (via birth of siblings and presence of younger siblings) on social relationships within the family. This focus on flexible social roles is made possible by the existing variation in captive hylobatid families. The composition of groups allows a comparison of the behaviour of one family before and after the birth of two different infants, as well as comparison of the behaviour of immatures with varied sibling compositions. Comparing the behaviour of immatures in differing sibling compositions improves understanding of the influence of social context on behavioural development, relative to the influence of chronological age.

CHAPTER 7: CONCLUSIONS AND GLOBAL DISCUSSION

In the final chapter, I outline how the adoption of a similar framework to that which has emerged from decades of discussion on human life history strengthens understanding of hylobatid family life. Many of the emergent themes in the thesis reflect similar discussions in humans, including: slow growth combined with overlapping dependents, and flexible social roles within a small, highly related kin group. Together, these life history and social characteristics reflect a cooperative breeding strategy that reduces the daily cost of reproduction for females, and allows faster reproductive rates than would be otherwise possible.

CHAPTER 2 THE SOCIAL PAIR BOND

CHAPTER 2 THE SOCIAL PAIR BOND

INTRODUCTION

Pair bonds are long-term associations between a male and female of the same species. Although there is no concrete definition of pair bonds that readily allows cross-species comparison (Kleiman 1981; Fuentes 2002), pair bonds are usually defined as social affiliations between a male and female that are distinct from bonds formed between other adults. Pair bond definitions often include close spatial proximity and synchronicity of activities, affiliative behaviour (grooming, play) and energetic investment in the mate (Eisenberg et al. 1972; see Table 2.1 for those relevant to hylobatids). In mammals, pair bonds have become synonymous with monogamy, as both a mating and a social system (Kleiman 1977; Fuentes 2002).

There are three interrelated components contributing to this association: exclusively monogamous mating (the sexual pair bond, as per Fuentes 2002), two-adult grouping patterns (a male and female occupying the same territory, as per Fuentes 1998), and specific affiliative and bonding behaviours between a single male and female (the social pair bond, as per Fuentes 2002). These components are logically connected because there are fitness advantages to social pair bonds for males that are already mating monogamously and occupying a female's territory (Palombit 1999). When males are limited to mating with only one female, mate guarding is both less costly and more crucial to reproductive success, and this can be achieved by maintaining close proximity to the female.

Table 2.1 Presence of behaviours that may function to maintain pair bonds in hylobatids

Behaviour	Present?	Species (source)
Contact calls	Yes	<i>H. lar</i> (Ellefson 1974)
Low aggression frequency	Yes	<i>H. lar</i> (Bartlett 2009a) <i>H. lar</i> , <i>S. syndactylus</i> , <i>N. leucogenys</i> (Bricknell 1992) <i>H. lar</i> , <i>H. agilis</i> and <i>S. syndactylus</i> (Gittins & Raemaekers 1980)
Duetting	Mostly	All species except <i>H. klossii</i> and <i>H. moloch</i> (Cowlshaw 1992)
Territorial display	Mostly	<i>H. lar</i> (Geissmann 2009) <i>S. syndactylus</i> (Chivers 1974, p. 238)
Assistance during aggressive encounters	Possibly	<i>H. lar</i> (Ellefson 1974)
Close spatial proximity	Variable	Present in <i>S. syndactylus</i> (Chivers 1976) <i>S. syndactylus</i> , <i>H. lar</i> (Palombit 1996) But less so in <i>H. klossii</i> (Dooley 2015)
Synchronous activity	Variable	Present in <i>S. syndactylus</i> (Chivers 1976) But less so in <i>H. klossii</i> (Dooley 2015)
Grooming	Variable	<i>H. lar</i> (Brockelman 2009)
Other physical contact (embrace)	Variable	<i>S. syndactylus</i> (Palombit 1996)
Play	Infrequent	<i>H. lar</i> (Bartlett 2003)
Copulation	Infrequent	<i>H. lar</i> (Ellefson 1974)
Food transfer	Infrequent	<i>H. lar</i> (Berkson & Schusterman 1964) <i>H. lar</i> , <i>S. syndactylus</i> , <i>N. leucogenys</i> (Bricknell 1992) <i>S. syndactylus</i> (Fox 1977)

Monogamous mating and two-adult groups therefore both entail some spatial or social association between a pair, but do not imply other behaviours that have been suggested to characterise pair bonds. Because many behaviours such as overt affiliative bonds, territoriality, duetting, and direct paternal care do co-occur with monogamous mating or two-adult groups in many species, monogamy and pair bonds have understandably been used as catch-all terms that imply a suite of life history and behavioural characteristics (Kleiman 1981; Fuentes 1998; Palombit 1999). This is problematic when applied to species which do not fit the mould (Fuentes 2000a; Komers 1996). For example, the small apes (family Hylobatidae) are usually considered to be pair bonded, monogamous primates (Palombit 1996; Fuentes 2000a). All hylobatid species occur primarily in two-

adult groups, but hylobatids are not exclusively monogamous maters and exhibit little direct paternal care (see Table 3.2 in Chapter 3). Substantial research has focused on the potential role of duetting in strengthening or advertising pair bonds in hylobatids, but the evidence is so far inconclusive (reviewed by Fuentes 2000a). In addition, two species of gibbon do not duet (Table 2.1), suggesting that there are additional mechanisms maintaining pair bonds beyond singing behaviour. Evidence for a pair bonding role of grooming in hylobatids is also yet to be provided, although it is often assumed (Ellefson 1974, p. 94; Brockelman & Srikosamatara 1984; Fischer & Geissmann 1990; Cowlshaw 1992). In captive *S. syndactylus*, Geissmann & Orgeldinger (2000) did find a correlation between grooming frequency and duetting frequency across 10 pairs, but no study has yet linked pair grooming to reproductive success. It is likely that the function and evolutionary history of pair bonding behaviours differ between species (Fuentes 1998; Kappeler & van Schaik 2002), especially given that strong male-female bonds also occur in polygynous primates (Palombit, 1999). It is therefore important to separate these characteristics (Gowaty 1996), because some of the selective pressures favouring two-adult groups (that is, a long term spatial association between a male and female) may not simultaneously select for other pair bonding behaviours (e.g. grooming).

Several hypotheses have been proposed to explain the occurrence of two-adult groups in mammals, and each has been associated with specific predictions for the appearance of the social pair bond (Malone & Fuentes 2009, summarised in Figure 2.1). The investment of each sex into maintaining spatial proximity and social interactions with their mate is suggested to reflect the ultimate reason for long-term associations between males and females across species. The “females as a limited resource” hypothesis states that ecological factors select for widely-dispersed females and it is therefore too costly for males to defend more than one female (Bartlett 2009b; Lukas & Clutton-Brock

2013; but see van Schaik & Dunbar 1990). Males that are limited to defend only one female are predicted to maintain close proximity to their mate for more effective mate guarding (Palombit 1999; Fuentes 2002), thus long term associations between a single male and female could simply be the result of widely dispersed females plus male mate guarding (Pathway A in Figure 2.1). If females do not otherwise benefit from this arrangement, this hypothesis predicts one-sided, male-biased associations between a male and female.

Alternatively, females might accept the presence of males in their territory when the benefits of social tolerance outweigh the costs of resource sharing and rejecting male guarding (van Schaik & Kappeler 1997). This balance might be tipped in favour of tolerance when males can provide a service that improves female reproductive success (Pathway B in Figure 2.1). This is suggested by the male defence hypotheses, which incorporate male defence of resources, and defence against predators, harassment and infanticide from male conspecifics (van Schaik & Dunbar 1990; van Schaik & Kappeler 1997; Palombit 1999; Fuentes 2002). In contrast to the “females as a limited resource” hypothesis, these hypotheses all predict greater female than male investment in maintaining the pair bond. Importantly, pathways A and B (Figure 2.1) focus on either male or female interests and assume that selective pressures on males and females operate independently. If both sexes benefit from cooperation, or if reproduction is not possible without it, then reciprocal social bonds may form (Kleiman 1977, pathway C in Figure 2.1).

Accumulating data on pair bonding behaviour has so far proven to be a difficult task, the result being that many generalisations about hylobatids are based on limited data from small numbers of individuals across few study populations (both captive and wild, Table 2.2). So far, there is no indication of a consistent sex-bias in maintaining the pair bond across hylobatid species (Table 2.2). Considering the position that hylobatids have

previously held in theoretical discussions over the evolution of monogamy and pair bonds (see Fuentes 2000a; Morino 2009 for a summary of research on monogamy in hylobatids), in this chapter I contribute to the literature quantifying pair bonding behaviour in hylobatids. One potential explanation for the variation in sex-biased investment among hylobatid pairs is that sex differences in behaviour depend on the socioecological context.

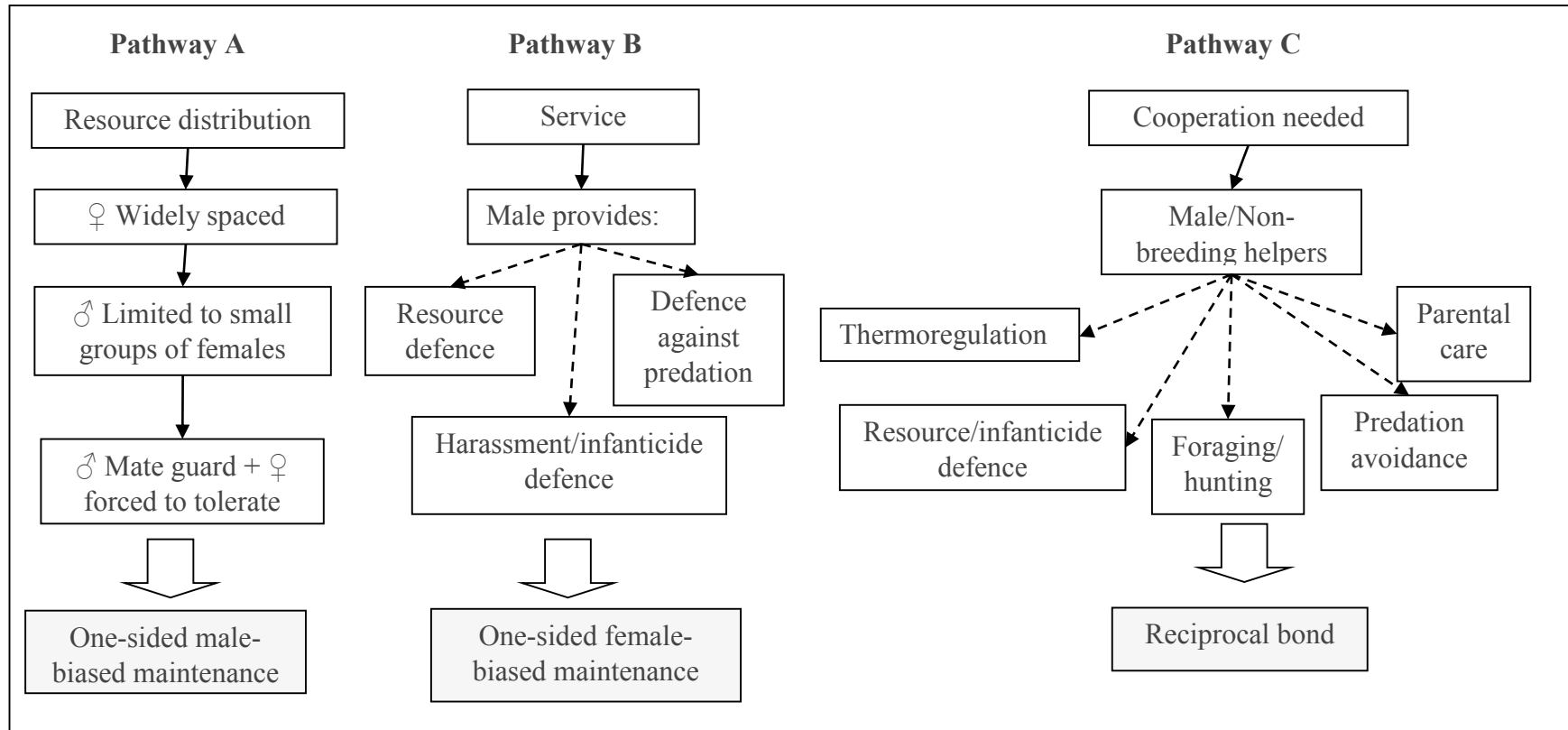


Figure 2.1 Hypotheses for the evolution of social pair bonds

Table 2.2 Sex differences in hylobatid mate grooming and proximity maintenance in the literature

Species	Context	Source ¹	Grooming ²			Proximity maintenance ²		
			Male-biased	Female-biased	Equal	Male-biased	Female-biased	Equal
<i>H. lar</i>	Wild	1, 2, 3, 4	3	2	1 ³			
	Captive	5, 6		6				
<i>S. syndactylus</i>	Wild	1, 7, 8	4			12	3	1
	Captive	9, 6, 10	10	3	2			
<i>N. leucogenys</i>	Captive	6, 11, 10, 12	1	9				1
<i>Hoolock hoolock</i>	Wild	13	3					
TOTAL # of pairs			9	> 12	> 3	17	> 2	2

¹1 = Palombit (1992), 2 = Ellefson (1974), 3 = Brockelman (2009), 4 = Bartlett (2009a), 5 = de Veer & van den Bos (2000), 6 = Bricknell (1992), 7 = Chivers (1974), 8 = Morino (2012), 9 = Fox (1972), 10 = Rosenkranz (2002), 11 = Lukas et al. (2002), 12 = Poyas (2008), 13 = Ahsan (2000)

²Numbers represent the number of pairs

³Brockelman (2009) notes variation in sex-bias of mate grooming with time since pair formation

Primates are known to be flexible in their behaviour (Chapman & Rothman 2009). Investment by an individual into maintaining a social bond requires either time or energy, both of which are limited resources. Other necessary daily activities (e.g. foraging) also require time and energy, therefore the expression of bonding behaviour at any point in time should depend on other demands on the individual's activity budget, as well as on the behaviour of the mate. That individuals respond variably to differing socioecological contexts predicts that primate pair bonding behaviour is sensitive to current conditions and pair bonds are therefore dynamic. Sex-biases in investment into the pair bond may therefore only occur in certain contexts. For example, female white-faced saki monkeys (*Pithecia pithecia*) are more responsible for maintenance of proximity to the mate during times of infant vulnerability (Thompson & Norconk 2011). Similarly, in white-handed gibbons, Brockelman (2009) notes that grooming patterns within pairs switch over time from female-biased to male-biased. Given the flexibility of primate behaviour and the observed variation in social behaviour among hylobatid pairs, it is likely that hylobatid pair bonding behaviour varies across the reproductive lifespan in a way which increases fitness.

In this chapter, I contribute to the discussion on hylobatid pair bonds in 2 ways: 1) by describing pair bonding behaviour in 13 captive hylobatid pairs using consistent behavioural observation methods, adding to the accumulation of data in the literature, and 2) by exploring how behaviours considered to be involved in pair bonding differ with the social and reproductive context. Specifically, I investigate whether investment of each sex into the pair bond and the pair bond itself differs depending on the presence of offspring, the length of time that the pair have been housed together, or the reproductive status of the female. I explore this question using a mixed sample of longitudinal and cross-sectional data from captive groups (i.e. comparing across pairs that differ in presence of offspring, length of pair bond and female reproductive status).

METHODS

STUDY ANIMALS

I collected behavioural observations on 13 pairs (six *N. leucogenys* pairs, two *H. moloch* pairs and five *S. syndactylus* pairs), including pairs with and without offspring, and longitudinal samples from some pairs in different years, or before and after a birth or mate change (Table 2.3). Three of the groups were also observed in 2005 (Dooley 2006). Pairs are labelled with a code that denotes the species (WC = white-cheeked gibbons, *N. leucogenys*, Silv = silvery gibbons, *H. moloch*, Siam = siamang, *S. syndactylus*), composition (F = family with offspring, P = pair with no offspring, StepF = step-family with unrelated offspring) and sampling period (T1-6) for pairs that were sampled longitudinally, see Table 2.3. One group contained an adopted immature that was unrelated to the adult pair; I included this pair with pairs that had their own biological offspring in the group. Some females were on oral contraceptives (combined pill microgynon®) for breeding management reasons. Adults were defined as being ≥ 6 years of age, removed from their natal groups and housed with at least an opposite sex adult. Adult females ranged in age from 6.1 to 31.7 years old, while adult males ranged from 7.9 to 38.5 years old (Table 2.3), and pair bond length ranged from 0 to 23 years since introduction (Table 2.3).

I assumed that all pairs were pair bonded despite the fact that captive gibbons have little, if any influence over their mate choice. This is a limitation of captive studies that is presently unavoidable; however, there is some limited assortment that occurs during pair introductions in captivity. For example, pairs that show sustained aggression or who avoid each other and are not seen mating are likely to be repaired with other individuals by keeping staff if possible. All pairs in this study except one were observed copulating and grooming. The outlying pair (Siam-P2) were never seen copulating and only the female groomed the male, but they did play with each other.

Table 2.3 Characteristics of pairs during each sampling period

Pair code ¹	Male + Female	Sampling date range	Length of pair bond (years)	Age of male (years)	Age of female (years)	N (10-day samples)		Female reproductive status ³
						Activity budget ²	Social activity ²	
WC-F1-T1	Phillip + Viann	18.07.2005 – 04.01.2006	5	33.3	12.6	36	-	Lactating
WC-F1-T2		14.02.2008 – 22.06.2008	8	35.8	15.1	22	-	OCP
WC-F1-T3		24.04.2010 – 21.08.2010	10	38	17.3	24	24	Cycling
WC-F1-T4		29.04.2011 – 06.08.2011	11	38.5	18.1	20	20	OCP
WC-P1	Kayak + Robyn	18.07.2005 – 28.07.2005	5.5	12.7	13.5	4	-	OCP
WC-P2-T1	Kayak + Nelly	27.09.2005 – 04.01.2006	0	12.9	9.5	19	-	Cycling
WC-P2-T2		14.02.2008 – 22.06.2008	3.25	15.4	12	22	-	OCP
WC-P3	Remus + Viet	01.10.2010 – 19.11.2010	4.08	14.5	11.6	10	10	Cycling
WC-P4	Vilson + Robyn	08.02.2011 – 19.03.2011	5.42	23.7	19.1	8	8	OCP
WC-StepF-T1	Tao + Jermei	13.06.2010 – 10.09.2010	0	8.1	8.1	16	16	Cycling
WC-StepF-T2		19.04.2011 – 15.09.2011	1	8.9	9	26	26	Pregnant
Silv-F1-T1	Jury + Hecla	18.07.2005 – 04.01.2006	13	19.5	22.6	36	-	Lactating
Silv-F1-T2		14.02.2008 – 25.05.2008	16	22.1	25.1	20	-	Pregnant
Silv-F1-T3		26.05.2008 – 02.07.2008	16	22.1	25.1	8	-	Lactating
Silv-F1-T4		24.04.2010 – 12.07.2010	18	24.3	27.3	17	17	Pregnant
Silv-F1-T5		13.07.2010 – 10.09.2010	18	24.3	27.3	10	10	Lactating
Silv-F1-T6		19.04.2011 – 15.09.2011	19	25	28	25	25	Lactating
Silv-F2-T1	Arjuna + Layar	14.01.2010 – 03.04.2010	1.16	9.4	8	16	16	Lactating
Silv-F2-T2		13.02.2012 – 03.04.2012	3.16	11.3	9.9	12	12	Pregnant
Siam-F1-T1	Armstrong + Fern	14.01.2010 – 03.04.2010	14	28.1	29.2	15	15	Lactating
Siam-F1-T2		13.02.2012 – 03.04.2012	16	29.8	30.8	12	12	Lactating
Siam-F2	Niran + Mang	01.10.2010 – 19.11.2010	13.25	21.7	22.3	10	10	Cycling
Siam-F3	Irian + Suli	01.10.2010 – 19.11.2010	4.75	9.6	10.6	10	10	Cycling
Siam-P1	Itam + Iuri	09.01.2011 – 07.02.2011	23	26.8	31.7	6	6	Cycling
Siam-P2	Iwani + Kera	10.12.2010 – 08.01.2011	1	7.9	6.1	6	6	Cycling

¹Pairs are labelled with a code that denotes the species (WC = white-cheeked gibbons, *N. leucogenys*, Silv = silvery gibbons, *H. moloch*, Siam = siamang, *S. syndactylus*), composition (F = family with offspring, P = pair with no offspring, StepF = step-family with unrelated offspring) and sampling period (T1-6) for pairs that were sampled longitudinally.
²Detail on data sets is available in Appendix C
³OCP = Oral contraceptive pill

BEHAVIOURAL OBSERVATIONS

Continuous focal animal sampling (Altmann 1974) was used to record the proportion of time spent doing activities (e.g. grooming) and the proportion of time spent with particular group members (e.g. time spent in proximity to mate). This was achieved using continuous recording on a laptop computer during 10-minute intervals. Ten minutes was decided to be the maximum possible length of recording sessions to avoid observer fatigue and all ten minute samples were separated by a 5 minute break.

Observations were generally conducted on weekdays at each zoo and ranged from 3-6 days a week in frequency, averaging 5 hours per day. Starting times varied during the week between dawn, 9am and 12 noon, and this pattern was followed consistently at each zoo so that results were comparable among groups. Each social group was observed once per day during these hours.

Individuals were sampled once or twice per day and never sampled twice in a row. Each day the observer cycled through group members in a pre-determined order. Focal samples were stratified such that all individuals were sampled across all times of day (from dawn to approximately 16:30) for the entire observation period. Event behaviours (e.g. grooming solicitation) were tallied during all focal observations and calculated as frequencies per hour of focal sampling. At the end of each focal sample the position of all individuals in the group was estimated and dyad distances were calculated using estimated enclosure maps (see Appendix B for details). Behaviours recorded for this study are listed in Appendix C.

Duration behaviours (Data sets 1 & 2, Appendix C) were calculated as proportions of in-sight-time:

$$\% \text{ time spent in behaviour A} = \text{duration of behaviour A} / (600 \text{ seconds} - \text{duration of out of sight time})$$

Only focal samples in which the focal animal was in view of the observer for ≥ 60 seconds were included in analyses. Observer reliability between the two different observers was assessed by comparing non-social behaviours of the same adults during 2005/2006 and 2008. Of the five behaviours in the comparison (eating, total movement, total play, total social grooming, and self-grooming), only the proportion of time spent eating differed between observers ($t(264.8) = 2.38$, $p = 0.018$). In addition, behavioural categories devised for this project were based on definitions from the 2005/2006 study by Helen M Dooley, and were defined in such a way that they could be directly compatible.

For data collected in 2010 onwards, during each 10-min focal sample, all approaches (approaching another individual to within arm's reach or ~ 1 m) and retreats (leaving from within arm's reach, or ~ 1 m, of another individual) by all individuals in the group were recorded. Only those approaches and retreats made by the focal animal are included in analyses. In most cases, approaches and retreats were one-sided (i.e. it was clear which individual was approaching and retreating, particularly when the other individual(s) involved were stationary). On the rare occasions when two or more individuals approached or retreated simultaneously, this was still scored as an approach or retreat for the focal animal. Since all group members were sampled equally often, this methodology is unlikely to bias the results.

STATISTICAL ANALYSES

All proportions were transformed using the arcsine square root transformation to improve normality, and all frequency behaviours were transformed using the square root function. Hinde's index for maintenance of proximity (Martin & Bateson 1993) was calculated for each 10-day period whenever the frequency of approaching and retreating for either member of the dyad was > 0 . The equation is as follows:

$$A's\ responsibility\ for\ maintaining\ proximity = U_A / (U_A + U_B) - S_A / (S_A + S_B)$$

Where:

U_A is the frequency per hour that A approached B;

U_B is the frequency per hour that B approached A;

S_A is the frequency per hour that A retreated from B;

and S_B is the frequency per hour that B retreated from A.

The resulting index ranges from -1 to +1; for all pairs, individual A is the male and individual B is the female, thus a value closer to +1 indicates greater male responsibility for maintaining proximity to the mate and a value closer to -1 indicates greater female responsibility for maintaining proximity to the mate.

Proportions, events, distances and Hinde's indices calculated for each 10-minute focal sample were aggregated across a 10-day period, in order to retain an adequate sample size for each individual while also homogenising samples taken at different times of day. The proportion of time spent grooming the mate was analysed using a two-step process due to the low frequency and duration of this behaviour. I first modelled the presence or absence of grooming during a 10-day period (logistic regression) and then modelled the proportion of time spent grooming when grooming did occur (truncated linear regression).

In *N. leucogenys* and *S. syndactylus* groups, length of pair bond was significantly shorter in non-parents compared to parents (pair $\mu = 4.29$, family $\mu = 7.27$, $t_{115.8} = -3.9$, $p < 0.001$, Figure 2.2). Because the presence of offspring may indirectly influence pair bonding behaviour via changes in activity budgets, I first compared the behaviour of pairs with and without offspring. Therefore, all behaviours were initially compared across group composition for *N. leucogenys* and *S. syndactylus* pairs using generalised linear mixed models (GLMM) via the function "lmer" in the R (v.2.15.2) package lme4

(version 0.999999-0) (Bates et al. 2012; R-Core-Team 2012). Models of individual behaviour included ‘individual ID’ as a random effect, and dyadic behaviour included ‘group ID’ as a random effect, due to repeat measures.

The limited sample size required pooling of species to investigate variation and plasticity in behaviour. ‘Species’ was included in all models throughout the thesis as a fixed effect, to control for underlying differences in behaviour frequency and duration. Although *S. syndactylus* are suggested to be different in some social behaviours, particularly in the occurrence of infant carrying by some fathers (Palombit 1996), the limited sample size precluded analysis of interaction effects between species and social/reproductive context. It is worth noting that the male *S. syndactylus* who had an infant (in two different sampling years) was never observed to carry either infant. Further, due to the overall similarities in ecology and social organisation across species, and the focus on plasticity of behaviour, I predicted that individual responses to variable social and reproductive contexts should be consistent across species. This should particularly be the case in captive groups, which are usually kept as socially monogamous groups in all species.

If pair bonding behaviour was not different between pairs with resident offspring and pairs without resident offspring, data were pooled to investigate whether pair behaviour varied with the length of the pair bond. Otherwise, I controlled for group composition in order to look independently at the influence of pair bond length by excluding pairs without offspring. Length of pair bond was also positively correlated with both male age (where age = mean age during sampling period, $r = 0.48$, $p < 0.001$, $N = 206$ 10-day samples), female age ($r = 0.97$, $p < 0.001$, $N = 211$ 10-day samples) and enclosure size ($r = 0.37$, $p < 0.001$, $N = 417$ 10-day samples). Newer pairs tended to be younger, and were kept in smaller enclosures due to introduction and quarantine protocols and smaller group sizes in young pairs with fewer offspring. As length of pair bond was the

predictor variable of interest, I did not include age or enclosure area in regression models.

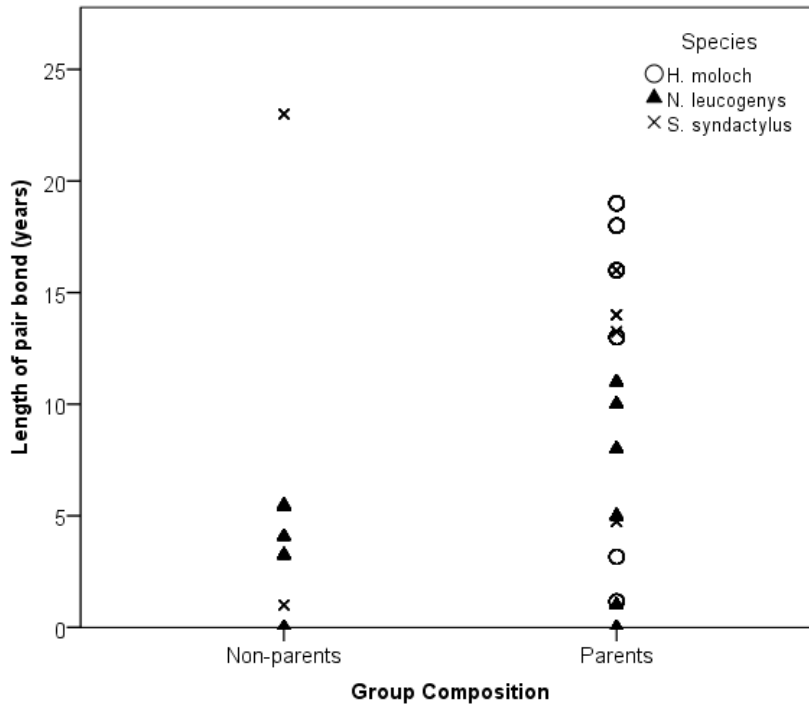


Figure 2.2 Length of the pair bond in groups with and without offspring $N = 25$ groups, but some markers overlap due to identical length of pair bond

Behaviours were analysed across length of pair bond and female reproductive status (cycling, pregnant/OCP, lactating) using GLMMs. Individual behaviours (e.g. grooming mate) were analysed within each sex. Females that were on oral contraceptives during the study were pooled with pregnant females under the assumption that the contraceptive method may alter the signals received by males as to the female’s fertility. Overall sex differences in individual behaviours were analysed cross-sectionally using GLMMs. Sex differences in behaviour were then analysed within pairs for each sampling period using t-tests. Due to the small sample size and uneven distribution of female reproductive status among species, interaction terms were not included in the models.

Residuals and fitted values were plotted for each model and visually checked for normality of residuals and homoscedasticity across the fitted values (Zuur et al. 2009). I calculated Markov-chain Monte Carlo (MCMC) p-values using the “pvals.fnc” function in the languageR package (v.1.4) (Baayen 2011). For predictor variables with more than 2 levels, I used the “aov.lmer” command in the lme4 package to determine whether that predictor had a significant effect on the response variable overall. P-values for the logistic models are based on the z-score. Degrees of freedom for t-tests are adjusted for unequal variances where Levene’s test for homogeneity of variances was significant. Significance was set at $\alpha = 0.05$ but I also report trends where $0.05 \leq p \leq 0.10$.

RESULTS

GENERAL DESCRIPTION OF DIURNAL PAIR BONDING BEHAVIOURS

Pair means (\pm S.D.), ranges and sample sizes are displayed in Table 2.4. On average, paired individuals spent 30% of their time within arm’s reach of each other, but only 10% of time was spent in physical contact with the mate, and an additional 3% of time was spent actively grooming the mate (Table 2.4). Play, initiation of play, solicitation for grooming and food transfers were infrequent between pair mates, and frequencies of aggression were also low (0.15 aggressive acts/hr on average between pair mates, Table 2.4). Maintenance of proximity was on average, equal between the two sexes (Table 2.4).

Table 2.4 Means for pair bonding behaviours per 10-day period, standard deviations, range and sample size across pairs

Type of data	Behaviour	Mean (all pairs)	S.D.	Range	Total N (pairs ¹)	N (10-day samples)
<i>Proportion of activity budget</i>	Time in proximity to mate	0.31	0.25	0.1 – 0.54	17	243
	Time in contact with mate	0.13	0.18	0.0006 – 0.38	15	212
	Time grooming mate	0.03	0.07	0 – 0.11	25	412
	Time in non-grooming contact with mate	0.10	0.18	0.006 – 0.30	15	212
	Time in non-contact proximity with mate	0.18	0.17	0.08 – 0.44	15	212
	Time playing with mate	0.002	0.01	0 – 0.01	11	243
<i>Frequency/hr of focal sampling</i>	Male solicitation of grooming	0.30	0.84	0 – 1.1	21	158
	Female solicitation of grooming	0.19	0.46	0 – 0.46	21	159
	Male grooms mate	2.12	3.41	0 – 6.7	17	121
	Female grooms mate	2.17	3.08	0 – 6.1	17	121
	Male initiation of play	0.26	1.93	0 – 1.8	17	121
	Female initiation of play	0.19	0.61	0 – 1.5	17	121
	Copulation	0.34	0.88	0 – 2.5	21	158
	Food transfer between mates	0.02	0.10	0 – 0.15	21	317
	Food transfer success (proportion of attempts that were successful)	0.75	0.40	0 - 1	11	27
	Aggression towards mate (male)	0.10	0.34	0 – 1.7	21	158
	Aggression towards mate (female)	0.19	0.43	0 – 0.92	21	159
	Approach mate (male)	2.21	2.31	0.46 – 5.5	17	121
	Approach mate (female)	3.46	6.05	0.56 – 20.9	17	121
	Retreat from mate (male)	2.85	4.45	0.24 – 13.9	17	121
	Retreat from mate (female)	2.52	2.36	0.76 – 5.3	17	121
<i>Distance</i>	Distance (metres)	3.16	1.67	1.7 – 4.8	20	145
<i>Frequency/10 days</i>	Duetting	2.2	2.8	0.5 – 13.7	14	105
<i>Index/10days</i>	Hinde's index (for male)	0.001	0.52	-0.68 – 0.64	17	100

¹Includes some longitudinal sampling periods for some groups

SEX DIFFERENCES IN PAIR BONDING BEHAVIOURS

There were no overall sex differences in the duration or frequency of individual pair bonding behaviours when all pairs were pooled. To investigate this further, I looked at sex differences within each pair during each of their sampling periods (if sampled more than once in different contexts) using t-tests. The number of pairs in which each behaviour was more female-biased, more male-biased, or in which there was no sex difference, are displayed in Table 2.5. Non-significant trends are included as sex-biases. The results were similar to the pooled results, showing very few sex differences in pair bonding behaviour and, where there was a difference, there was no consistent direction towards a male or female bias (Table 2.5).

VARIATION IN PAIR BONDING BEHAVIOURS AMONG PAIRS

Most of the pair bonding behaviours measured showed variation among pairs, and also within pairs that were sampled in different group compositions. Figures 2.3 A-G show the means for pair behaviours for each pair in each sampling period. Figures 2.4 A-E show the means for individual behaviours for males and females of each pair in each sampling period.

Table 2.5 Sex differences in pair bonding behaviour

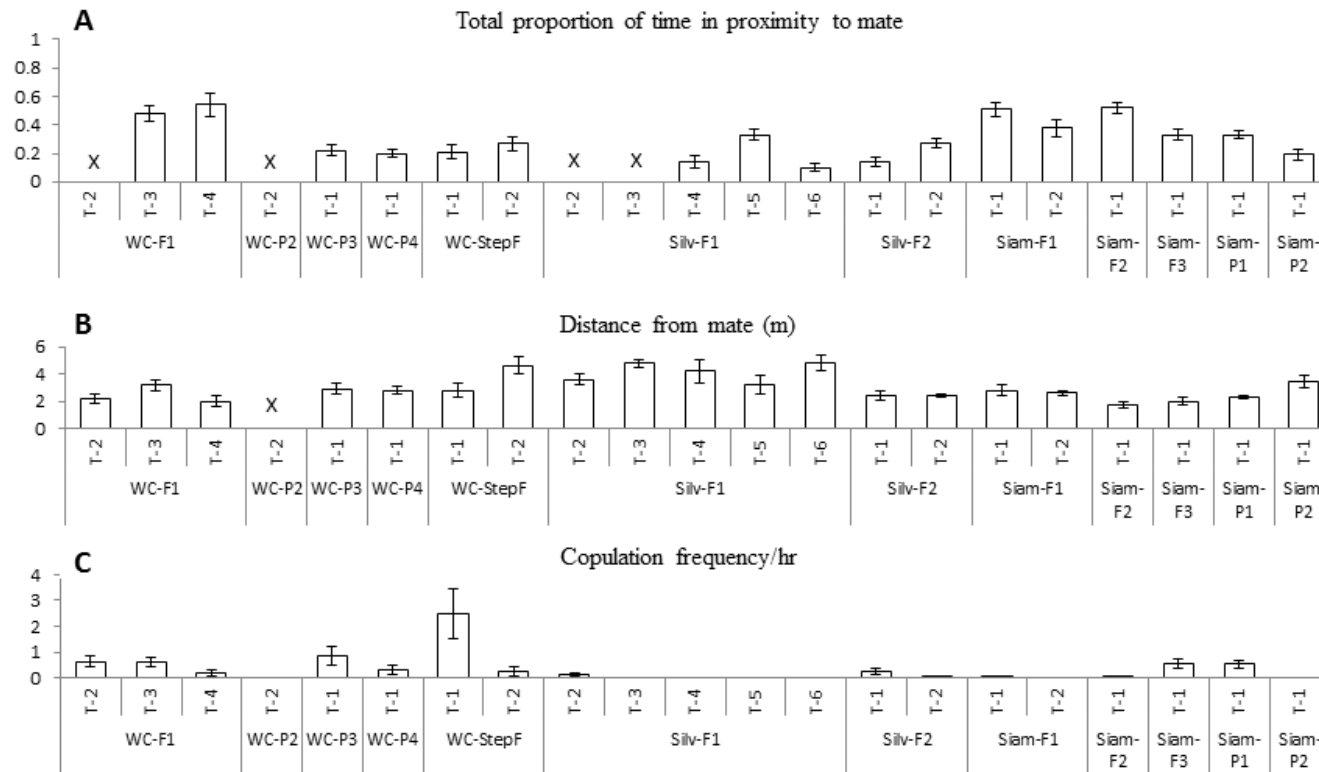
	Truncated grooming duration	Grooms mate F/hr ¹	Solicit grooming F/hr	Approach mate F/hr	Leave mate F/hr	Initiate play F/hr	Aggression F/hr
No sex difference	78%	63%	94%	65%	53%	89%	81%
Female-biased ²	17%	18.5%	0%	24%	29%	11%	19%
Male-biased ²	5%	18.5%	6%	11%	18%	0%	0%
TOTAL # pairs	18	16	18	17	17	9	16

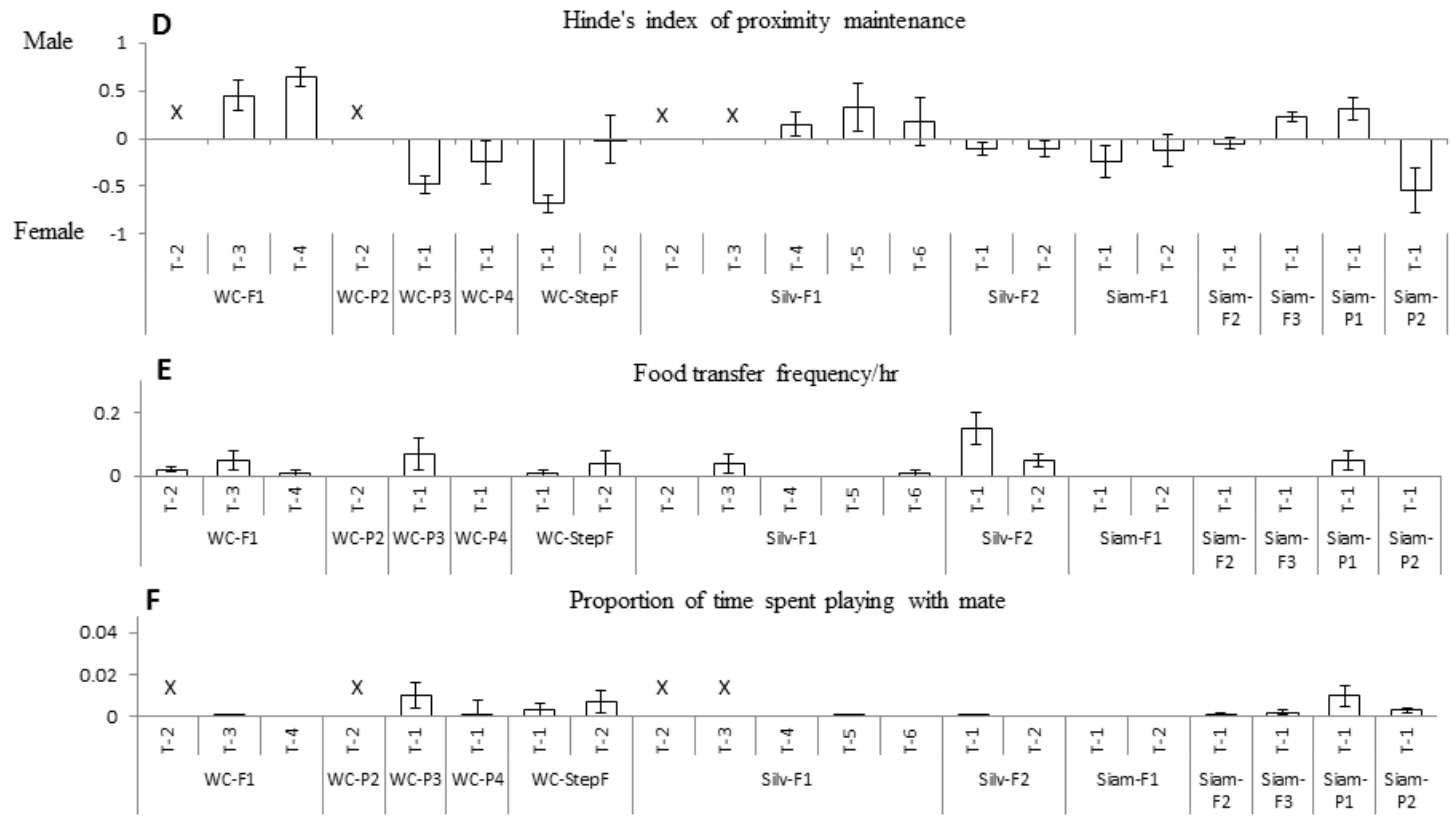
¹F/hr = frequency per hour of focal sampling

²Non-significant trends ($0.05 \leq p \leq 0.10$) are included as sex-biases

INFLUENCE OF PARENTAL STATUS ON PAIR BONDING BEHAVIOURS

There was a trend for non-parents to spend less time in close proximity compared to parents (Table 2.6). Despite this, there was no difference in the average distance between mates across pairs with and without offspring. Non-parents duetted more frequently and initiated play more frequently than did parents (Table 2.6). There was a trend for females without offspring to spend a smaller proportion of time grooming their mate compared to females with offspring (Table 2.6). Males without offspring spent significantly less time grooming their mates than did males with offspring (Table 2.6). There was no difference between parents and non-parents in any other pair bonding behaviour (Table 2.6).





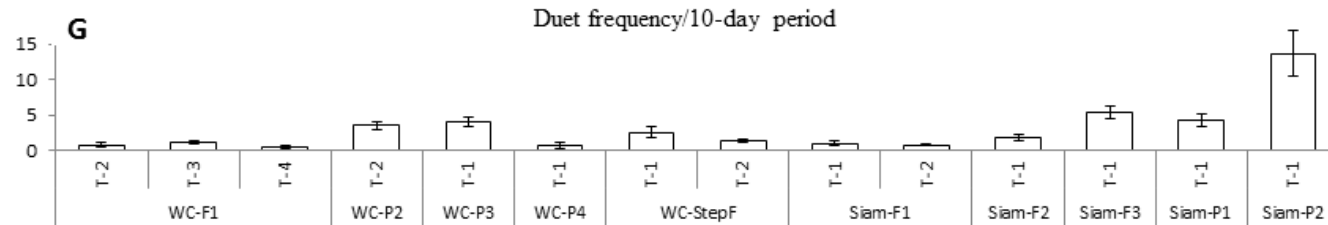
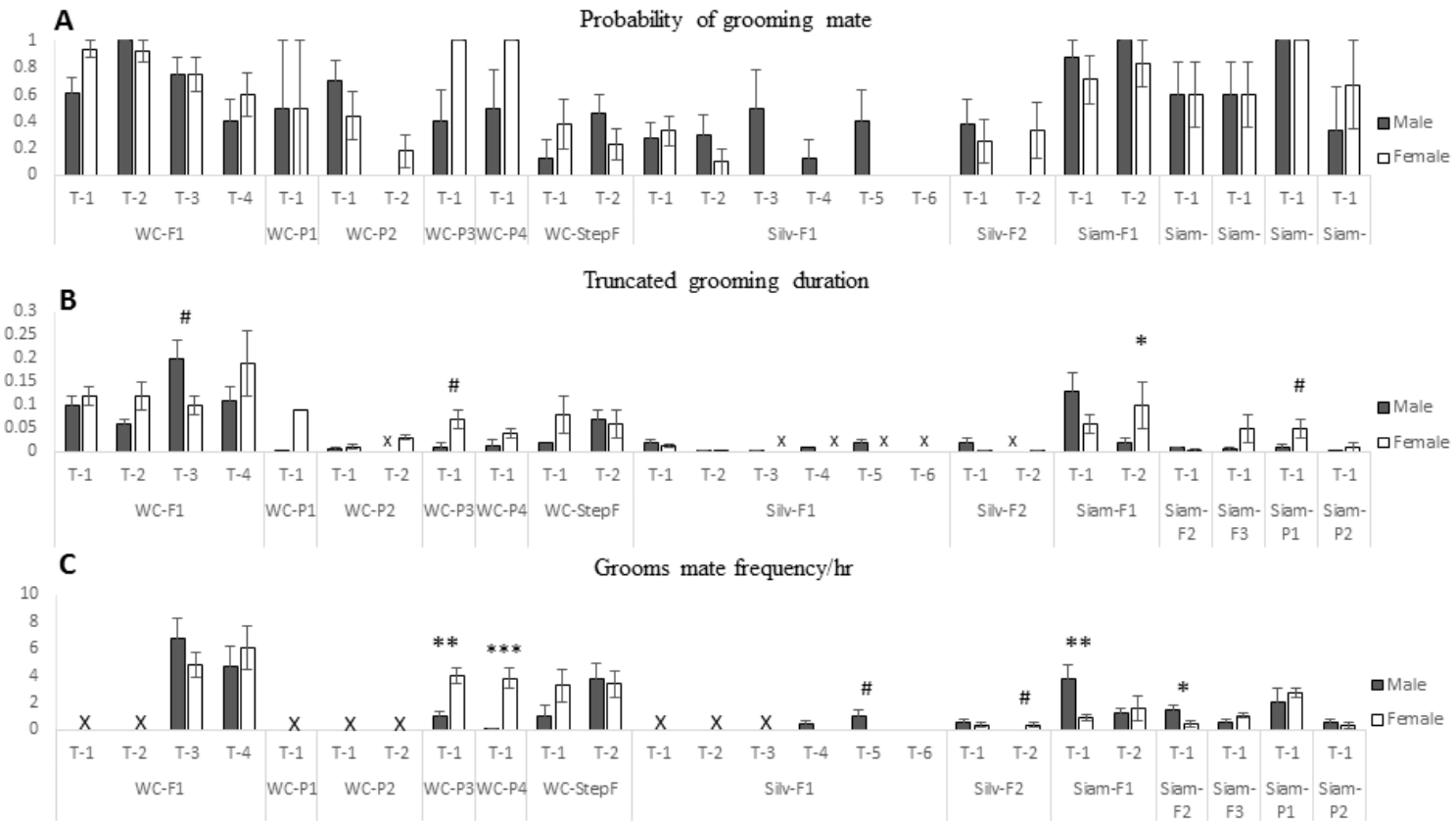


Figure 2.3 A – G Means \pm S.E. for pair behaviours in each pair during each sampling period (T-1 to T-4, for details see Table 2.3): proportion of time spent within arm's reach of mate (A), distance from mate (m) (B), copulation frequency per hour of focal sampling (C), Hinde's index of proximity maintenance (D), food transfer frequency per hour of focal sampling (E), proportion of time spent playing with mate (F) and duet frequency per 10-day period (G). Hinde's index of proximity maintenance can range from -1 to 1 and is calculated from the male's perspective wherein values closer to 1 indicate male responsibility for maintaining pair proximity and values closer to -1 indicate female responsibility for maintaining pair proximity. Duet frequency shown only for *N. leucogenys* and *S. syndactylus* pairs since *H. moloch* pairs do not perform a duet. An 'X' on the graph indicates missing data, to distinguish from sampling periods in which pairs did not engage in a behaviour (i.e. true zeros).



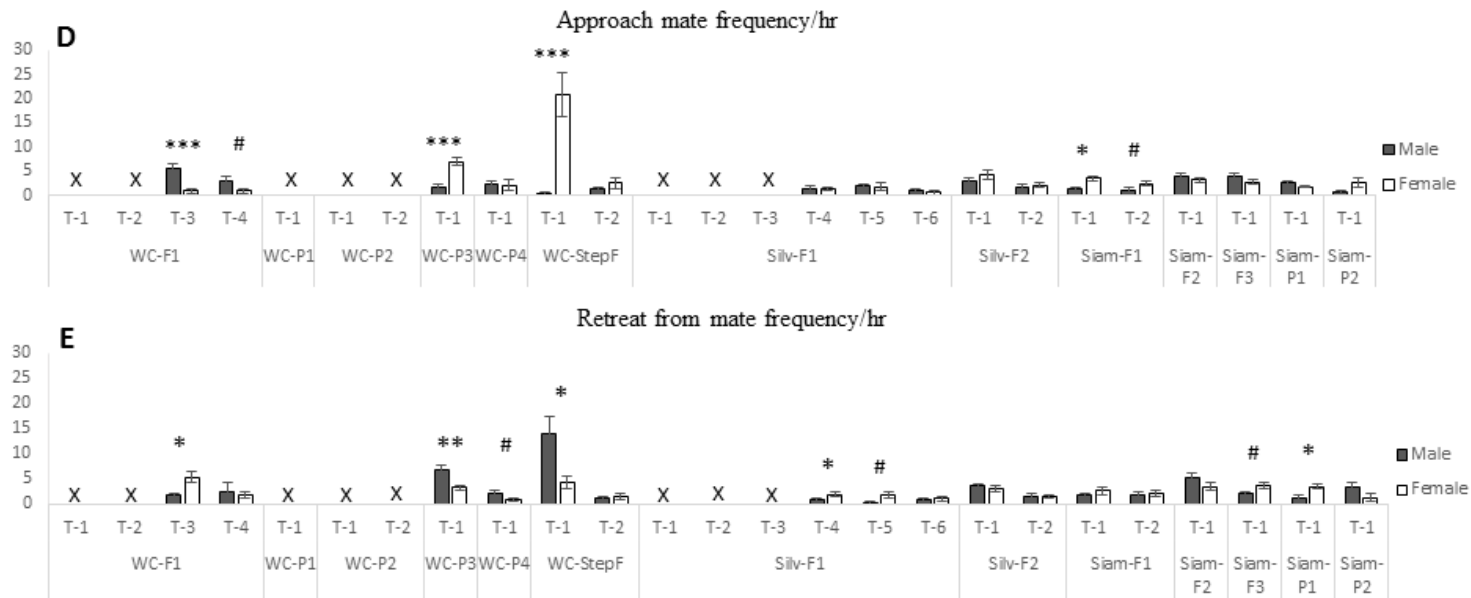


Figure 2.4 A – E Means \pm S.E. for individual behaviours of each pair during each sampling period for each sex (T-1 to T-4, for more details see Table 2.3): probability of grooming the mate in a 10-day period (A), proportion of time spent grooming mate when they did allogroom during a 10-day period (B), frequency of grooming mate per hour of focal sampling (C), frequency of approaching the mate to within arm's reach per hour of focal sampling (D), frequency of retreating from within arm's reach of mate per hour of focal sampling (E). Symbols denote sex differences within pairs based on t-tests (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, # $0.05 \leq p \leq 0.10$)

Table 2.6 Influence of parental status on pair bonding behaviours

Behaviour ¹		Estimate ± S.E. (non-parents) ²	t	p	N individuals (N 10-day samples)
% Proximity to mate	↓	-0.18 ± 0.08	-2.1	0.08	9 (163)
Duet frequency	↑	+0.93 ± 0.39	2.4	0.008**	10 (105)
♀ Play initiation frequency	↑	+0.49 ± 0.16	3.1	0.01*	9 (81)
♂ Play initiation frequency	↑	+0.41 ± 0.16	2.6	0.04*	9 (82)
♀ Truncated grooming duration	↓	-0.12 ± 0.03	-3.6	0.08	10 (86)
♂ Truncated grooming duration	↓	-0.20 ± 0.04	-5.7	0.007**	10 (78)

¹Group composition did not influence the distance between mates ($p = 0.61$), copulation frequency ($p = 0.59$), Hinde's index ($p = 0.22$), the probability of grooming their mates (p [females] = 0.46, p [males] = 0.25), frequency of mate grooming (p [females] = 0.52, p [males] = 0.11), frequency of aggression towards mate (p [females] = 0.40, p [males] = 0.32), frequency of approaching mate (p [females] = 0.69, p [males] = 0.83), frequency of retreating from mate (p [females] = 0.67, p [males] = 0.43), and grooming solicitation frequency (p [females] = 0.48, p [males] = 0.42)

²Estimate for non-parents compared to parents (reference category)

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, bold p values indicate a trend ($0.05 \leq p \leq 0.10$)

INFLUENCE OF LENGTH OF PAIR BOND ON PAIR BONDING BEHAVIOURS

Time in proximity, duet frequency, grooming duration and play initiation differed by group composition, therefore I excluded pairs without offspring to look at the associations of these behaviours with pair bond length (see Figure 2.2 for the spread of pair bond length in groups with offspring). For all other behaviours, pairs with and without offspring were pooled to look at associations with pair bond length. Duet frequency was lower in *N. leucogenys* and *S. syndactylus* parents who had been together for longer (Table 2.7, Figure 2.5). Initiation of play by females towards the mate was lower in females that had been with their mates for longer (Table 2.7); play initiation by males towards the mate did not differ by pair bond length. Maintenance of proximity was more equal for pairs that had been together longer, compared to newer pairs in which females were more responsible for proximity (Table 2.7, Figure 2.6). The difference in Hinde's index resulted from both decreased female approach rates and decreased male retreat rates with increased length of pair bond (Table 2.7). Males who had been with their mates for longer were less aggressive towards them (Table 2.7).

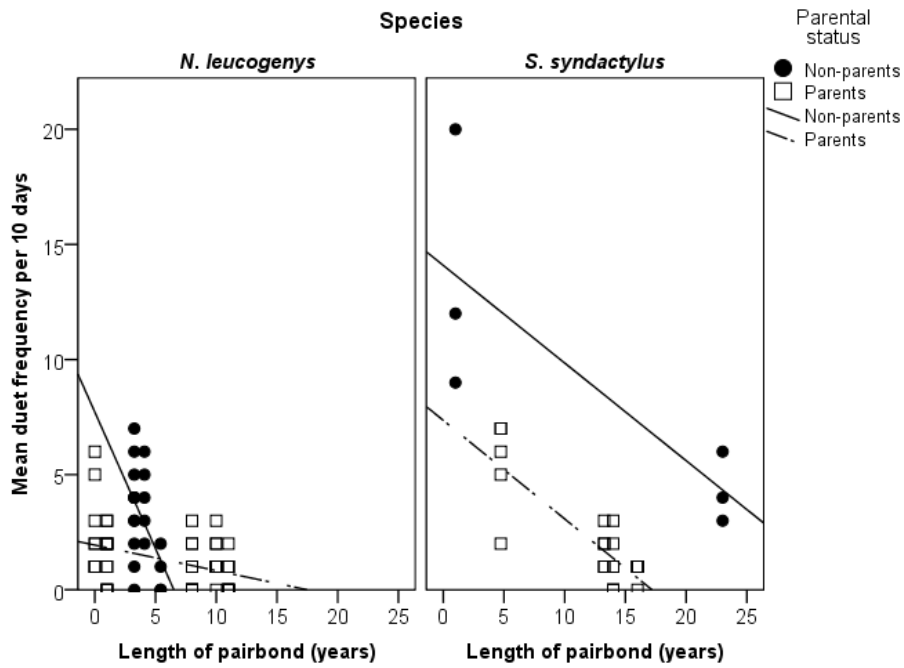


Figure 2.5 Duet frequency in *N. leucogenys* and *S. syndactylus* pairs with and without offspring, across the length of the pair bond.

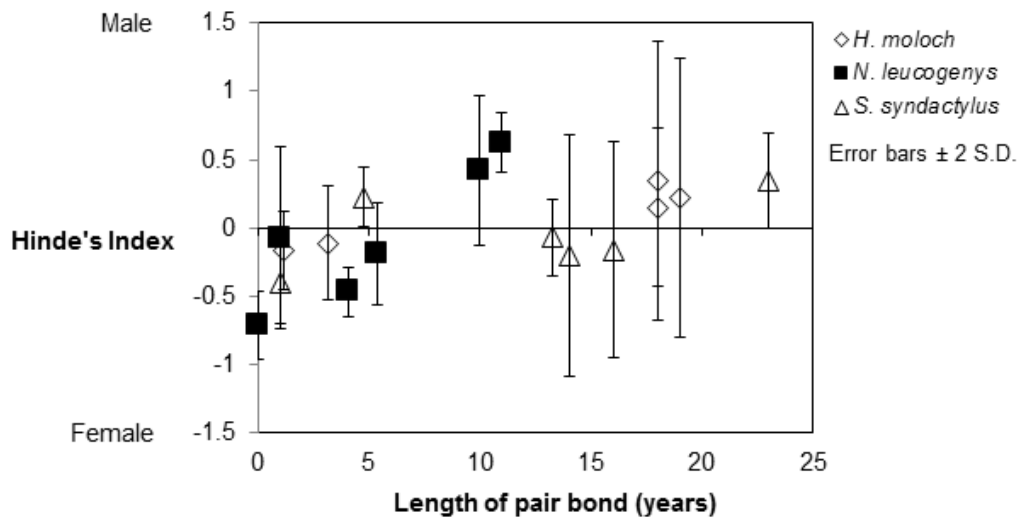


Figure 2.6 Hinde's index across length of pair bond for pairs of each species (more positive = more male-biased responsibility for maintaining proximity).

Table 2.7 Influence of length of pair bond on pair bonding behaviours

Behaviour ¹		Estimate ± St. Error (length of pair bond)	t	p	N pairs/individuals (N 10-day samples)
Duet frequency	↓	-0.05 ± 0.02	-3.0	0.06	5 (79)
Hinde's index	↑	+0.03 ± 0.01	2.6	0.02*	11 (100)
♀ Approach mate frequency	↓	-0.07 ± 0.02	-3.0	0.02*	11 (121)
♀ Play initiation frequency	↓	-0.02 ± 0.005	-3.3	0.02*	7 (106)
♂ Aggression to mate frequency	↓	-0.02 ± 0.006	-2.9	0.005**	12 (158)
♂ Retreat from mate frequency	↓	-0.06 ± 0.01	-4.3	0.02*	11 (120)
♂ Probability grooms mate	↑	0.07 ± 0.04	2.0	0.04*	12 (206)

¹Length of pair bond did not influence the % time pairs spent in proximity (p = 0.56), the distance between mates (p = 0.60), frequency of copulation (p = 0.26), ♀ probability of grooming mate (p = 0.45), truncated duration of grooming (p[females] = 0.21, p[males] = 0.12), frequency of grooming mate (p[females] = 0.52, p[males] = 0.28), ♀ frequency of aggression to mate (p = 0.27), ♀ frequency of retreating from mate (p = 0.90), grooming solicitation frequency (p[females] = 0.74, p[males] = 0.19), ♂ play initiation frequency (p = 0.31) and ♂ frequency of approaching mate (p = 0.68)

* p < 0.05, ** p < 0.01, *** p < 0.001, bold p values indicate a trend (0.05 ≤ p ≤ 0.10)

INFLUENCE OF FEMALE REPRODUCTIVE STATUS ON DYADIC PAIR BONDING BEHAVIOURS

Copulations were more frequent in groups with cycling females, compared to groups with pregnant or lactating females (Table 2.8). *N. leucogenys* and *S. syndactylus* pairs in which the female was pregnant duetted less frequently than pairs in which the female was cycling (Table 2.8). The proportion of time the pair spent in proximity, the average distance between mates, and Hinde's index for maintenance of proximity did not differ with female reproductive status (Table 2.8).

INFLUENCE OF FEMALE REPRODUCTIVE STATUS ON FEMALE PAIR BONDING BEHAVIOURS

Females that were pregnant or lactating during the sampling period retreated from their mates (out of arm's reach) less frequently than did cycling females (Table 2.9). Pregnant females initiated play with their mates less frequently than cycling females did (Table 2.9). Lactating females were more likely to groom their mate during a 10-day period, compared to pregnant females, but there was no difference in grooming probability between lactating and cycling females (Table 2.9). There was no difference in the duration of mate grooming, the frequency of mate grooming, aggression, approaching the mate or solicitation for grooming by females in different reproductive states (Table 2.9).

Table 2.8 Influence of female reproductive status on dyadic pair behaviours

Behaviour ¹	Reference group (N _p , N _o) ²	Test group (N _p , N _o) ²	Estimate ± S.E.	t	p	Overall p
Copulation frequency	Cycling (7, 47)	Pregnant (5, 57)	↓ -0.35 ± 0.1	-3.5	0.0002***	0.003**
	Cycling	Lactating (3, 43)	↓ -0.32 ± 0.12	-2.7	0.01*	
	Pregnant	Lactating	0.03 ± 0.10	0.27	0.80	
Duet frequency	Cycling (4, 36)	Pregnant (2, 29)	↓ -0.37 ± 0.16	-2.3	0.03*	0.04*
	Cycling	Lactating (1, 14)	-0.71 ± 0.26	-2.7	0.13	
	Pregnant	Lactating	-0.34 ± 0.29	-1.2	0.50	

¹Female reproductive status did not influence % time in proximity (p = 0.75), distance from mate (p = 0.64) or Hinde's index (p = 0.95)
²Sample sizes for number of pairs (N_p) and number of 10-day samples (N_o)
* p < 0.05, ** p < 0.01, *** p < 0.001, bold p values indicate a trend (0.05 ≤ p ≤ 0.10)

Table 2.9 Influence of female reproductive status on female pair bonding behaviours

Behaviour ¹	Reference group (N _i , N _o) ²	Test group (N _i , N _o) ²	Estimate ± S.E.	t	p	Overall p
♀ Retreat from mate frequency	Cycling (7, 47)	Pregnant (5, 35)	↓ -0.86 ± 0.20	-4.2	< 0.001 ***	< 0.001 ***
	Cycling	Lactating (3, 39)	↓ -0.71 ± 0.25	-2.9	0.006 **	
	Pregnant	Lactating	+0.15 ± 0.22	0.7	0.61	
♀ Play initiation frequency	Cycling (7, 47)	Pregnant (5, 35)	↓ -0.24 ± 0.10	-2.5	0.01 *	0.04 *
	Cycling	Lactating (3, 39)	-0.14 ± 0.13	-1.0	0.26	
	Pregnant	Lactating	+0.13 ± 0.08	1.5	0.16	
♀ Probability grooms mate	Cycling (8, 56)	Pregnant (6, 71)	-0.41 ± 0.50	-0.8	0.41	N/A
	Cycling	Lactating (4, 79)	+0.57 ± 0.64	0.9	0.38	
	Pregnant	Lactating	↑ +0.98 ± 0.57	1.7	0.09	

¹Female reproductive status did not influence truncated grooming duration (p = 0.15), frequency of grooming mate (p = 0.94), frequency of aggression to mate (p = 0.47), frequency of approaching mate (p = 0.13) and grooming solicitation by females (p = 0.44)

²Sample sizes for number of individuals (N_i) and number of 10-day samples (N_o)

* p < 0.05, ** p < 0.01, *** p < 0.001, bold p values indicate a trend (0.05 ≤ p ≤ 0.10)

INFLUENCE OF FEMALE REPRODUCTIVE STATUS ON MALE PAIR BONDING BEHAVIOURS

Males with pregnant mates retreated from their mate less often compared to males with cycling mates (Table 2.10). There was a trend for males with lactating mates to be more likely to groom them during a 10-day period, and to groom them for longer, compared to males with pregnant mates (Table 2.10). There was a trend for males to groom pregnant mates for a smaller proportion of time compared to cycling mates (Table 2.10). Male grooming frequency, play initiation, aggression, approaches to the mate and grooming solicitations did not differ with the female's reproductive status (Table 2.10).

Table 2.10 Influence of female reproductive status on male pair bonding behaviours

Behaviour ¹	Reference group (N _i , N _o) ²	Test group (N _i , N _o) ²		Estimate ± S.E.	t	p	Overall p
♂ Retreat from mate frequency	Cycling (7, 47)	Pregnant (5, 35)	↓	-0.80 ± 0.23	-3.4	0.001**	0.006**
	Cycling	Lactating (3, 38)		-0.39 ± 0.27	-1.5	0.14	
	Pregnant	Lactating		0.41 ± 0.25	1.6	0.17	
♂ Probability grooms mate	Cycling (8,57)	Pregnant (6, 70)		-0.27 ± 0.42	-0.64	0.52	N/A
	Cycling	Lactating (4, 79)		0.48 ± 0.46	1.04	0.30	
	Pregnant	Lactating	↑	0.75 ± 0.42	1.80	0.07	
♂ Truncated grooming duration	Cycling (8, 32)	Pregnant (5, 26)	↓	-0.07 ± 0.04	-1.7	0.07	0.09
	Cycling	Lactating (4, 36)		0.02 ± 0.04	0.49	0.99	
	Pregnant	Lactating	↑	0.09 ± 0.04	2.4	0.06	

¹Female reproductive status did not influence frequency of grooming mate (p = 0.72), frequency of play initiation (p = 0.19), frequency of aggression to mate (p = 0.24), frequency of approaching mate (p = 0.19) or grooming solicitation frequency (p = 0.74) by males

²Sample sizes for number of individuals (N_i) and number of 10-day samples (N_o)

* p < 0.05, ** p < 0.01, *** p < 0.001, bold p values indicate a trend (0.05 ≤ p ≤ 0.10)

DISCUSSION

‘Strong’ pair bonds are often associated with socially monogamous species, and invoke ideas of close spatial proximity, and large amounts of time devoted to affiliative behaviours including grooming and several other forms of physical contact between breeding pairs (Kleiman 1981; Palombit 1999; Zeifman & Hazan 1997). Gibbons and siamangs have accrued a reputation of being inflexibly monogamous and exhibiting ‘strong’ pair bonds between males and females that mate for life. More recent research in the last few decades reveals that hylobatids are not strictly monogamous in their sexual or social behaviour, and some flexibility in hylobatid social organisation is widely accepted (Malone & Fuentes 2009; Reichard 2009; Whittaker & Lappan 2009). In contrast, hylobatids are still considered to exhibit pair bonds and therefore are expected to display ‘strong’ social bonds within breeding pairs. This reputation is potentially problematic in the context of captive breeding and rehabilitation programs, since husbandry teams may look for high frequencies of affiliative interactions as a measure of the success of forming pairs. There is an implicit assumption that pairs who spend more time together, are more synchronous in their activities, groom more frequently and are less aggressive may be more successful breeders.

The pairs in the current study were similar to one another in the expression of some pair bonding measures; hylobatid pairs in captivity clearly have a tendency to spend time close together, and engage in infrequent though usually affiliative interactions, rather than ignoring each other (Table 2.4). Social play, food transfers, solicitation for grooming, copulation and aggression were relatively infrequent in all pairs, confirming that they play a limited role in long term pair bond maintenance (Table 2.4). It was not possible to assess whether relationships between pair mates differ from other potential adult relationships, since no groups contained multiple adults. However, the mean distance between mates for each pair ($\bar{x} = 3.16 \pm 1.67\text{m}$, range = 1.7 – 4.8m, Table 2.4)

varied less than the mean distance between parents and offspring in family groups (unpublished data, mother-offspring: $\bar{x} = 3.7 \pm 2.4$, range = 0.3 – 7.7m, father-offspring: $\bar{x} = 4.5 \pm 2.1$, range = 1.8 – 7.8m), suggesting that adult pairs do maintain very close spatial proximity. Despite this, the amount of time that pairs spent in close proximity was highly variable, ranging from 10 to 54% of the activity budget (Figure 2.3A). Similarly, some pairs spent considerable proportions of time in physical contact or grooming each other, while others spent very little time in contact with and/or grooming their mates (Figures 2.4A, B). This variation supports the separation of different aspects of pair bonding behaviour (Gowaty 1996), such that pairs can maintain close proximity without also engaging in high rates of affiliative bonding behaviour.

DO PAIRS VARY ACCORDING TO CONTEXT?

The variation in the degree of social interaction among these hylobatid pairs, and the variation in sex-biased maintenance of the pair bond in the literature (Table 2.2) could be explained by varying social contexts. Adults may alter their investment in the pair bond when offspring are present if successful offspring development relies on the social bond between the parents (Brockelman et al. 1974). For example, Brockelman (2009) hypothesised that grooming patterns in hylobatid pairs are related to the relative value of grooming to the fitness of the recipient. He argues this as an explanation for why grooming patterns within pairs switch from female-biased to male-biased with time after pair formation. If this is the case, then females should reduce their investment in their mate as a result of time budget constraints associated with care of offspring.

Herein, play initiation and grooming duration differed with the presence or absence of offspring (Table 2.6). However, these differences were observed in both sexes, and those with offspring groomed their mates for longer, indicating that the presence of offspring in captivity does not influence sex differences in mate-directed behaviour as

predicted. None of the other pair-directed behaviours differed for either sex with the presence or absence of offspring (Table 2.6).

Similarly, the length of the pair bond had a minimal impact on the contribution of each sex to the pair bond, except that proximity maintenance in newer pairs was more female-biased, while in older pairs, proximity maintenance was more equal (Table 2.7, Figure 2.6). Likewise, the spatial cohesion of the pair, and many of the individual behaviours were unaffected by the reproductive status of the female (Tables 2.8, 2.9, and 2.10), and those that differed did not result in sex differences in investment. For example, the greater likelihood of mate grooming by males as well as females in pairs with infants does not provide clear support for females investing more in the pair bond in order to prevent infanticide. The overall lack of sex differences in this captive sample (Table 2.5) and others (Table 2.2) suggests mutual maintenance of proximity and grooming relationships, rather than reflecting a universal sex-bias in pair bond maintenance.

So far the evidence does not suggest that the presence of offspring, length of pair bond, or female's reproductive status makes the pair bond more valuable to either sex. The mutual maintenance of proximity and social interaction in these groups indicates that the pair bond is not more important to one sex than the other. But it is possible that this comparison is too simplistic; after all, most pairs in the wild would be non-reproductive for only a short period of time after pair formation, after which they would almost always have offspring present in their social group. Similarly, the production of overlapping dependent offspring means that most groups would usually have an infant present in the group. Investment by each sex into pair bond maintenance may therefore change on a more subtle, short term basis. In particular, male investment into the pair bond might depend on more subtle cues of female reproductive status. Recent evidence from *H. lar* (Barelli et al. 2011) provides some support for male grooming being

exchanged for reproductive opportunities on a more short-term basis. Additionally, males might solicit or receive more grooming from their mates during inter-group conflicts (Ellefson 1974). In captivity, the impact of social context on the investment by each sex into the pair bond may also be limited if some predicted sex differences are the result of time budget constraints in the wild. I.e., when time budgets are not limited by other necessary activities (e.g. defence or foraging), as in captivity, sex differences in behaviour may be less pronounced.

Alternatively, the general lack of sex differences and the variation in sex-biased investment into the hylobatid pair bond could result from many of the ultimate reasons for social pair bonds being intertwined (see Figure 2.7). Spatial pair bonds require that females are tolerant of males occupying their territory. This also does not necessarily imply social tolerance of male proximity within that territory, but does imply shared access to resources in space. Consequently, the nature of social interactions between the breeding pair should reflect the selective pressures favouring female tolerance (Kleiman 1981), and this becomes extremely important when ecological pressures favour smaller groups (as in hylobatids).

The important question then becomes: why do females tolerate the presence of a male instead of forcing males to feed and travel elsewhere? As previously noted, there are several hypothetical pathways through which social pair bonds might evolve. Each pathway alone predicts female tolerance of males in their territories but each predicts a different type of relationship between the pair through divergent selective pressures. When considered separately, only pathway C leads to reciprocal pair bonds (Figure 2.1), but the three pathways are not mutually exclusive. Selection for one-sided male-biased relationships via pathway A changes the cost/benefit ratio of pathway B, and vice versa. Similarly, selection for pathway A or B may make pathway C more beneficial.

The “females as a limited resource” hypothesis (pathway A in Figure 2.7) predicts that males should maintain proximity to females in order to guard them from other males (Palombit 1999). In its simplest form, this hypothesis treats females as resources (Brockelman 2009) and implies that females do not benefit from the presence of the male in any way such that any “territorial defence” provided by males solely reflects mate guarding. Females under resource pressure should therefore not tolerate the presence of a guarding male, unless the cost of expelling males from the territory is considerably higher (Wrangham 1979; Gowaty 1996). Thus, mate guarding as an ultimate reason for pair bonds is likely to produce unstable bonds that are solely maintained by males and presumably unwelcome to females (Figure 2.7). In addition, the “females as a limited resource” hypothesis suggests that single females defend territories themselves, and that males join them only to mate guard. The occurrence of sex-specific territoriality has been suggested as evidence for this hypothesis (Reichard 2003; van Schaik & Kappeler 2003). However, the occurrence of female-biased investment in the pair bond in many groups (Tables 2.2 and 2.5) and the absence of single females defending territories before pairing (Brockelman 2009) indicate that pathway A is not a satisfactory explanation for the pattern of two-adult groups in this taxon.

In contrast, the male defence hypotheses (pathway B in Figure 2.7) inherently assume that females benefit from tolerating a male in their territory. Alone, this pathway predicts greater female investment in retaining males in their territory, but if females are successful at retaining a male, males again benefit from continuous mate guarding in the absence of a ranging strategy. This is particularly important if social monogamy and male provision of services increases male paternity certainty, in which case the fitness benefit to males of defending a female and her offspring approaches the fitness benefit to the female. Thus, pathways A and B are interrelated, because selection for either sex-

biased pair bond changes the cost/benefit ratio of investment by the other sex. This can result in a pair bond that appears to be reciprocally maintained by both individuals (i.e. a cooperative relationship), but is actually a result of independent strategies and benefits (e.g. Kubitza et al. 2015; Figure 2.7).

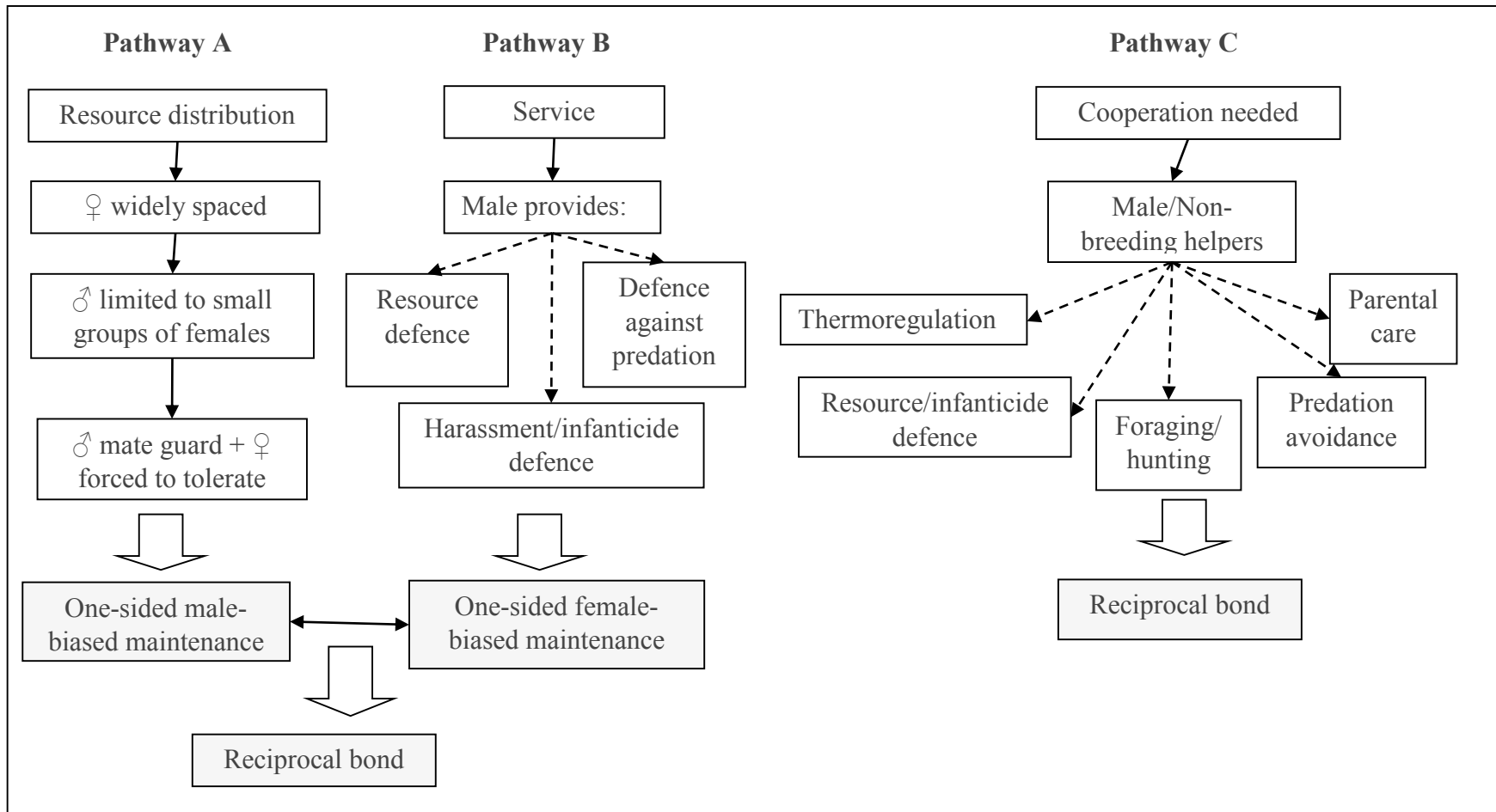


Figure 2.7 Interactions between hypothesised pathways leading to social pair bonds

Alternative hypotheses for female tolerance incorporate some form of cooperation being necessary for the reproductive success of all individuals involved (Kleiman 1977, pathway C in Figure 2.7). Thus, even if some ecological pressures favour solitary ranging, the benefits obtained through cooperation may promote female tolerance and investment by both sexes into the pair bond. It is likely that many of the activities outlined in pathway C benefit both sexes in hylobatids, since paternity certainty for primary males is relatively high (~ 90%, Barelli et al. 2013). In contrast to pathways A and B, selective pressures favouring cooperation between a male and female do not predict any asymmetry in maintaining the relationship. Importantly this selective pressure does not predict greater social investment by either individual, merely coordination of pair activities to achieve a common goal. Thus, the hylobatid pair bond may be characterised only by coordination of activities and close spatial proximity between pair mates, rather than specific patterns of sex-biased investment and high frequencies of affiliation. This could explain why maintenance of the pair bond in some hylobatid pairs appears male-biased, while in others it appears female-biased or mutual (Table 2.2; Table 2.5).

COOPERATION AS A DRIVER OF PAIR BONDING IN HYLOBATIDS

If the development of a unique relationship with a specific female requires a substantial amount of investment, then this further increases the cost of mate desertion and roving strategies for males (Brockelman & Srikosamatara 1984). The length of the pair bond in oystercatchers (a wading bird, *Haematopus ostralegus*), independent of age and breeding experience, is positively associated with greater reproductive success (van de Pol et al. 2006). This appears to be achieved through increased competency with time, via improved coordination within the pair (van de Pol et al. 2006). Similarly, in a monogamous lizard, familiar pairs are able to mate earlier than are unfamiliar pairs (Leu et al. 2015). This suggests that familiarity with the partner's behavioural patterns

facilitates coordination that ultimately increases reproductive success. In the current study, this coordination is reflected in the difference in the responsibility for maintaining proximity in newer compared to established pairs (Table 2.7). The more equal responsibility for maintaining close proximity in established pairs resulted from efforts by both individuals to coordinate their proximity.

Despite the lack of direct paternal care in hylobatids, the duration of pair bonds may still be an important (if indirect) factor in the appearance of the social pair bond, given the importance of synchronisation and coordination in duetting (as an advertisement of pair bond strength, Maples et al. 1989; Geissmann 1999), territory defence, and/or predation avoidance (Dooley & Judge 2014). The lower rates of duetting with longer length of pair bond in the current study support previous findings that new pairs duet more frequently than more established pairs and that this frequency decreases over time, along with development of the duet into a more cohesive or synchronised form (Arrowood 1988; Geissmann 1999). Geissmann (1999) logically explained that the high frequency of duetting (a loud auditory signal) would be particularly adaptive, as it reduces the length of time that new pairs spend advertising their newness to neighbouring groups. Likewise, new pairs should establish coordination as quickly as possible, to reduce their vulnerability to neighbouring groups.

In addition to duet frequency, aggression by males towards their mates was more frequent in newer pairs (Table 2.7). Fox (1977) also reported intense aggressive behaviour by a captive *S. syndactylus* male during introduction to his mate. Similarly, the most severe aggression between mates in the current study was reported by keepers during the introduction of a young pair of *N. leucogenys* (WC-StepF). These instances of aggression were not recorded during focal observations but the nature was so severe as to inflict wounds that required stitches (Holly Thompson, Perth Zoo, personal communication). The recorded frequency of aggression for this pair was, despite this,

relatively low at 0.3 acts/hr of focal sampling. A higher frequency and/or intensity of aggression during pair formation facilitates quicker establishment of dominance within the pair and allow mates to learn how to interact with each other. For example, Barelli & Heistermann (2012), and Reichard (2009) note that aggression between males in polyandrous groups is rarely seen once dominance is established; this may be similar during pair formation. This restriction of aggression to a short time period during establishment of social bonds could improve coordination of activities and thus increase a pair's ability to successfully defend their territory against other individuals. Further research on changes in aggression over time within pairs could prove valuable for captive breeding and rehabilitation programs, with implications for the success of pair introductions.

CONCLUSION

All of the hylobatid pairs in the current study maintained close spatial relationships with one another. However, pairs varied in how much time they spent engaging in physical contact, and grooming with their mate. Social interactions between mates most commonly involved passive physical contact or grooming. Interestingly, grooming of the pair mate averaged only 6.7% (male + female effort) of the activity budget of a pair, despite the abundance of time for grooming in captivity. The variation in social interaction among mates, contrasted with the close spatial proximity of all pairs, suggests that physical contact and grooming are not necessary to maintain close spatial proximity between a male and female. Very little of the variation among pairs could be explained by the presence of offspring, length of pair bond or reproductive status of the female, and I found no evidence of a consistent sex-bias in maintenance of the bond. The mutual maintenance displayed by many hylobatid pairs might reflect that the social pair bond is ultimately important to both sexes. If both sexes benefit from maintaining

close proximity to their mate, then males and females should attempt to coordinate their behaviour, and this should be reflected in the appearance of the social pair bond.

CHAPTER 3 PARENTAL BEHAVIOUR

CHAPTER 3 PARENTAL BEHAVIOUR

INTRODUCTION

Parental care (Clutton-Brock 1991) can be defined as any behaviour of parents which improves the fitness of offspring. Within this, many researchers find it useful to distinguish direct from indirect care, particularly for inter-specific comparisons of the impact of parental care on social organisation (Kleiman 1977). Most definitions of direct parental care include behaviours such as: active feeding, transporting, huddling/co-sleeping, grooming, socialising and direct defence of offspring. Indirect forms of care generally include defence of resources and indirect defence of offspring against predation and infanticidal males. A further distinction could be made between forms of direct care that have a relatively higher return on fitness (feeding, transporting and huddling/co-sleeping) and those that have a relatively lower return on fitness (grooming and socialising, Table 3.1). Moreover, some types of parental care can only be performed by certain individuals (e.g. lactation), while others can be substituted by other group members (termed 'substitutive care' here, see Table 3.1).

Table 3.1 Types of parental care in primates

Parental care type		Return on fitness ¹	Who can perform? ²	Relative energetic cost ¹	Relative time cost ¹	
Direct	Feeding (lactation)	H	M	H	L	
	Feeding (other)	H	S(A)	I	I	
	Direct defence (requires “babysitting”)	H	S(AD)	L	H	
	Transport	H	S(AD)	I	I	
	Huddling/Co-sleeping	I	S(AD)	I	L	
	Grooming	I	S(A)	L	H	
	Play	I	S(A)	H	H	
	Other socialisation (requires proximity)	L	S(A)	L	I	
	Indirect	Defence of resources	H	S(AD)	H	H
		Indirect defence of offspring	H	S(AD)	H	H

¹L = low, I = intermediate, H = high
²M = mother only, S(A) = substitutive by any group member, S(AD) substitutive by adult sized group members

The small apes live in nuclear family groups most commonly consisting of a single female, a single male and their offspring. Inter-birth intervals can be as short as 3.5 years, but offspring take between 7 and 11 years to reach maturity and disperse from the natal group (Palombit 1995; Brockelman et al. 1998; Reichard & Barelli 2008). This means that the average lactating female will have at least one older semi-dependent offspring as well as an infant, after the birth of her first offspring. This pattern of overlapping dependent offspring increases the daily burden on females for providing parental care for each offspring (Kramer & Ellison 2010; Kramer & Otárola-Castillo 2015). This reproductive strategy is interesting, considering that the ecological niche of the hylobatids is similar to that of orang-utans (Harrison & Marshall 2011; Malone et al. 2012) and that other aspects of their social organisation suggest strong limitations on group size in response to resource availability (Brockelman et al. 2014). Beyond investment in lactation and transport for a younger offspring, hylobatid mothers also

have to provide thermoregulatory care, food transfers, social support, grooming, play and defence for older offspring.

An obvious candidate for substitutive care of these older offspring in hylobatids is the father; the contribution of males to direct care of offspring has been a topic of substantial interest, due to hylobatid social organisation (Fuentes 2000a). In a socially monogamous group it is logical to assume that males will contribute to direct offspring care due to the higher paternity certainty associated with continuous mate guarding (Trivers 1972). Contrary to this prediction, most hylobatid males contribute less direct care of offspring compared to males in many other socially monogamous species (Kleiman 1977; Wright 1990; van Schaik & Paul 1996; Table 3.2). Male hylobatids are often noted to contribute only indirect care of offspring in the form of defence (including defence of resources and against predation and infanticide, Brockelman 2009; Morino 2009). Males can contribute to direct care through huddling/co-sleeping, facilitating food transfer, play, grooming and direct defence of older offspring, but direct care by males is individually variable and often negligible (Table 3.2). The opposing contributions of males and females to direct care of offspring might be related to other demands on each individual's activity budget.

Table 3.2 Presence/absence of types of direct care by male hylobatids

Species	Context	Infant transport ¹	Co-sleeping ¹	Grooming ¹	Play ¹	Proximity (“babysitting”) ¹	Food transfer ¹	Sources ²
<i>S. syndactylus</i>	Wild	V (N – F)	F	F	M	?	?	1, 2, 3, 4, 5
	Captive	V (N – F)	?	V (I – F)	V (I – F)	?	?	6, 7, 8, 9, 10
<i>Nomascus spp.</i>	Wild	N	F	?	?	?	?	11
	Captive	V (N – I)	?	V (I – F)	V (I – F)	I	I	6, 12, 13, 14, 15
<i>Hylobates spp.</i>	Wild	N	N	F	V (N – F)	?	I	16, 17, 4, 18, 21
	Captive	V (N – M)	?	I	F	M	I	8, 12, 19, 20

¹V = variable (range), N = no contribution, I = infrequent/minimal contribution, M = moderate contribution, F = frequent/substantial contribution (> 50%)

²1 = Morino (2014), 2 = Lappan (2008), 3 = Chivers (1974), 4 = Gittins & Raemaekers (1980), 5 = Palombit (1992), 6 = this study, 7 = Alberts (1987), 8 = Fischer & Geissmann (1990), 9 = Braendle & Geissmann (1997), 10 = Dal Pra & Geissmann (1994), 11 = Fan & Jiang (2008), 12 = Burns (2009), 13 = Poyas (2008), 14 = Ingmanson (2007), 15 = Dooley (2006), 16 = Bartlett (2009a), 17 = Prime & Reichard (2008), 18 = Nettlebeck (1998), 19 = Clemens et al. (2008), 20 = Klein (1997), 21 = Reichard (1998)

THE RELATIONSHIP BETWEEN PARENTAL CARE TYPES AND ACTIVITY BUDGETS

Trivers (1972), in his original definition of parental investment, specified that investment in one offspring by a parent comes at the cost of investment into other offspring. This is true of most direct forms of parental care but precludes defining any indirect care as investment, since most indirect care produces shared benefits for all offspring. The distinction between direct and indirect care makes it difficult to assess the investment costs to each parent, because the two forms of care are not directly comparable. For example, some forms of parental investment require substantial energetic costs (e.g. transporting infants), while others require substantial time/opportunity costs (e.g. vigilance for defence of offspring, Table 3.1).

In addition, it is difficult to compare measurable impacts on offspring fitness (e.g. growth improved via provisioning) with theoretical reductions in mortality risks (e.g. decreased risk of predation via vigilance). Even though indirect care can be shared among offspring, investing in indirect care limits the time available for other activities and thus influences parental activity budgets. Both energy- and time-costly care could produce a similar increase in offspring fitness, but the investment cost to the individual of engaging in each type of care may differ. From the perspective of an individual parent, the fitness benefits obtained from direct and indirect, high- and low-return forms of offspring care should depend on the energetic or opportunity cost to the individual. The impact of energetic and time costs associated with different types of parental care depend on the current ecological, social and reproductive context as well as the phylogenetic history of a species. Investment by individual parents should thus vary predictably with local conditions, bounded by constraints set during evolutionary history.

MATERNAL ENERGETIC INVESTMENT VARIES

The degree of energetic investment into parental care by a female primate at any point in time depends on her reproductive status. Pregnancy and lactation influence female energy balance primarily through the diversion of caloric resources into the fetus/infant (Speakman 2008) and the associated maternal support tissue and ‘running costs’ (Dufour & Sauther 2002). Lactation is the most energetically expensive phase of reproduction for female primates (McCabe & Fedigan 2007; Key & Ross 1999). This additional energy must be acquired from somewhere; thus, reproduction in females requires some compensatory strategy in either energy acquisition or in allocation.

Two such strategies have been defined in relation to the timing of this energetic compensation relative to reproduction; these are the ‘income’ and ‘capital’ breeding strategies (Jönsson 1997). These terms were originally used to describe evolutionary rules governing clutch size in birds (Drent & Daan 1980), and have since been applied to mammals in a slightly different way (Stearns 1989b; Jönsson 1997). Their usefulness in primates has been criticised (Lewis & Kappeler 2005; Emery Thompson 2013) because application of either term to a species or individual depends on the definition of ‘reproduction’; however, the concept can be useful as long as strategies and reproductive phases are carefully defined (Brockman & van Schaik 2005).

Income breeders increase acquisition of energy during the reproductive period of highest energy demand. Primate examples include increasing the time spent feeding (Dunbar 1988) or increasing food intake rate during lactation (McCabe & Fedigan 2007), and/or timing lactation with periods of high quality food availability (Lee 1987). Alternatively, capital breeders store energy before reproduction and/or use somatic energy stores during lactation and regain that energy later (Vasey 2005). Importantly, seasonal timing of the most expensive phase of reproduction (mid to late lactation) is not possible for species in which the lactation period exceeds one seasonal cycle of food

productivity (van Noordwijk et al. 2013). Hylobatid infants are weaned at 2 – 3 years of age; hence, like most large primates, female hylobatids cannot easily rely on an income breeding strategy to support this long lactation period (additional to a 7 month gestation).

Behavioural evidence from wild *S. syndactylus* supports this; females neither increase their time spent feeding nor utilise higher quality foods during early lactation (Lappan 2009). Instead, female *S. syndactylus* may sacrifice somatic stores during lactation, and utilise the post-weaning period (when infants are no longer carried by the female) to recoup energy for the next reproductive effort (Lappan 2009). Females can also reduce energy expenditure during pregnancy or lactation instead of increasing energy intake (Emery Thompson 2013); for example, wild *S. syndactylus* females rest more when lactating (Lappan 2009). In captivity, the reproduction of many pairs is carefully managed. Captive groups therefore provide an opportunity to compare the behaviour of reproductive and non-reproductive females of similar age, in a context where food is not limiting. In this chapter, I explore the impact of female investment into fetal/infant care on female activity budgets in captivity. I predict that female hylobatids in captivity show behavioural evidence of a capital breeding strategy. Thus, I expect that cycling females spend more time feeding than reproductively active (pregnant or lactating) females (Lappan 2009), and that energy expenditure is reduced in reproductively active females.

THE IMPACT OF MATERNAL REPRODUCTIVE STATUS ON ACTIVITY BUDGETS AND PARENTAL CARE

The substantial investment of females into fetal and infant care may also produce sex differences in general activity budgets that reflect the energetic cost of this investment. In wild white-handed gibbons (*H. lar*), males spend more time resting and less time feeding overall, compared to females (Chivers et al. 1975; Bartlett 2009a). Similarly,

male siamang (*S. Syndactylus*) spend less time feeding and feed slower compared to females (Chivers 1977). Thus, sex differences in activity budgets may reflect the impact of female investment into reproduction on female activity levels. Comparing the activity budgets of adults who have and have not reproduced could also give a general indication of the cost of parenthood as reflected in variation in adult activity budgets. Herein, I compare the impact of offspring presence and female reproductive status on adult activity budgets and on sex differences in activity budgets. Male activity budgets and sex differences in activity are predicted to reflect that male energy requirements are lower and less variable, and that males generally invest more of their activity budget into indirect than direct care of offspring.

Given the greater energetic constraints on activity by reproductively active females, any parental care that can be substituted by the adult male, by older siblings or by other individuals may also reduce the costs to the mother. Some evidence from *S. syndactylus* indicates that this is not the case for investment into infant care (Lappan 2008); females in polyandrous groups received *less* direct care for their infants from group males (in total) compared to females in monogamous groups. But males and additional adults may also contribute to direct care of older offspring, and/or contribute indirectly to the reproductive success of the breeding pair via resource defence. In light of the variation in paternal care and social behaviour among hylobatids (Table 3.2), I explore the social context of varying parental roles in captivity. I explore how maternal care of older offspring differs in association with reproductive status, and whether fathers or siblings contribute to offspring care in a complementary way. I predict that hylobatid parents will alter their behaviour according to the behaviour of other group members. If male resource defence plays a large role in hylobatid monogamy (Bartlett 2009a) and hence in the reproductive success of both sexes, males should avoid direct care of offspring when the female is already investing. Males can subsidise care of infants/older offspring

when it becomes too costly for the female (Lappan 2008), and/or when no one else is available.

METHODS

STUDY ANIMALS

I observed six pairs without offspring (*N. leucogenys* and *S. syndactylus* only) and seven pairs (including all three species) with offspring. The seven pairs with offspring were used to assess changes in parental behaviour with female reproductive status and family composition (one or more offspring). Details of the female's reproductive status and family composition for each family group are provided in Table 3.3. Some females were on oral contraceptives (combined pill microgynon®) for breeding management reasons. Females who were on oral contraceptives at the time of sampling are included with cycling females for analysis, since differences in behaviour with female reproductive status are predicted to be associated with the energy requirements of reproductively active (pregnant/lactating) females. All females without offspring were either cycling or on oral contraceptives during the study period.

Table 3.3 Characteristics of families during each sampling period

Pair code ¹	Father + Mother	Sampling date range	Age of male	Age of female	# of offspring	♀ Reproductive status ²
WC-F1-T1	Phillip + Viann	18.07.2005 – 04.01.2006	33.3	12.6	2F	Lactating
WC-F1-T2	Phillip + Viann	14.02.2008 – 22.06.2008	35.8	15.1	2F	OCP
WC-F1-T3	Phillip + Viann	24.04.2010 – 21.08.2010	38	17.3	1F	Cycling
WC-F1-T4	Phillip + Viann	29.04.2011 – 06.08.2011	38.5	18.1	1F	OCP
WC-StepF-T1	Tao + Jermei	13.06.2010 – 10.09.2010	8.1	8.1	1F ³	Cycling
WC-StepF-T2	Tao + Jermei	19.04.2011 – 15.09.2011	8.9	9	1F ³	Pregnant ⁴
Silv-F1-T1	Jury + Hecla	18.07.2005 – 04.01.2006	19.5	22.6	2M	Lactating
Silv-F1-T2	Jury + Hecla	14.02.2008 – 25.05.2008	22.1	25.1	2M	Pregnant
Silv-F1-T3	Jury + Hecla	26.05.2008 – 02.07.2008	22.1	25.1	2M,1F	Lactating
Silv-F1-T4	Jury + Hecla	24.04.2010 – 12.07.2010	24.3	27.3	1M,1F	Pregnant
Silv-F1-T5	Jury + Hecla	13.07.2010 – 10.09.2010	24.3	27.3	1M,2F	Lactating
Silv-F1-T6	Jury + Hecla	19.04.2011 – 15.09.2011	25	28	1M,2F	Lactating
Silv-F2-T1	Arjuna + Layar	14.01.2010 – 03.04.2010	9.4	8	1F	Lactating
Silv-F2-T2	Arjuna + Layar	13.02.2012 – 03.04.2012	11.3	9.9	1F	Pregnant
Siam-F1-T1	Armstrong + Fern	14.01.2010 – 03.04.2010	28.1	29.2	2M,1F	Lactating
Siam-F1-T2	Armstrong + Fern	13.02.2012 – 03.04.2012	29.8	30.8	3M,1F	Lactating
Siam-F2	Niran + Mang	01.10.2010 – 19.11.2010	21.7	22.3	1M	Cycling
Siam-F3	Irian + Suli	01.10.2010 – 19.11.2010	9.6	10.6	1M	Cycling

¹Families labelled with a code that denotes the species (WC = white-cheeked gibbons, *N. leucogenys*, Silv = silvery gibbons, *H. moloch*, Siam = siamang, *S. syndactylus*), composition (F = family with offspring, StepF = step-family with unrelated offspring) and sampling period (T1-6) for pairs that were sampled longitudinally.

²OCP = oral contraceptive pill

³Adopted immature, unrelated to Tao + Jermei

⁴This female had a stillbirth towards the end of the study period

BEHAVIOURAL OBSERVATIONS

Behaviour of individuals was recorded using continuous focal animal sampling (see methods in Chapter 2).

STATISTICAL ANALYSES

Behavioural variables were prepared as outlined in Chapter 2. I pooled males and females to compare the general differences in activity between parents and non-parents in *N. leucogenys* and *S. syndactylus* (Model 1, Table 3.4), and to compare overall sex differences in activity (Model 1, Table 3.4). If there was an interaction between adult sex and presence of offspring, sex differences were further investigated within non-parents and within parents. Maternal activity budgets were compared across female reproductive status (cycling, pregnant, lactating, Model 2, Table 3.4). Maternal and paternal behaviour were analysed separately to compare offspring care across the female's reproductive status and the sibling composition (one offspring vs. multiple) for all 3 species (Model 3, Table 3.4). Finally sex differences in direct offspring care were analysed, controlling for the reproductive status of the adult female and species (Model 4, Table 3.4). If there was a significant interaction between sex and reproductive status for parents, sex differences for that behaviour were analysed within reproductive status categories.

Table 3.4 Predictors included in regression models

Model	Dependent variables	Fixed effects
1	Adult activity budgets	Presence of offspring (Y/N) Species (<i>S. syndactylus</i> , <i>N. leucogenys</i>) Sex (M/F) Age (years) ¹ Interaction term: Presence of offspring x Sex
2	Maternal activity budgets	Female reproductive status (cycling, pregnant, lactating) Species (<i>S. syndactylus</i> , <i>N. leucogenys</i> , <i>H. moloch</i>)
3	Maternal and paternal direct care	Female reproductive status Species Family composition (one offspring/multiple offspring)
4	Sex differences in direct care	Female reproductive status Species Sex Interaction term: Female reproductive status x Sex

¹Age was only included when analysing time spent resting, moving, in solo and social play

All models were estimated using generalised least squares regression (fit by REML) via the “nlme” package (v.3.1-105) in R (Pinheiro et al. 2012). Residuals and fitted values were plotted for each model and visually checked for normality of residuals and homoscedasticity across the fitted values (Zuur et al. 2009). Where residuals showed heteroscedasticity across the fitted values and fixed effects, I included a weighted variance structure that allowed the variance to be modelled separately for each combination of factor levels (where needed). This was achieved using the ‘varIdent’ function in the “nlme” package (Zuur et al. 2009). Final models that included a weighted variance function had a significantly better fit compared to the uniform variance model (based on a likelihood ratio test of the two models and the AIC, Zuur et al. 2009). Significance was set at $\alpha = 0.05$ but I also report trends where $0.05 \leq p \leq 0.10$.

RESULTS

OFFSPRING PRESENCE AFFECTS CAPTIVE MALE AND FEMALE ACTIVITY BUDGETS

Adult *N. leucogenys* and *S. syndactylus* of both sexes who did not have offspring present in their social group spent more time resting and moving, compared to parents (Table 3.5). Both male and female non-parents spent less time self-grooming, in total social play, grooming others and being groomed than did parents (Table 3.5, Figure 3.1 A,B). Non-parents also spent more time alone, compared to parents (Table 3.5). Males without offspring spent more time singing compared to males with offspring; in contrast, the proportion of time spent singing was the same for females with and without offspring (Table 3.5). Females without offspring spent more time in solo play compared to females with offspring, but there was no difference in solo play between fathers and males without offspring (Table 3.5).

Table 3.5 Influence of parental status on activity budgets

Behaviour ¹		Estimate ± S.E. (non-parents) ²	t	p	N individuals (10-day samples) ³
♀ % Rest	↑	0.17 ± 0.02	8.6	< 0.001 ***	NP: 5 (37) P: 5 (101)
♂ % Rest	↑	0.11 ± 0.03	4	< 0.001 ***	NP: 5 (38) P: 5 (97)
% Movement	↑	0.08 ± 0.02	4.2	< 0.001 ***	NP: 10 (75) P: 10 (198)
% Self groom	↓	-0.07 ± 0.02	-3.9	< 0.001 ***	NP: 10 (75) P: 10 (198)
% Social play	↓	-0.04 ± 0.02	-2.8	0.006 **	NP: 10 (75) P: 10 (198)
% Allogroom	↓	-0.21 ± 0.03	-8.4	< 0.001 ***	NP: 10 (75) P: 10 (198)
♀ % Groomed	↓	-0.19 ± 0.02	-8.2	< 0.001 ***	NP: 5 (37) P: 5 (101)
♂ % Groomed	↓	-0.11 ± 0.03	-4.5	< 0.001 ***	NP: 5 (38) P: 5 (97)
% Time alone	↑	0.43 ± 0.06	7.5	< 0.001 **	NP: 10 (52) P: 10 (162)
♂ % Sing	↑	0.085 ± 0.03	3.3	0.001 **	NP: 5 (38) P: 5 (97)
♀ % Solo play	↑	0.02 ± 0.01	3.1	0.003 **	NP: 5 (37) P: 5 (101)

¹Parental status had no influence on time spent feeding ($p = 0.19$) and on solo play by males ($p = 0.75$)

²Estimate for non-parents compared to parents (reference category)

³NP = non-parents, P = parents

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, bold p values indicate a trend ($0.05 \leq p \leq 0.10$)

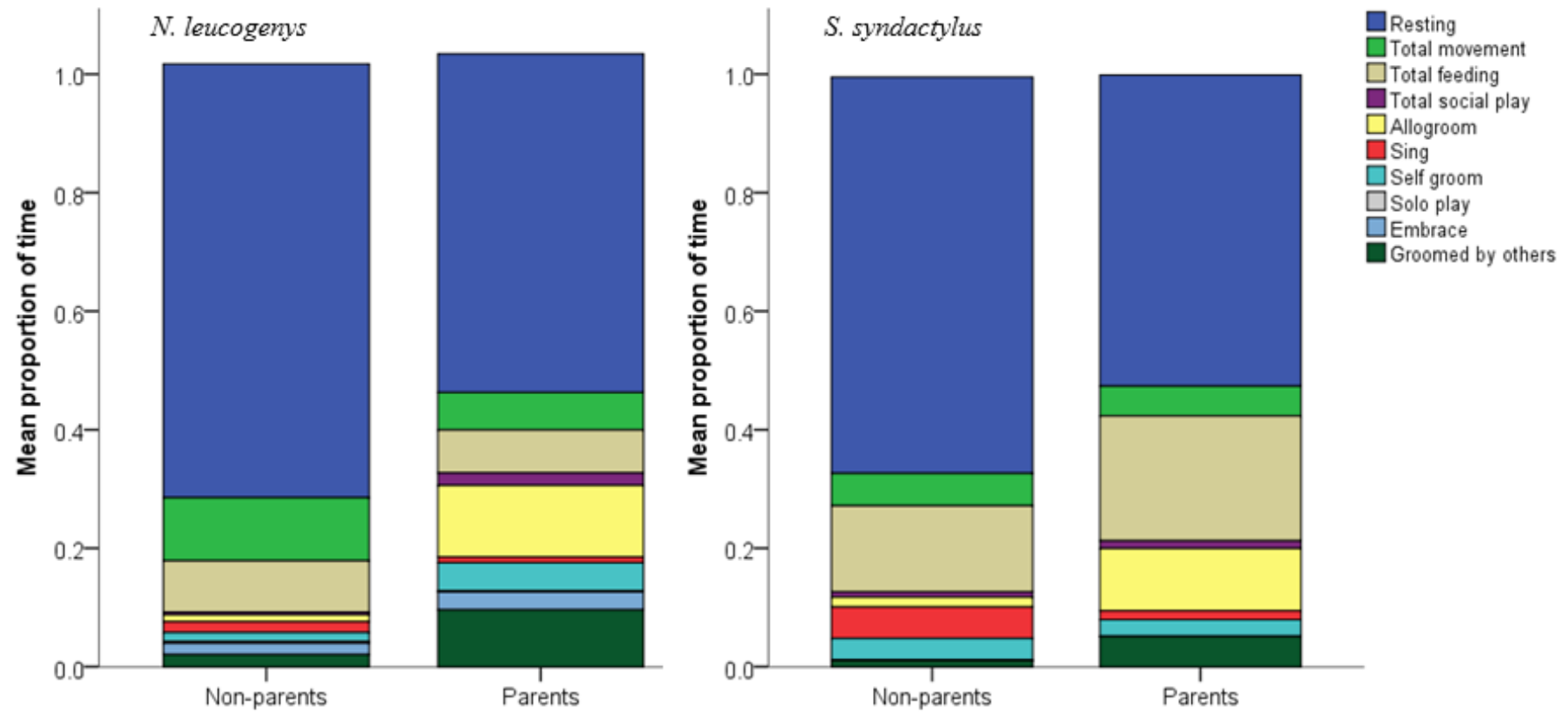


Figure 3.1 Activity budgets of parents and non-parents for *N. leucogenys* and *S. syndactylus*. Data shown are raw proportions of time.

SEX DIFFERENCES IN ACTIVITY BUDGETS

Males spent less time grooming and less time solo playing than did females, irrespective of parental status (Table 3.6, Figure 3.2, Figure 3.3). There was no difference overall between the sexes in the proportion of time spent self-grooming. Sex differences in singing, being groomed, resting, feeding, moving, and social play depended on the parental status. In non-parents, males spent more time singing (trend) and more time being groomed compared to females (Table 3.6, Figure 3.2). There was no difference in the proportion of time that male and female non-parents spent resting.

In family groups, fathers spent more time resting compared to mothers, and there was a trend for fathers to also spend more time feeding than did mothers, regardless of the reproductive status of the female (Table 3.6, Figure 3.3). Fathers spent less time moving compared to mothers, when mothers were lactating, but there were no sex differences in movement in groups with cycling or pregnant mothers (Table 3.6, Figure 3.4). Fathers spent more time engaged in social play when mothers were pregnant or lactating; there was no sex difference in social play when mothers were cycling (Table 3.6, Figure 3.4).

Table 3.6 Sex differences in activity budgets

Sample	Behaviour ¹		Estimate (males) ²	St Error	t	p	N individuals (10-day samples) ³
All adults	% Allogroom	↓	-0.06	0.03	-2.12	0.03*	M: 10 (135) F: 10 (138)
	% Sing	↑	0.05	0.03	1.89	0.06	M: 5 (38) F: 5 (37)
Non-parents	% Groomed	↑	0.07	0.02	3.28	0.002**	M: 5 (38) F: 5 (37)
	% Solo play	↓	-0.03	0.01	-2.8	0.007**	M: 5 (38) F: 5 (37)
Parents	% Rest	↑	0.06	0.02	3.4	< 0.001***	M: 5 (97) F: 5 (101)
	% Feed	↑	0.04	0.02	1.94	0.05	M: 5 (97) F: 5 (101)
	% Solo play	↓	-0.005	0.002	-2.4	0.02*	M: 5 (97) F: 5 (101)
	% Move (female lactating)	↓	-0.06	0.01	-4.7	< 0.001***	M: 4 (79) F: 4 (79)
	% Social play (female pregnant)	↑	0.05	0.02	2.7	0.009**	M: 3 (31) F: 3 (32)
	% Social play (female lactating)	↑	0.05	0.01	4.8	< 0.001***	M: 4 (79) F: 4 (79)

¹Sex had no influence overall on time spent self-grooming (p = 0.96), feeding (p = 0.79), moving (p = 0.17), and social play (p = 0.51) and had no influence on time spent resting in non-parents (p = 0.29), on time spent moving when females were cycling (p = 0.63) or pregnant (p = 0.75), and on time spent in social play when females were cycling (p = 0.65)

²Estimate for males compared to females (reference category)

³M = males, F = females

* p < 0.05, ** p < 0.01, *** p < 0.001, bold p values indicate a trend (0.05 ≤ p ≤ 0.10)

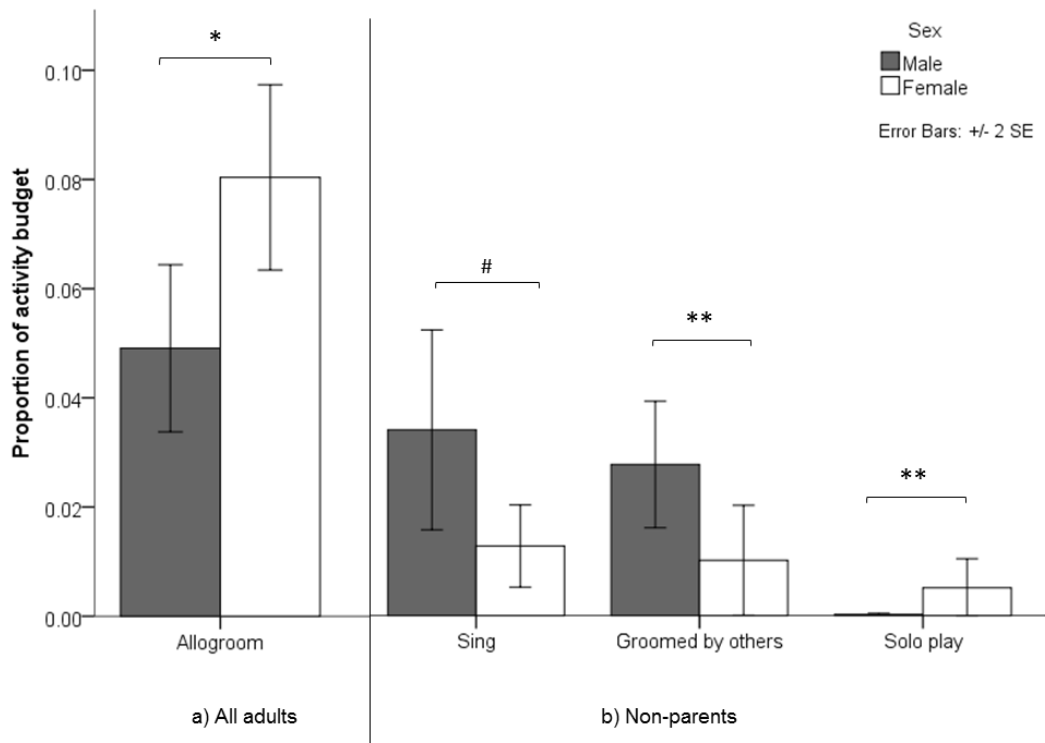


Figure 3.2 Sex differences in the activities of a) all adults, irrespective of parental status and b) non-parents only. Data shown are raw proportions of time (± 2 standard errors), and significant differences are derived from GLS regression models. # $0.05 \leq p \leq 0.1$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

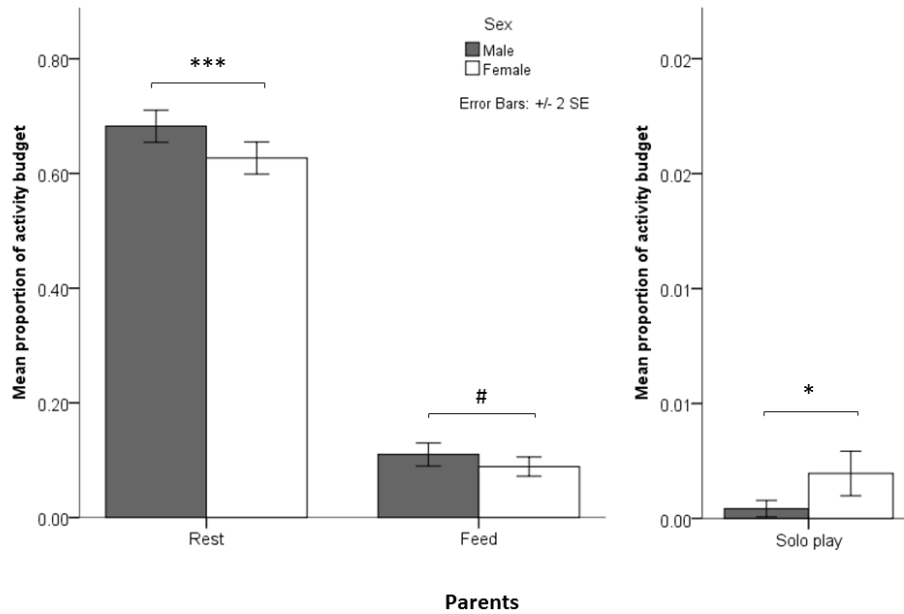


Figure 3.3 Sex differences in activities of parents only, showing a) Resting and feeding and b) Solo play. Data shown are raw mean proportions of time (± 2 standard errors) and significant differences are derived from GLS regression models, # $0.05 \leq p \leq 0.1$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. NB: a different scale is required to illustrate solo play, due to the infrequency of this behaviour relative to resting and feeding.

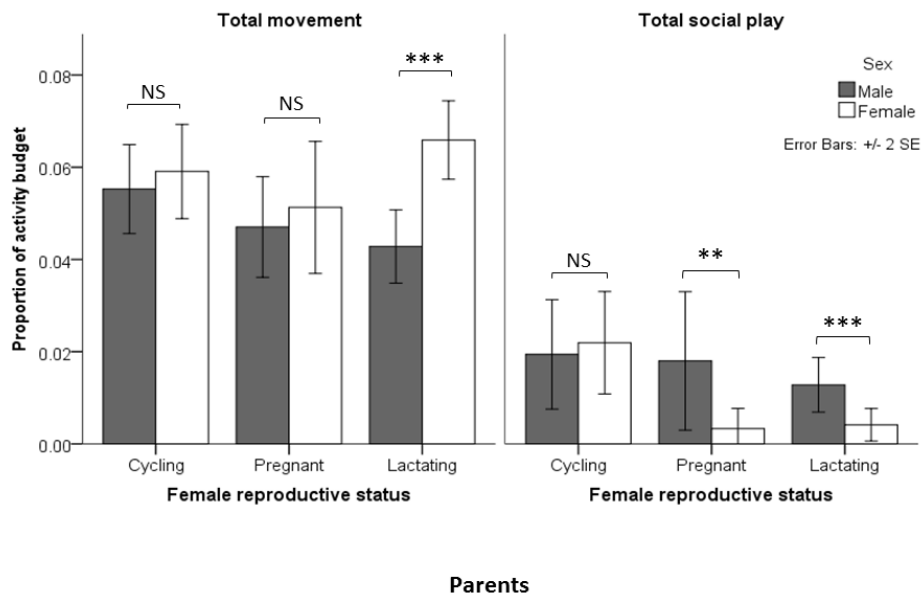


Figure 3.4 Sex differences in activities of parents only, relative to the reproductive status of the adult female. Data shown are raw mean proportions of time (± 2 standard errors) and significant differences are derived from GLS regression models, NS $p > 0.1$, # $0.05 \leq p \leq 0.1$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

MATERNAL ACTIVITY BUDGETS DEPEND ON REPRODUCTIVE STATUS

The reproductive status of the adult females influenced all maintenance behaviours (i.e. required non-social behaviours) in mothers, except for total feeding time (Table 3.7). Pregnant and lactating mothers spent more time resting than did cycling mothers (Table 3.7, Figure 3.5). There was a trend for pregnant mothers to spend more time resting compared to mothers who were lactating (Table 3.7, Figure 3.5). Lactating mothers spent more time moving compared to both pregnant and cycling mothers (Table 3.7, Figure 3.5). Pregnant mothers spent the most time self-grooming, followed by lactating females, with cycling females spending the smallest proportion of time self-grooming (Table 3.7, Figure 3.5). Solo play was lower in pregnant females compared to cycling females, but there was only a trend for pregnant females to spend less time in solo play than lactating females (Table 3.7, Figure 3.5). Pregnant and lactating females spent less time in social play compared to cycling females (Table 3.7, Figure 3.5).

Table 3.7 Influence of female reproductive status on maternal activity budgets

Behaviour ¹	Reference group (N _i , N _o) ²	Test group (N _i , N _o) ²		Estimate ± S.E.	t	p
% Rest	Cycling (4, 63)	Pregnant (3, 32)	↑	0.16 ± 0.04	3.8	< 0.001 ***
	Cycling	Lactating (4, 79)	↑	0.10 ± 0.03	3.3	0.001 ***
	Pregnant	Lactating	↓	-0.06 ± 0.03	-1.9	0.06
% Move	Cycling (4, 63)	Pregnant (3, 32)		0.008 ± 0.02	0.3	0.737
	Cycling	Lactating (4, 79)	↑	0.04 ± 0.02	2.9	0.004 **
	Pregnant	Lactating	↑	0.04 ± 0.02	2.1	0.04 *
% Self-groom	Cycling (4, 63)	Pregnant (3, 32)	↑	0.15 ± 0.03	4.5	< 0.001 ***
	Cycling	Lactating (4, 79)	↑	0.07 ± 0.02	3.0	0.004 **
	Pregnant	Lactating	↓	-0.08 ± 0.02	-3.3	0.001 **
% Solo play	Cycling (4, 63)	Pregnant (3, 32)	↓	-0.02 ± 0.01	-2.1	0.04 *
	Cycling	Lactating (4, 79)		-0.007 ± 0.008	-0.9	0.386
	Pregnant	Lactating	↑	0.01 ± 0.01	1.7	0.09
% Social play	Cycling (4, 63)	Pregnant (3, 32)	↓	-0.04 ± 0.02	-2.0	0.05
	Cycling	Lactating (4, 79)	↓	-0.04 ± 0.02	-2.1	0.04 *
	Pregnant	Lactating		-0.00003 ± 0.01	-0.003	0.99

¹Female reproductive status had no influence on time spent feeding (p = 0.53)
²Sample sizes for number of individuals (N_i) and number of 10-day samples (N_o)
* p < 0.05, ** p < 0.01, *** p < 0.001, bold p values indicate a trend (0.05 ≤ p ≤ 0.10)

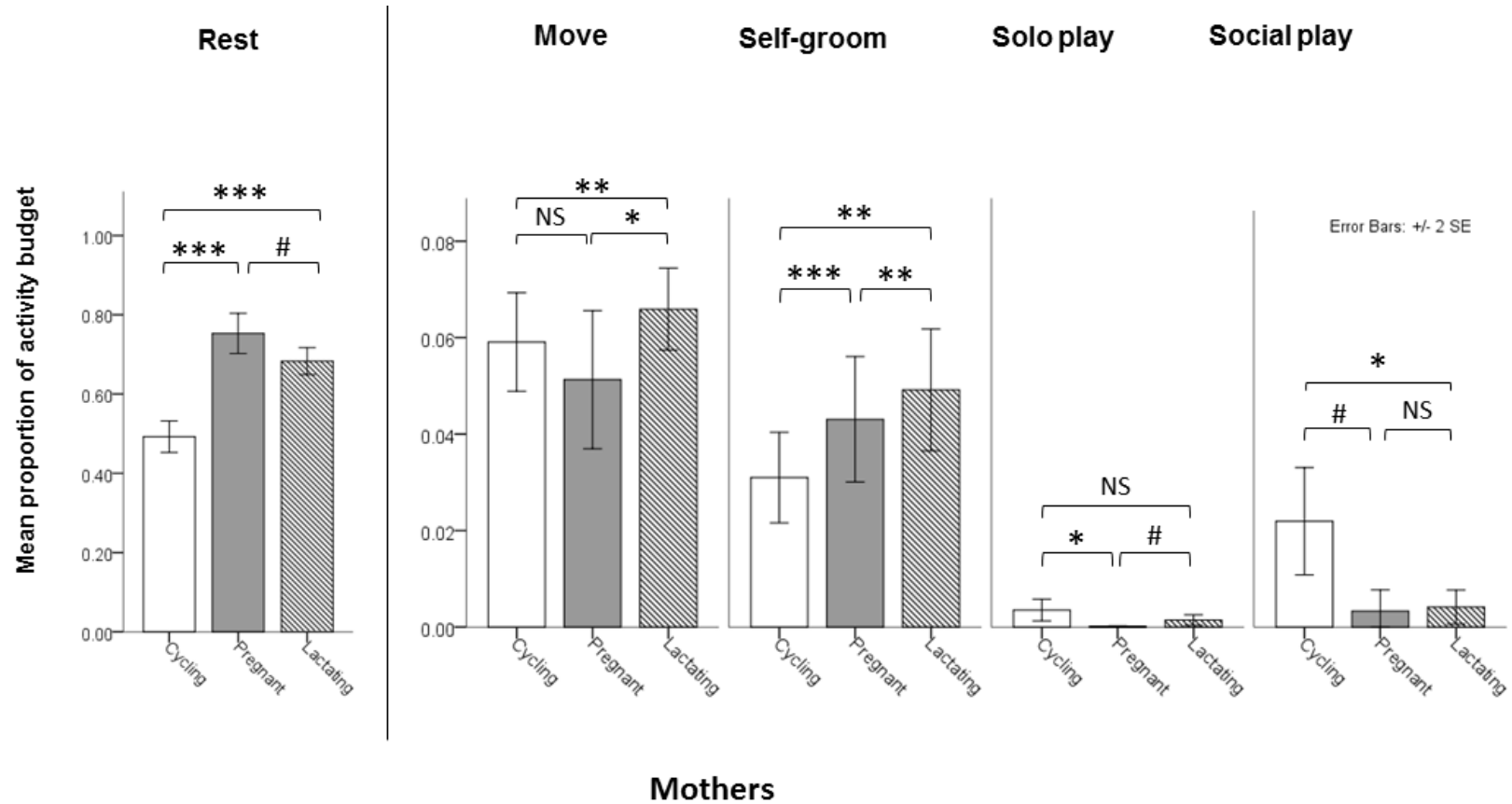


Figure 3.5 Influence of reproductive status on maternal activities. Data shown are raw mean proportions of time (± 2 standard errors). The proportion of time that mothers spent feeding did not differ by reproductive status. Significant differences (shown by symbols) are derived from GLS regression models. NS $p > 0.1$, # $0.05 \leq p \leq 0.1$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. NB: a different scale is required to illustrate the proportion of time spent resting, relative to the other behaviours. Differences in self grooming between pregnant and lactating mothers do not reflect the regression results due to the inclusion of 'species' as a control variable in regression analyses, see Table 3.7.

MATERNAL DIRECT CARE DEPENDS ON REPRODUCTIVE STATUS

Both pregnant and lactating mothers spent less time playing with offspring compared to cycling mothers (Table 3.8, Figure 3.6). There was a trend for lactating mothers to spend more time playing with offspring compared to pregnant mothers (Table 3.8).

Lactating mothers spent less time alone compared to non-lactating mothers (Table 3.8).

There were no differences across reproductive status in the proportion of time that mothers spent grooming offspring, or the frequencies per hour of grooming offspring, and initiating play with offspring.

PATERNAL DIRECT CARE DEPENDS ON MATERNAL REPRODUCTIVE STATUS

Fathers spent more time playing with offspring and initiated play with offspring more frequently when their mate was pregnant, compared to fathers whose mates were cycling (Table 3.8, Figure 3.6). There was a trend for males with pregnant mates to spend more time playing with offspring compared to males with lactating mates (Table 3.8). Males with lactating mates initiated play with offspring more frequently compared to males with cycling mates, but did not spend a greater proportion of time playing with offspring (Table 3.8). Fathers with pregnant or lactating mates spent more time grooming offspring, and there was a trend for males with lactating mates to groom offspring more frequently, compared to those with cycling mates (Table 3.8). Fathers whose mates were lactating spent more time alone compared to fathers with pregnant mates (Table 3.8).

Table 3.8 Influence of female reproductive status on maternal and paternal direct care of offspring

Subset	Behaviour ¹	Reference group (N _i , N _o) ²	Test group (N _i , N _o) ²		Estimate ± S.E.	t	p
Maternal	% Play with offspring	Cycling (4, 51)	Pregnant (3, 22)	↓	-0.11 ± 0.02	-4.5	< 0.001 ***
		Cycling	Lactating (3, 39)	↓	-0.10 ± 0.02	-4.2	< 0.001 ***
		Pregnant	Lactating	↑	0.01 ± 0.01	1.69	0.09
	% Alone	Cycling (4, 63)	Pregnant (3, 32)		0.005 ± 0.08	0.07	0.95
		Cycling	Lactating (3, 43)	↓	-0.46 ± 0.08	-5.5	< 0.001 ***
		Pregnant	Lactating	↓	-0.46 ± 0.06	-8.2	< 0.001 ***
Paternal	% Play with offspring	Cycling (4, 46)	Pregnant (3, 21)	↑	0.10 ± 0.04	2.7	0.007 **
		Cycling	Lactating (3, 39)		0.06 ± 0.03	1.6	0.11
		Pregnant	Lactating	↓	-0.04 ± 0.02	-1.9	0.06
	Play initiation frequency	Cycling (4, 46)	Pregnant (3, 21)	↑	1.17 ± 0.29	4	< 0.001 ***
		Cycling	Lactating (3, 39)	↑	0.75 ± 0.22	3.4	< 0.001 ***
		Pregnant	Lactating		-0.42 ± 0.27	-1.6	0.12
	% Grooms offspring	Cycling (4, 58)	Pregnant (3, 31)	↑	0.09 ± 0.04	2.5	0.01 *
		Cycling	Lactating (4, 79)	↑	0.10 ± 0.03	3.1	0.002 **
		Pregnant	Lactating		0.01 ± 0.02	0.40	0.69
	Frequency grooms offspring	Cycling (4, 46)	Pregnant (3, 21)		0.33 ± 0.20	1.6	0.11
		Cycling	Lactating (3, 39)	↑	0.34 ± 0.18	1.9	0.06
		Pregnant	Lactating		0.01 ± 0.13	0.08	0.94
% Alone	Cycling (4, 58)	Pregnant (3, 31)		-0.04 ± 0.09	-0.48	0.63	
	Cycling	Lactating (3, 43)		0.10 ± 0.08	1.33	0.19	
	Pregnant	Lactating	↑	0.14 ± 0.07	2.04	0.04 *	

¹Female reproductive status did not influence maternal time spent grooming offspring (p = 0.82), frequency of grooming offspring (p = 0.78), or frequency of initiating play with offspring (p = 0.12)

²Sample sizes for number of individuals (N_i) and number of 10-day samples (N_o)

* p < 0.05, ** p < 0.01, *** p < 0.001, bold p values indicate a trend (0.05 ≤ p ≤ 0.10)

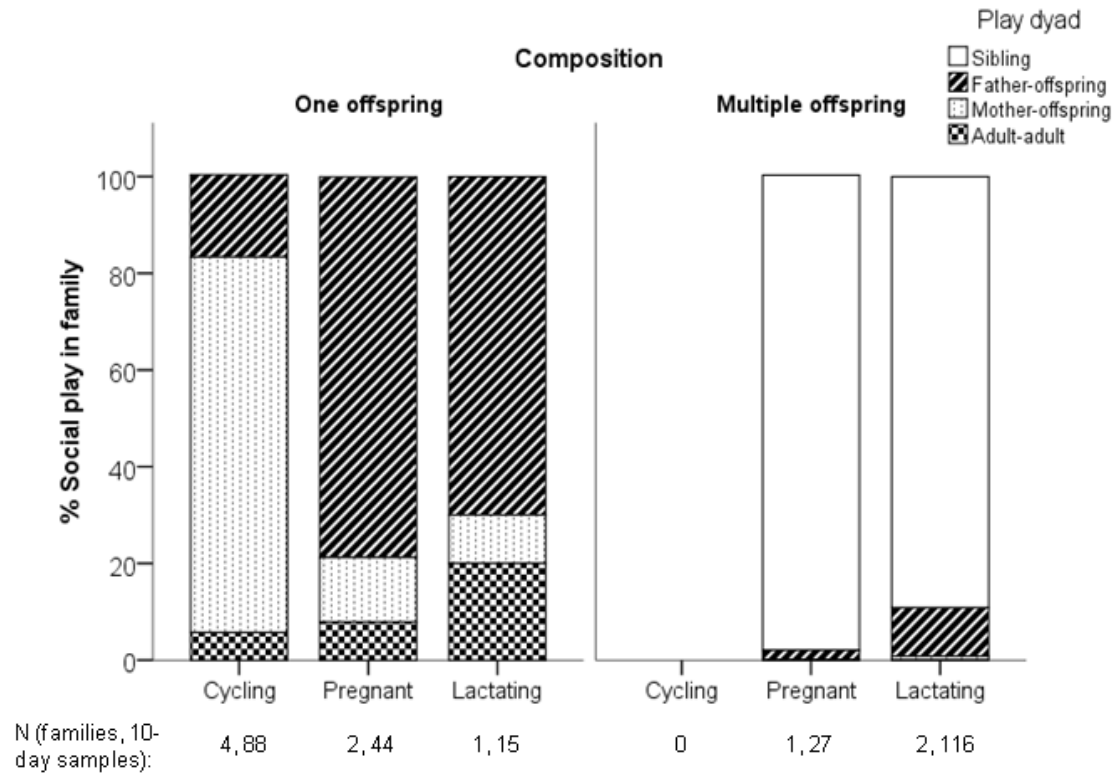


Figure 3.6 Percentage of total social play in families represented by siblings, father-offspring dyads, mother-offspring dyads and adult-adult dyads, according to the number of offspring in the group and the reproductive status of the adult female

SEX DIFFERENCES IN OFFSPRING CARE

There was no interaction between parental sex and reproductive status for the frequency of grooming offspring ($p = 0.49$) and the proportion of time spent grooming offspring ($p = 0.70$). Females always groomed offspring more frequently, and for greater proportions of time than did males (Table 3.9). In groups in which females were cycling, mothers spent a greater proportion of time playing with offspring than did fathers (Table 3.9, Figure 3.6), but there was no sex difference in the frequency of initiating play with offspring (Table 3.9). Fathers spent a greater proportion of time playing with offspring than did mothers when mothers were pregnant (Table 3.9, Figure 3.6). Fathers also initiated play with their offspring more than did mothers when mothers were pregnant or lactating (Table 3.9). There was no sex difference in the proportion of time spent playing with offspring in groups with lactating females. Fathers spent more time alone than did mothers when mothers were lactating (Table 3.9). There was no sex difference in the proportion of time spent alone when the mother was cycling or pregnant.

Table 3.9 Sex differences in direct offspring care

Subset	Behaviour ¹		Estimate ± S.E. (males) ²	t	p	N individuals (10-day samples) ³
All parents	% Grooms offspring	↓	-0.07 ± 0.02	-4.5	< 0.001 ***	M: 7 (168) F: 7 (174)
	Frequency grooms offspring	↓	-0.41 ± 0.08	-4.9	< 0.001 ***	M: 7 (106) F: 7 (111)
Female cycling	% Play with offspring	↓	-0.09 ± 0.03	-3.4	0.001 **	M: 4 (46) F: 4 (51)
Female pregnant	% Play with offspring	↑	0.08 ± 0.03	3.1	0.004 **	M: 3 (21) F: 3 (22)
	Play initiation frequency	↑	1.02 ± 0.31	3.3	0.002 **	M: 3 (21) F: 3 (21)
Female lactating	Play initiation frequency	↑	0.17 ± 0.07	2.3	0.02 *	M: 3 (39) F: 3 (39)
	% Alone	↑	0.38 ± 0.05	7.3	< 0.001 ***	M: 3 (43) F: 3 (43)

¹Sex had no influence on the frequency of initiating play with offspring (p = 0.54) or time spent alone (p = 0.37) when females were cycling, time spent alone when females were pregnant (p = 0.17), and time spent playing with offspring when females were lactating (p = 0.17)

²Estimate for males compared to females (reference category)

³M = males, F = females

* p < 0.05, ** p < 0.01, *** p < 0.001, bold p values indicate a trend (0.05 ≤ p ≤ 0.10)

EFFECT OF SIBLING PRESENCE ON PARENTAL CARE

Only the frequency of play initiation differed between mothers with one offspring and mothers with more than one offspring; mothers with one offspring initiated play with offspring more frequently compared to mothers with more than one offspring (Table 3.10). There was a trend for mothers with more than one offspring to be more frequently aggressive towards offspring, compared to mothers with only one offspring (Table 3.10). There was no difference in the proportion of time that mothers spent playing with offspring or grooming offspring, or the frequency of grooming offspring between mothers with one offspring and mothers with more than one offspring. Fathers with more than one offspring spent less time engaged in social play with offspring and initiated play with offspring less often compared to fathers with only one offspring (Table 3.10, Figure 3.6). In contrast, fathers with more than one offspring spent more time grooming offspring (total proportion of time) compared to fathers with only one offspring (Table 3.10). Fathers with one offspring spent more time alone than fathers with more than one offspring (Table 3.10). In contrast, there was a trend for mothers with one offspring to spend *less* time alone, compared to mothers with more than one offspring (Table 3.10). Paternal aggression did not differ between those with one offspring and those with more than one.

Table 3.10 Influence of number of offspring (one offspring or more than one offspring) on maternal and paternal direct care

Subset	Behaviour ¹		Estimate ± S.E. (one offspring) ²	t	p	N individuals (10-day samples) ³
Maternal	Play initiation frequency	↑	0.37 ± 0.13	2.8	0.006**	OO: 5 (72) MO: 2 (39)
	Frequency of aggression towards offspring	↓	-0.13 ± 0.08	-1.7	0.097	OO: 5 (67) MO: 3 (66)
	% Alone	↓	-0.07 ± 0.04	-1.7	0.097	OO: 5 (72) MO: 3 (66)
Paternal	% Play with offspring	↑	0.05 ± 0.01	5.6	< 0.001***	OO: 5 (67) MO: 2 (39)
	% Groom offspring	↓	-0.06 ± 0.02	-3.2	0.002**	OO: 5 (67) MO: 3 (101)
	Play initiation frequency	↑	0.91 ± 0.15	5.8	< 0.001***	OO: 5 (67) MO: 2 (39)
	% Alone	↑	0.20 ± 0.04	4.5	< 0.001***	OO: 5 (67) MO: 3 (65)

¹Number of offspring had no influence on maternal time spent playing with offspring (p = 0.18), grooming offspring (p = 0.52), and frequency of grooming offspring (p = 0.12), and no influence on paternal frequency of grooming offspring (p = 0.93), and frequency of aggression towards offspring (p = 0.18)

²Estimate for parents with one offspring compared to parents with more than one offspring (reference group)

³OO = one offspring, MO = multiple offspring

* p < 0.05, ** p < 0.01, *** p < 0.001, bold p values indicate a trend (0.05 ≤ p ≤ 0.10)

DISCUSSION

In this chapter I explored the variation in male and female activity budgets in differing social and reproductive contexts, and the impact that this variation has on sex differences in activity and participation in parental care of weaned offspring. I predicted that the presence of offspring in the social group and the reproductive status of the female would influence female activity budgets more so than male activity budgets, and that sex differences in activity would be more pronounced when offspring are present and/or when females are pregnant or lactating. Additionally, I predicted that male participation in parental care of weaned offspring would depend on the current reproductive status of the female and the contributions of the female and older siblings to parental or alloparental care of offspring. The following discussion explores this variation in activity budgets and parental care in the context of the unusual reproductive strategy and ecological niche of the small apes.

GREATER INTRA-GROUP SOCIALITY WHEN OFFSPRING ARE PRESENT

I predicted that the presence of offspring in captive groups would have a greater influence on female activity budgets than on male activity budgets, due to the division of labour observed in wild groups between offspring care (females) and territory defence (males, Chivers 1974; Gittins 1980; Brockelman & Srikosamatara 1984; Palombit 1993; Orgeldinger 1997; Reichard & Sommer 1997; Heine & Geissmann 2000; Bartlett 2003; Brockelman 2009). Interestingly, offspring presence influenced the activity budgets of both males *and* females in captivity. Parents in the current study spent less time resting and moving, and spent more time in social activities like social play and grooming, compared to adults without offspring, irrespective of sex. Additionally, fathers spent less time singing than did non-fathers. These results are consistent with the suggestion by Orgeldinger (1997) that captive parents are less attentive to external stimuli compared to adults with no offspring, due to the time

needed for offspring care. Orgeldinger (1997) noted reduced territorial behaviour and activity in captive siamang parents, compared to adults without offspring.

Combined, these results suggest that both parents shift their focus internally when offspring are present in the social group. However, this finding may not be wholly applicable to wild groups, since wild hylobatids spend much less time playing and grooming compared to captive groups (Dooley 2006). The lower frequency of play in the wild may be associated with available energy, since play frequency in wild groups varies with fluctuations in resource availability (Bartlett 2003), while the lower frequency of grooming may be more related to the time required for foraging. In the absence of these pressures, the presence of offspring might have a greater impact on parental activity budgets in captivity. Nevertheless, wild hylobatid adults may still exhibit a shift in social focus when offspring are present, or when new offspring are born. This could be investigated further in wild groups.

SEX DIFFERENCES IN BEHAVIOUR ARE GREATER WHEN OFFSPRING ARE PRESENT

If sex differences in behaviour are related to parental investment and the associated division of labour, then there should be few differences in male and female behaviour in pairs with no offspring. Although the presence of offspring influenced both male and female behaviour in captivity, there *were* greater sex differences in activity budgets in parents than in non-parents (Table 3.6), indicating that the presence of offspring does differentially influence the activity budgets of adults. Regardless of the mother's reproductive status, fathers spent more time resting than mothers (Figure 3.3), consistent with observations from wild *H. lar* in which males spend more time resting than females (Bartlett 2009a). But males in groups with offspring spent *more* time feeding compared to females (Figure 3.3), in contrast to the greater feeding by wild female than male *H. lar* (Bartlett 2009a).

It is possible that provisioning by keeping staff (to reproductively active females) reduces the proportion of time that reproductive females spend on eating their regular feed and browse items. This extra feeding is likely to be underrepresented in focal samples, because extra items were often given when females were out of the observer's sight in holding cages. In addition, females consumed these extra food items quickly, because they were often a preferred food type. As a result of these limitations, the proportion of time spent feeding is probably not a useful measure of sex differences in energy intake in a captive setting, unless feeding is more carefully monitored. Further sex differences in parental activity budgets depended on the female's reproductive status, and were associated with variation in maternal behaviour.

MATERNAL ACTIVITY BUDGETS DEPEND ON REPRODUCTIVE STATUS

I predicted that female activity budgets would reflect a capital breeding strategy involving increased feeding and decreased resting during the recovery (weaning, post-weaning) period. Wild *S. syndactylus* females spend more time feeding during the weaning and post-weaning periods than when lactating (Lappan 2009). I therefore expected that mothers who were cycling during the observation period would spend more time feeding and less time resting compared to pregnant or lactating mothers. This was not observed; I did not find any differences in the proportion of time devoted to feeding by mothers in different reproductive states. There may be several reasons for this: firstly, fat reserves tend to be higher in captive primates than in wild populations (Dufour & Sauther 2002). Secondly, females in captivity could increase their food intake without substantially increasing the time spent feeding due to the easier access to food items. Thirdly, changes in the diet of females implemented by veterinary and keeping staff (such as the allocation of extra nutrition like bananas to pregnant and lactating females) may reduce the need for females to change their behaviour by reducing the impact of gestation and lactation on female energy reserves.

The lack of a difference in feeding behaviour across reproductive status is therefore not wholly surprising, but a more detailed analysis of female feeding behaviour in relation to relevant husbandry practices and physiological measures of energy balance would be worthwhile in captive groups. It is also possible that the increased time spent feeding during weaning and post-weaning periods in wild *S. syndactylus* are actually a result of *decreased* feeding during the lactation phase, due to the physically suppressive impact of infants on female foraging activity (Lappan 2009; van Noordwijk 2012). However, in the current study, lactating females spent the most time moving, suggesting that infants do not limit female activity in captivity.

Pregnant and lactating females were less active than non-reproductive females. Mothers rested more and played less during pregnancy and lactation, compared to cycling mothers (Table 3.7). Pregnant mothers also reduced their solo play compared to both lactating and cycling mothers. However, extensive reductions in activity levels may not be possible in wild hylobatids due to the travel requirements of foraging. This is suggested by the lack of a sex difference in daily path length in wild *S. syndactylus*, despite the greater resting by lactating females (Lappan 2009). In the absence of this pressure (in captivity), females are able to rest more and are less inclined to be active during pregnancy and lactation. Similarly, in other captive non-human primates energy intake does not vary with reproductive status, in contrast to wild populations; this is suggested to result from the greater ability of primates to reduce activity levels in captivity, thus reducing the need for increased energy intake during gestation and lactation (Dufour & Sauther 2002). This difference between captive and wild populations is important to consider for captive management of female energy balance.

In the current study, pregnancy seemed to have a greater impact on female activity than did lactation (which includes infant carrying), and lactating mothers spent the most time moving. It is possible that the time spent resting was lower, and time spent moving

higher in lactating than pregnant mothers due to the monitoring required for semi-dependent infants. In captivity, reasons for travelling through the enclosure include moving towards food, and moving to and from social partners or preferred resting sites. For females with semi-dependent infants, more frequent movement may also be required to retrieve wandering infants. This is somewhat supported by a trend for mothers with older infants to spend more time moving (Pearson's $R = 0.7$, $p = 0.053$, $N = 8$ mother-infant dyads). Thus, females could be less able to reduce energy expenditure during lactation due to their involvement in maintaining proximity to semi-dependent infants.

SEX DIFFERENCES IN PARENTAL ACTIVITY BUDGETS DEPEND ON FEMALE REPRODUCTIVE STATUS

I predicted that sex differences in feeding behaviour between parents would be greatest when females were cycling, based on the feeding patterns observed in wild *S. syndactylus* females (Lappan 2009). But female reproductive status had no impact on sex differences in feeding behaviour, presumably because female feeding behaviour itself did not differ with reproductive status. I also predicted that sex differences in other activity budget behaviours would vary with maternal reproductive status. In support of this hypothesis, females only spent less time in social play than did males when females were currently physiologically investing in a fetus or infant (Figure 3.4). In contrast, the only sex difference in time spent moving was seen in groups with lactating mothers; lactating females spent more time moving than did males (Figure 3.4). Again, this could be related to the presence of a semi-dependent infant that requires monitoring.

VARIABLE MATERNAL INVESTMENT IN ENERGY-COSTLY BUT NOT TIME-COSTLY OFFSPRING CARE

I predicted that the role of each parent would be dynamic, with mothers reducing additional social care of existing offspring (play and grooming) when their transport and

nutritional care costs were the greatest (i.e. during pregnancy and lactation). Play is an energetically costly behaviour; therefore, maternal play with offspring is likely to be reduced during the most expensive reproductive phases. Females indeed spent less time engaged in social play in general, and specifically, in play with offspring, when pregnant or lactating compared to cycling females (Figure 3.6). Grooming of offspring, which is comparatively less energetic than play, did not differ with female reproductive status. The lack of a difference between mothers of differing reproductive status may simply be a result of the less constrained time budget of captive hylobatids. Whilst play still has an energetic cost in captivity, grooming mostly incurs a time cost, and time is much more plentiful in a captive environment compared to the wild, due to the reduced need to forage (Hosey 2005).

PATERNAL OFFSPRING CARE COMPLEMENTS VARIATION IN MATERNAL CARE

As socialisation can be provided by fathers, I also predicted that when maternal social care was the lowest, direct care by fathers would be the highest. Paternal play with offspring reflected the differences in maternal activity budgets; fathers contributed the most to active care of offspring when mothers were pregnant, and therefore might have been less responsive to offspring play solicitations. Similarly, in a *H. lar* group with a newborn infant and only one older offspring, play activity of the juvenile shifted to the father after the birth (Schessler & Nash 1977).

In contrast, fathers in groups with lactating mothers did not spend more time playing or initiating play with offspring compared to males with cycling mates, despite the fact that their mates spent less time playing with offspring compared to cycling mothers. This can be explained by the group composition: of those groups in which the mother was lactating, 80% of samples represented families with more than one offspring. This was not the case for groups with pregnant mothers, in which families with more than one offspring constituted only 38% of samples. Therefore, the majority of families with

lactating mothers also contained older offspring who could play with siblings. This suggests that paternal play behaviour is sensitive to both the female's reproductive state and the availability of younger play partners. The contribution of males should persist if no older siblings (or other group members) are present, as in Schessler & Nash's (1977) *H. lar* family.

Although mothers spent the same proportion of time grooming offspring regardless of reproductive status, fathers spent more time grooming offspring and groomed offspring more frequently when mothers were pregnant or lactating. This variation in paternal grooming of offspring suggests that something other than maternal care influences how much offspring grooming males do. Regardless of the mother's reproductive state, mothers were the main provider of grooming for offspring (Table 3.9). This contrasts with some observations of wild *H. Lar* in which the adult male contributes the most to offspring grooming (Bartlett 2009a), although Brockelman (2009) notes in the same population that males groom offspring less than do females. Females in captivity may have more time available for offspring grooming than do wild females. In the current study, fathers, but not mothers, spent more time grooming offspring (in total) when they had more than one offspring, compared to fathers with only one offspring. If more offspring means more required grooming, fathers may contribute additional grooming, and thus lighten the (otherwise increased) load on mothers. The input of fathers to offspring grooming therefore depends on the number of offspring in the group and may function to limit maternal grooming time to an optimal amount.

This possible compensation by males is interesting considering that time costs should have greater consequences for males than they do for females in the wild. If male hylobatids have to spend a large proportion of time being vigilant for successful territory defence (Orgeldinger 1997; Heine & Geissmann 2000), then the more time they spend attending to intra-group activities (like grooming offspring), the less time is

available to attend to extra-group stimuli (conspecifics and/or predators). The low frequency of grooming in hylobatids compared to other primates (particularly in the smaller hylobatid species), and the clustering of grooming bouts in some wild groups at the end of the activity period (Ellefson 1974, p.94) may limit the impact that grooming has on vigilance and foraging efficiency in the wild. For this reason, grooming behaviour may be less dependent on the contributions of others compared to play, due to its already limited impact on activity budgets. Further research on factors surrounding paternal grooming could shed light on the observed variation in this behaviour.

OLDER SIBLINGS SUBSIDISE THE COST OF PLAY BUT NOT GROOMING

There is some evidence that the contribution of older offspring to play with siblings can minimise the time (and associated energy) that mothers and fathers devote to playing with offspring (see Figure 3.6). Mothers and fathers with multiple offspring in the current study initiated play with offspring less frequently than those with one offspring (Table 3.10). Fathers with more than one offspring also spent less time playing with offspring compared to those with only one offspring (Table 3.10). These differences in play initiation suggest that parents alter their behaviour when offspring have no alternative play partners. This may be because offspring solicit play more frequently from parents when no-one else is available, or perhaps parents are more likely to respond to only-offspring play solicitations regardless of the frequency with which that offspring demands play. For fathers, the presence of siblings reduced the proportion of the activity budget spent on play, but this was not the case for mothers. It is difficult to distinguish between the influence of reproductive phase and sibling presence on maternal play, since my sample did not include any cycling females with multiple offspring. Similar reductions in paternal care occur in common marmosets (*Callithrix jacchus*); fathers reduce their participation in infant carrying when older siblings are available (Ximenes & Sousa 1996).

It is unlikely that older offspring reduce the cost of offspring grooming for either parent. Neither mothers nor fathers decreased the proportion of time that they spent grooming offspring when more than one offspring was present. This suggests that parents continue to groom each offspring despite the presence of additional grooming partners who could be contributing. A greater contribution by older offspring towards play with siblings, rather than grooming of siblings is logical, given the intrinsic benefits of those activities to the individual performing them. Older immatures presumably still gain intrinsic benefits in locomotor and parenting skills through play with younger siblings, but gain less from grooming activities which require less practise. Alternatively, although the actions involved in grooming may not require much learning, inexperienced older offspring may be less effective at identifying parasites in the hair. Younger offspring may thus gain more of a hygienic benefit from being groomed by parents than by older siblings.

CONCLUSION

I have shown that offspring presence and female reproductive status influence hylobatid activity budgets in captivity and contributions to parental care by group members complement variation in maternal care. The investment of mothers into gestation and lactation resulted in a more energy-conserving activity profile, and suppressed maternal investment in active substitutive care (play with offspring), but not passive substitutive care (grooming offspring). Accordingly, the parent contributing the most to play with offspring depended on the reproductive phase of the mother (Figure 3.6). Mothers who were cycling were the main parental play partner for offspring, while in groups with pregnant or lactating mothers, fathers devoted more time to offspring play than did mothers. Lastly, the presence of more than one offspring also suppressed active substitutive care by both parents, but did not influence grooming of offspring. The impact of reductions in the already infrequent play and grooming in wild hylobatid

groups may not be as substantial; however, variation in other types of direct offspring care may depend on the energy- and time-budgets of individuals and the group composition in a similar way.

CHAPTER 4 THE TIMING OF DEVELOPMENT

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INTRODUCTION

The pre-reproductive period in primates is variably divided into infancy, juvenescence, adolescence, and subadulthood (Caine 1986). Many primates display delayed sexual maturity in comparison to the relatively early onset of reproduction in other mammals (Plant 1994). Zoological definitions of adulthood are variable, with 3 major components: attainment of adult body size, sexual maturity and social maturity (with the last being particularly prominent in the primate literature). The transition to adulthood is thus multifactorial, consisting of both physiological and behavioural components that interact. In addition, the timing of each aspect of maturity differs among species, and depends on the definition used (Caine 1986; Setchell & Lee 2004). Data on development in hylobatids is lacking in comparison to other apes. Most of the few existing data on somatic markers of development in hylobatids of known age are obtained from hand-raised captive individuals (e.g. Suzuki et al. 2003) or individuals of unknown origin or rearing history. Behavioural data are more abundant, but are also difficult to obtain in the field and are often descriptive in nature. Researchers currently divide the dependent period in hylobatids into a variable number of categories (Table 4.1); the ages at which transitions occur depend on the differing criteria used, particularly in early field studies lacking individual birth histories.

Table 4.1 Commonly used age class categories for hylobatids

Source	Species (context)	Age classes
(Ellefson 1974)	<i>Hylobates lar</i> (wild)	Infant (0 – 2 years), juvenile (2 – 4 years), adolescent (4 – 6 years), subadult (6+ years), adult
(Brockelman et al. 1998)	<i>H. lar</i> (wild)	Infant (0 – 2 years), juvenile I (2 – 5 years), juvenile II/adolescent (5 – 8 years), subadult (8+ years), adult
(Reichard 2003)	<i>H. lar</i> (wild)	Infant (0 – 2 years), juvenile (2.1 – 4 years), adolescent (4.1 – 6 years), subadult (6.1 – 8 years), adult, old adult
(Chivers 1974)	<i>Symphalangus syndactylus</i> (wild)	Infant I, infant II, juvenile, subadult (6/7 – 9 years), adult
(Geissmann 1993)	Various (captive)	Infant (0 – 2 years), juvenile (2.1 – 4 years), subadult (4.1 – 6 years), adult

Herein, I outline the range of estimates for the timing of developmental transitions currently available in the literature for hylobatids. In this chapter, I 1) provide the first comprehensive review of developmental timing in captive and wild hylobatids, and 2) describe changes in behaviour with age in a longitudinal and cross-sectional sample of captive immatures of three species: *Hylobates moloch*, *Nomascus leucogenys* and *Symphalangus syndactylus*. In this captive sample, I investigate whether the frequencies of social interactions (play, food transfer, aggression, sexual behaviour and proximity to/distance from parents) change across the developmental period in a way which would suggest puberty onset and attainment of sexual and social maturity. Since developmental data is difficult to obtain for hylobatids, this chapter serves as a preliminary review that highlights the significant gaps in our knowledge of developmental timing in hylobatids. Compilation of this data from both wild and captive groups provides valuable insights into the developmental process in this taxon.

REVIEW OF MARKERS OF DEVELOPMENTAL TIMING IN HYLOBATIDS

The available markers for which we can also estimate chronological age in hylobatids are summarized below, and outlined in Table 4.2. Physiological, physical and

behavioural maturation are summarized separately due to evidence of dissociation between these aspects of maturity in other primates (Dixson 2012). For example, primary sexual function is achieved without the development of secondary sexual characteristics in some male mandrills (Dixson et al. 1993) and in unflanged male orang-utans (Maggioncalda et al. 1999). In addition, the offspring of many family-living vertebrates show a delay in sexual or social maturity while living in the natal group (Kleiman 1977), such that individuals are sexually mature (and thus *could* reproduce), but continue to associate with parents, or become non-breeding helpers (Goldizen 1990; Emlen 1995; Asa 1997). In many species the timing of reproductive maturity is also flexible among individuals depending on either developmental or current social environments, and traits develop variably in time (e.g. in tamarins, Ziegler et al. 1987; humans, Belsky et al. 1991; rodents, Gudermuth et al. 1992). To facilitate discussion of the variable age estimates for maturity in hylobatids, I present the range of estimates in a visual format (Figure 4.1).

Table 4.2 Age ranges for physiological and behavioural markers of development in captive and wild gibbons from the literature

Developmental transition	Marker	Age range in captivity (years)	Species	Age range in wild (years)	Species	
Infancy to juvenescence	M1 eruption	1.4	<i>H. agilis</i> ¹	-	-	
		1.8	<i>N. concolor</i> ³⁶	-	-	
		2.3	<i>S. syndactylus</i> ²⁴	-	-	
	Dental stress	1.5	<i>H. lar</i> ²	-	-	
		IGF-1	1.2 – 1.4	<i>H. agilis</i> ³	-	-
	Pelage colour change	0.5 – 1.5	<i>N. leucogenys</i> ⁴	0.5-1.5	<i>N. concolor</i> ⁵	
				0 – 0.5	<i>N. hainanus</i> ⁶	
	Behavioural weaning (completion)		1.2 – 2	<i>H. agilis</i> ³	2.2 – 2.5	<i>Hoolock hoolock</i> ⁷
					1.75 - 2.3	<i>H. lar</i> ^{8,9,10}
					1.5	<i>N. hainanus</i> ⁶
Locomotor independence		1.75 – 2.2	<i>S. syndactylus</i> ^{11,24}	1 – 1.5	<i>S. syndactylus</i> ^{12,13}	
				2.2	<i>H. hoolock</i> ⁷	
				2.3	<i>H. lar</i> ⁸	
Puberty onset	First sexual swelling ♀	5.6 – 7.5	<i>H. moloch</i> ¹⁵	8	<i>H. lar</i> ¹⁶	
		≥ 2	<i>H. albibarbis</i> , <i>H. meulleri</i> ¹⁷	-	-	
		7.5	<i>S. syndactylus</i> ¹¹	-	-	
	Menarche ♀	5 – 7.5	<i>H. moloch</i> ¹⁵	> 9	<i>H. lar</i> ¹⁶	
		7	<i>H. hoolock</i> ¹⁸			
	↑ Testosterone ♂	2.6 - 3.5	<i>H. agilis</i> ³	< 9	<i>H. lar</i> , <i>H. pileatus</i> ¹⁹	
	Testosterone to adult level	5	<i>H. lar</i> , <i>H. pileatus</i> ¹⁹			
	Receipt of parental aggression/exclusion from food sources/peripheralisation	5+		<i>Various</i> ^{20,37}	4 – 6	<i>H. lar</i> ⁸
					5 – 8+	<i>H. lar</i> ²¹
					5.5	<i>N. hainanus</i> ²²
	6	<i>S. syndactylus</i> ¹¹	6 – 9 +	<i>S. syndactylus</i> ^{12,23}		
Sexual maturity: potential for reproduction	Emergence of last M3	4.6 – 6.9	<i>H. agilis</i> ¹	6.1	<i>H. lar</i> ²⁴	
	Emergence of last canine	5.2 – 6.2	<i>H. agilis</i> ¹	5.2	<i>S. syndactylus</i> ²⁴	
				-	-	
				8 – 9+	<i>H. lar</i> ^{10,16}	
Regular sex-skin swelling ♀	-	-	-	<i>H. lar</i> ^{10,16}		
Regular ovulatory cycling pattern	7.7 – 8	<i>H. moloch</i> ¹⁵	> 9	<i>H. lar</i> ¹⁶		

Table 4.2 Cont.

Developmental transition	Marker	Age range in captivity (years)	Species	Age range in wild (years)	Species Source
Look like an adult	Adult body size	5.75	<i>Hylobates</i> spp. ²⁵	8	<i>H. lar</i> ¹⁰
		7.5	<i>S. syndactylus</i> ²⁵	8 – 10	<i>S. syndactylus</i> ^{26,23}
	Completed eruption of canines	7 – 8	<i>N. leucogenys</i> ²⁷	-	-
	Completed eruption of permanent dentition	9	<i>H. lar</i> ²⁸	-	-
	Pelage colour change ♀ <i>Nomascus</i>	5 – 9	<i>N. leucogenys</i> ^{27,35}	6 – 7	<i>N. concolor jingdongensis</i> ²⁸
		6 +	<i>N. leucogenys</i> ⁴		
	Dark chest plate ♀ <i>H. moloch</i>	5	<i>H. moloch</i> ²⁹		
Act like an adult	Copulation ♂	5.8 - 7.3	<i>Various</i> ²⁰	-	-
		7.6	<i>S. syndactylus</i> ¹⁴	-	-
	Sexual presentation ♀	8	<i>S. syndactylus</i> ¹¹	-	-
		Copulation ♀	8.6	<i>Various</i> ²⁰	-
	8		<i>S. syndactylus</i> ¹¹	9 ⁴	<i>S. syndactylus</i> ²³
	Mature song structure ♀	-	-	6 – 8	<i>H. agilis</i> ³⁰
	Decline in co-singing for ♀	-	-	8+	<i>H. lar</i> ¹⁰
	Regular solo singing ♂	-	-	6 – 8	<i>H. lar</i> ¹⁰
	Dispersal ♀	-	-	7 – 9	<i>H. lar</i> ^{16,31,32}
		-	-	10	<i>H. pileatus</i> ³³
	Dispersal ♂	-	-	10	<i>H. lar</i> ³¹
		-	-	7 – 8	<i>H. pileatus</i> ³³
	First reproduction (birth) ♀	-	-	5.5	<i>N. hainanus</i> ²²
		5.7 – 9.8	<i>Hylobates, Nomascus</i> spp. ³⁴	8.4 – 12.8	<i>H. lar</i> ^{31,32}
	First reproduction (birth) ♂	5.7 – 10	<i>S. syndactylus</i> ³⁴	-	-
		4.6 – 9.8	<i>Various</i> ^{34,20}	12.9 - >14	<i>H. lar</i> ³¹
4.9 – 10		<i>S. syndactylus</i> ³⁴	-	-	

1 = (Uchikoshi & Matsuzawa 2007), 2 = (Dirks 1998), 3 = (Suzuki et al. 2003), 4 = (Mootnick & Fan 2011), 5 = (Sheeran 1993), 6 = (Liu et al. 1989), 7 = (Ahsan 2004), 8 = (Ellefson 1974), 9 = (Reichard & Barelli 2008), 10 = (Reichard 2003), 11 = (Fox 1977), 12 = (Chivers 1980), 13 = (Lappan 2009), 14 = this study, 15 = (Hodgkiss et al. 2010), 16 = (Barelli et al. 2007), 17 = (Cheyne & Chivers 2006), 18 = (Matthews 1946), 19 = (Barelli & Heistermann 2012), 20 = (Mootnick et al. 2005), 21 = (Bartlett 2009a, p. 60), 22 = (Zhou et al. 2008), 23 = (Lappan 2005), 24 = (Dirks & Bowman 2007), 25 = (Leigh & Shea 1995), 26 = (Chivers 1974), 27 = (Deputte & Leclerc-Cassan 1981), 28 = (Huang et al. 2013), 29 = (Mootnick 2006), 30 = (Koda et al. 2013), 31 = (Brockelman et al. 1998), 32 = (Reichard et al. 2012), 33 = (Srikosamatara & Brockelman 1987), 34 = (Geissmann 1991), 35 = (Schilling 1984), 36 = (Schultz 1933), 37 = (Burns et al. 2011)

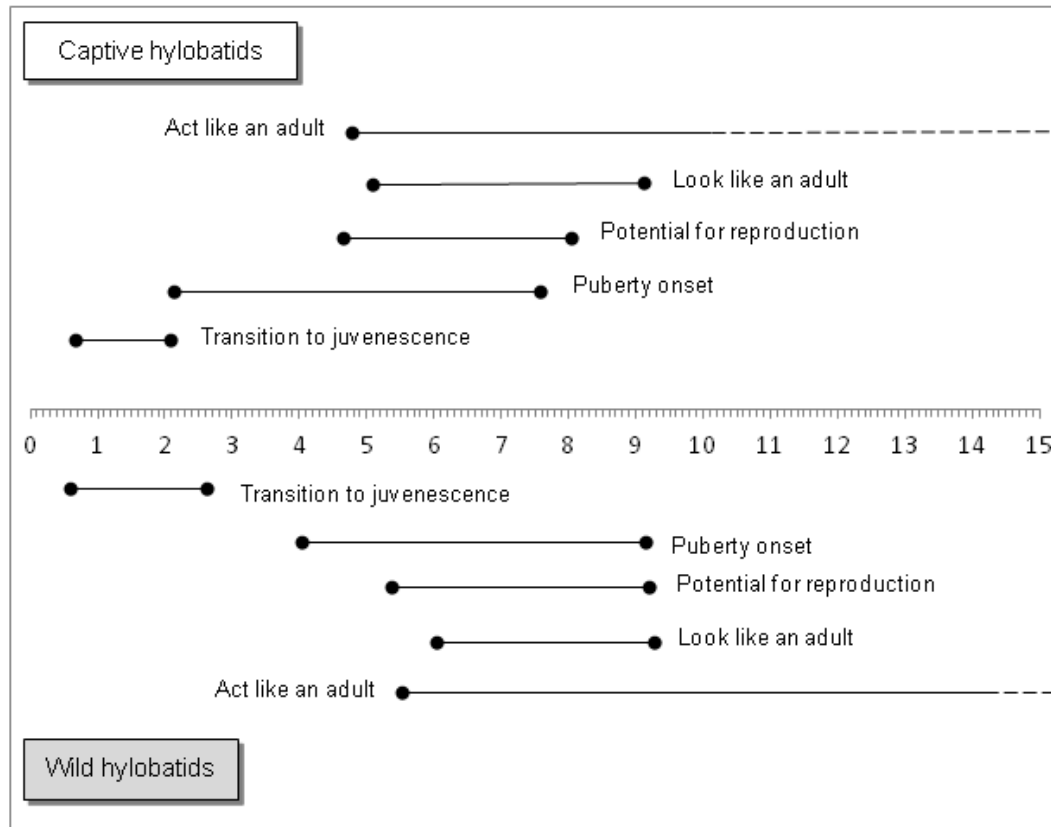


Figure 4.1 Range for ages at onset of developmental events in captive (top) and wild (bottom) hylobatids. Lines indicate the age range from various markers in multiple species (listed in Table 4.2). The transition between the solid and dashed lines for “Act like an adult” represent the latest observed ages at first reproduction.

BIRTH TO PUBERTY ONSET

Infancy is defined by dependence on maternal milk and this is reflected in measurable anatomical markers of physiological development (e.g. dental markers, Dirks 1998). In most anthropoid primates the eruption of the first molar (M1) corresponds with the onset of weaning (Dirks & Bowman 2007). This occurs at 1.4 – 2.3 years of age in captivity in hylobatids (Table 4.2). Dental histology and peaks in plasma levels of IGF-1 (an important somatic growth hormone) provide a similar estimate (Dirks 1998; Suzuki et al. 2003). In some species infant pelage colour changes during this stage; the timing of the first coat colour change in *Nomascus* spp. occurs between 0.5 – 1.5 years of age in both wild and captive individuals (Liu et al. 1989; Sheeran 1993; Mootnick & Fan 2011). Behavioural estimates of the transition to juvenescence are similar, ranging from 1 – 2 years in captivity, and 1 – 2.5 years in the wild (Table 4.2). Estimates of complete locomotor independence range from about 1 year of age in captivity to 2.2 – 2.3 years of age in the wild (Table 4.2).

The juvenile period in hylobatids is less well defined. In primates, play behaviour peaks during late infancy and early juvenescence (Fagen 1993) and juveniles engage in learning of foraging and social skills that may continue into adolescence and adulthood (Joffe 1997). Juveniles can also be characterised by feeding and travelling independently although they are not yet adult size (Lonsdorf & Ross 2012). The few observations from field research suggest that hylobatids display typical “juvenile” primate behaviour but do not clearly indicate the ages at which this behavioural pattern peaks and declines. In the wild, Ellefson (1974) characterized juvenile *Hylobates lar* by their interest in play and being groomed more than they groomed others. Schessler and Nash (1977) reported that juvenile *H. lar* engage in higher frequencies of food transfer attempts, which may facilitate the transition to self-feeding following weaning. In addition, juveniles tend to maintain closer proximity to their mother than do older

offspring (Brockelman et al. 1998; Reichard 2003), and still receive help when crossing large gaps in the canopy during group travel (Palombit 1992). Using these measures of juvenile behaviour, we provide the first age estimates of “juvenile” hylobatid behaviour in captivity using quantitative methods.

ADOLESCENCE: FROM PUBERTY ONSET TO SEXUAL MATURITY

Adolescence extends from the start of puberty to the completion of sexual maturation, the completion of body growth, or first reproduction (Watts & Pusey 1993).

Adolescence is a widely accepted life history phase in primates during which physical, sexual and social maturation are completed (Spear 2000; Setchell 2003). Behaviourally, this process involves increasing autonomy from parents and widening of the social sphere (Kipke 1999; Galdikas 1995). Puberty is the re-activation of the hypothalamic-pituitary-gonadal axis and associated increases in leutenising hormone (LH), follicle stimulating hormone (FSH), and gonadal steroid hormones (Saltzman et al. 2010).

There are no longitudinal data on androgen levels and testicular development in hylobatids that span the entire period of body growth. Suzuki et al (2003) reported that two hand-raised agile gibbons (*Hylobates agilis*) reached adolescence at 2.6 and 3.5 years based on the levels of plasma IGF-1, testosterone, and proportion of adult weight (Table 4.2). However, their data extended only to age 4, and growth continues for another 2 years in captive *Hylobates*. In female hylobatids the external signs of puberty (first sexual swellings and menarche indicated by menstrual bleeding) are more obvious than in males (Barelli et al. 2007; Hodgkiss et al. 2010). Estimates for the first appearance of swelling and menstrual bleeding for captive females in their natal groups suggest that adolescence begins as early as 5 – 5.6 or as late as 7.5 years (Hodgkiss et al. 2010, Table 4.2). Sexual swellings have also been reported in females as young as 2 years of age who were housed with unrelated males (Cheyne & Chivers 2006, Table 4.2). Estimates from wild *H. lar* suggest that first sexual swellings occur close to

cessation of body growth (~8 yrs), but that females may not experience menarche while residing in their natal groups (Barelli et al. 2007, Table 4.2).

Adolescence in most primates is associated with less frequent play (Pereira & Altmann 1985; Caine 1986; Pusey 1990; Kraemer et al. 1982), reduced tolerance from adults in feeding contexts (Pereira & Altmann 1985), increased aggressive behaviour (Coe et al. 1988; Kraemer et al. 1982), increased sexual behaviour (Lonsdorf & Ross 2012; Kraemer et al. 1982) and increased conflict and distancing between parents and offspring (in humans, Steinberg 1989), or between breeding adults and adolescents (in nonhuman primates, Caine 1986). There are no published quantitative data on rates of play across the immature period in wild hylobatids; some researchers note a decrease in play behaviour between the ages of 5 and 8 in wild *H. lar* (6 - 8 years, Reichard 2003; 5 - 8 years, Bartlett 2003). Ellefson (1974, p. 87) noted that intolerance by parents of food transfer attempts by offspring begins when offspring reach 4 – 6 years old, with increasing intensity as offspring get older. These observations are descriptive and it is unclear just how marked differences in frequencies are with age. Other reports suggest that parental aggression, exclusion of immatures from food sources and peripheral spacing of immatures occurs between 5 – 6 years of age in captive hylobatids, and 5 – 9 years of age in wild hylobatids (Table 4.2).

SEXUAL MATURITY: REPRODUCTIVE POTENTIAL

The end of the adolescent phase is difficult to define, since menarche is followed by a period of subfertility in most primates, including hylobatids (Spear 2000; Hodgkiss et al. 2010). For this reason, sexual maturation in females is defined either by the presence of complete ovulatory cycles, pregnancy, or first birth, depending on the available data. Since conception and reproduction generally do not occur in the natal group in hylobatids, only complete ovulatory cycling can be used to determine reproductive potential in females living at home. This occurs between 7.7 and 8 years of age in

captivity (Hodgkiss et al. 2010), and may not be observed in the natal group in the wild (up to 9 years of age, Barelli et al. 2007). Reproductive capability is more difficult to measure for males and would require data on testis size or sperm production. Currently, there is no evidence on which to base estimates of the age at which male hylobatids in the natal group are capable of successful conception. Males that were removed from their natal groups and housed with females were able to conceive offspring between 4 – 5 years of age (Geissmann 1991).

Dental emergence can also be used as a marker of sexual maturity; evidence from other primates suggests the emergence of the third molar (M3) is closely followed by first reproduction (Dirks & Bowman 2007). However, estimates of M3 emergence for wild hylobatids (5.2 in *S. syndactylus* and 6.1 in *H. lar*, Table 4.2) are much earlier than any estimates of first reproduction in wild populations (Dirks & Bowman 2007; see also Table 4.2). Zihlman et al. (2011) consider a captive 6.5 year old *Hylobates pileatus* male as adult based on M3 eruption and fusion of the proximal humerus. This age is similar to the age at body growth completion in captive *Hylobates* spp. (Table 4.2). Similarly, Uchikoshi & Matsuzawa (2007) note that an M3 was the last permanent tooth to erupt in one male *H. agilis* at 6.9 years, while a canine was the last tooth to erupt in another male *H. agilis* at 6.2 years of age (Table 4.2).

PHYSICAL MATURITY: LOOKING LIKE AN ADULT

Adult body size is reached by 5.75 years of age in captive *H. lar* and by 8 years of age in the wild (Table 4.2). In the larger *S. syndactylus*, adult body size is reached by 7.5 years in captivity and 8 – 10 years in the wild (Table 4.2). In some hylobatid species, males or females undergo changes in coat colour that are associated with sexual maturity. In captive *N. leucogenys* females, colour change begins between 5 – 9 years of age (Table 4.2), which is close to other estimates of puberty, and cessation of growth for *Hylobates* females in captivity (Table 4.2). Wild *N. concolor* females change pelage

colour between 6 – 7 years of age (Table 4.2), slightly earlier than estimates of first sexual swellings and attainment of adult body size in wild *H. lar* females (Table 4.2). Completed canine eruption produces corresponding changes in facial appearance to a more adult-like form, as was noted by Carpenter (1964, p. 208), who described the juvenile face as “not ruggedly contoured by canine teeth as is the case with adults”. Evidence of the age at which this occurs is extremely limited, even in captive individuals (Table 4.2).

SOCIAL MATURITY: ACTING LIKE AN ADULT

The transition to adulthood requires both the behavioural repertoire needed to achieve reproduction, and a change in the social environment. In family-living species the social contexts allowing reproduction include the absence of parents and the presence of appropriate mating partners, both of which are associated with natal dispersal (Ziegler et al. 1987). Behaviours that facilitate this social transition in hylobatids of both sexes include the onset of appropriate sexual behaviour, and peripheralisation (spatial distancing from parents, Reichard 2003), and dispersal (leaving the natal group and obtaining a mate and territory). Some researchers use mature singing as an indicator of maturity in either sex, particularly solo singing in males (Tilson 1981; Bleisch & Chen 1991; Reichard 2003; Guan et al. 2013; Dooley et al. 2013). Copulatory behaviour is observed between 5.8 – 8 years in captivity, but is rarely observed in the natal group in the wild (Table 4.2). Mature singing behaviour occurs between 6 – 8 years of age in the wild (Table 4.2). Estimates of the age at dispersal in wild hylobatids range from 5.5 (*N. hainanus*, Zhou et al. 2008) to 10 years of age (*H. pileatus*, Srikosamatara & Brockelman 1987, Table 4.2; *H. lar*, Brockelman et al. 1998). Estimates for age at first birth are generally older than estimates of age at dispersal, ranging from 8.4 – 14 years or more in the wild (Table 4.2). Age ranges for first birth in the wild could be more variable than this, since minimum estimates could underestimate the reproductive

success of males (Brockelman et al. 1998), and some individuals could take even longer to reproduce.

VARIATION IN DEVELOPMENTAL TIMING

There is little variability in the reported timing of the transition between the infant and juvenile stages (Figure 4.1), and estimates from captive and wild hylobatids are remarkably similar (Table 4.2). In contrast, age estimates for the onset of puberty and sexual maturation are far more diverse (Figure 4.1), suggesting that there is more plasticity in later development. This has resulted in variable and confusing definitions of age classes in hylobatids (Table 4.1). Later developmental milestones may be highly variable for two reasons; firstly, some developmental markers are reached at earlier ages in captive primates compared to individuals in the wild (Caine 1986). Given that hylobatids are not strict seasonal breeders, it is expected that endogenous condition thresholds are important for the establishment and maintenance of full reproductive function in females (Brockman & van Schaik 2005). Moreover, activation of the hypothalamic-pituitary-gonadal axis at puberty is also related to somatic growth thresholds in male primates (Plant 2008). As such, we expect developmental milestones to occur earlier in captivity where access to food is more constant, and food items are higher in nutritional value. Variation in available nutrition may also contribute to inter-individual variability in the wild.

Secondly, the variation in puberty onset and other developmental milestones within captive populations indicates the influence of additional factors, (e.g. social group composition) on the timing of maturation in individual hylobatids (Geissmann 1991). Hylobatids live in simple family groups and fit the conditions in which we might expect flexible sexual and social maturity (Emlen 1995). In wild hylobatid groups, offspring are mother-reared, and most offspring remain in their natal groups until dispersal after 7 – 8 years of age (mean, Table 4.2). In contrast, some captive animals for whom

developmental markers are recorded develop in different social environments (i.e. with same-aged peers, with only one parent, with siblings, hand-raised), or are removed from the natal group before 7 – 8 years of age (Geissmann 1991). Developmental markers may not be comparable to estimates from wild born individuals when the age at removal from the natal group is not noted. Thus, comparisons should only be made between markers obtained from immatures in the natal group during both infancy and activation of the reproductive system at puberty. The literature is currently limited in two ways: firstly, developmental markers from wild individuals of known age are only recently emerging from long term monitoring of wild groups. Secondly, published data from captive animals are often not accompanied by information on rearing history of individuals and the social context of developmental markers. This chapter is the first step in exploring possible sources of variation in developmental milestones in hylobatids. I integrate the available data from the literature with quantitative behavioural observations on 12 captive individuals in their natal groups and suggest a framework for investigating the proximate causes of variation in hylobatid development.

METHODS

STUDY ANIMALS

Subjects included 12 non-infant immatures (four *H. moloch*, three *N. leucogenys* and five *S. syndactylus*) and longitudinal data were collected for eight of these immatures (demographic information for the adolescents and subadults are displayed in Table 4.3). One subadult *S. syndactylus* and one juvenile *H. moloch* were the only immatures to be classified in the same age class in different sampling years. The remaining six longitudinally sampled immatures were observed in more than one age class such that there were 20 combinations of individuals and age classes. I used approximately 2 year age brackets to compare the behaviour of immatures, loosely corresponding to

Ellefson's (1974) age class descriptions (Table 4.1): infant (~0 – 2 years), juvenile (~2 – 4 years), adolescent (4 – 6 years) and subadult (6 – 9 years).

Nine *juveniles* ranged from 1.8 - 3.3 years of age (\bar{x} = 2.8 years). The youngest juvenile was never observed suckling (although once appeared to try and was rebuffed by the mother) and was not carried. Six *adolescents* ranged from 4.1 - 5.9 years of age (\bar{x} = 5.1 years) and five *subadults* ranged from 6.1 - 9.5 years of age (\bar{x} = 7.7 years). All subadults lived in their natal groups. The youngest *H. moloch* and *N. leucogenys* subadults were 6 years of age, while the youngest *S. syndactylus* subadult was 7.6 years of age, which closely fits with the end of body growth in captivity for *Hylobates* and *Symphalangus* spp., respectively; thus, all subadults were roughly adult size.

Table 4.3 Demographics of 4 – 9 year olds included in the study (details for juveniles available in Chapter 5)

Species	Individual (studbook #)	Date of birth	Age class	Age (start)	Age (end)	Parents (studbook #) ¹	Rearing status ²	Sample size (# 10-day samples)	Location
<i>H. moloch</i>	♂ Arjuna (#66)	24/11/2000	Adolescent	4.7	5.2	F: Jury (#36) M: Hecla (#32)	MR	18	
			Subadult	7.3	7.7			10	
	♂ Nakula (#137)	30/05/2005	Adolescent	5.0	5.3	MR	14		
		Subadult	6.0	6.3	13				
<i>N. leucogenys</i>	♀ Jermei (#28)	05/07/2002	Adolescent	5.7	6.1	F: Phillip (#2) M: Viann (#13)	HR: 6 – 20wks MR: > 20 wks	13	Perth Zoo
	♀ Kit (#29)	16/01/2005	Adolescent	5.4	5.7		MR	12	
			Subadult	6.3	6.5		10		
	♀ Li-Lian (#44)	02/06/2007	Adolescent	3.9	4.3	F: Kayak (#21) M: Nelly (#16) SF: Tao (#147) ³ , SM: Jermei (#28)	HR: 0 – 3yrs SMR: > 3yrs	6	
<i>S. syndactylus</i>	♂ Jambi (#72)	13/09/2002	Subadult	7.5 9.4	7.6 9.6	F: Armstrong (#70) M: Fern (#65)	MR	14	Mogo Zoo
	♀ Tunku (#79)	22/01/2007	Adolescent	5.1	5.2		MR	6	
	♂ Jars (#59)	26/10/2001	Subadult	9.1	9.2	F: Niran (#43), M: Mang (#41)	MR ⁴	5	Adelaide Zoo

¹Studbook numbers for *H. moloch* from the International Studbook for Javan Silvery Gibbons (2009), studbook numbers for *N. leucogenys* from the Australasian Regional Studbook for White-Cheeked Gibbons (2009), studbook numbers for *S. syndactylus* from the Australasian Regional Studbook for Siamang (2011). SF = step-father, SM = step-mother.

²Rearing status: MR = mother-reared, HR = hand-reared by keeping staff, SMR = step-mother-reared

³Studbook number for this individual obtained from the European Studbook (2008)

⁴According to studbook

BEHAVIOURAL OBSERVATIONS

Behaviour of individuals was recorded using continuous focal animal sampling (see methods in Chapter 2).

STATISTICAL ANALYSES

Behavioural variables were prepared as outlined in Chapter 2. Behaviours were compared across age class categories (infant, juvenile, adolescent, subadult, adult) using generalized linear mixed models (GLMM) via the function “lmer” in the R (v.2.15.2) package lme4 (version 0.999999-0) (Bates et al. 2012; R-Core-Team 2012). Immatures of both sexes were pooled, due to the small sample sizes within the older age class categories. Regression analyses were used in order to include ‘species’ as a fixed control variable and mixed models were chosen to account for the longitudinal nature of some of the data. ‘Individual ID’ nested in ‘group ID’ were used as random variables to account for repeated measures for some individuals in different age classes and for nesting of related individuals within the same family. Residuals and fitted values were plotted for each final model and visually checked for normality of residuals (in linear models) and homoscedasticity across the fitted values (Zuur et al. 2009). Age class had a significant influence on all behaviours (determined using the ‘aov.lmer’ command in “lme4”), and ‘species’ was only kept in the model if it had a significant impact on model fit (determined using a likelihood ratio test via the ‘anova.lme’ command). To obtain pairwise differences between age classes, I calculated Markov-chain Monte Carlo (MCMC) p-values using the ‘pvals.fnc’ function in the “languageR” package (v.1.4) (Baayen 2011). Significance was set at $\alpha = 0.05$ but I also report trends where $0.05 \leq p \leq 0.1$.

RESULTS

AGE-RELATED BEHAVIOUR OF 2 – 9 YEAR OLD CAPTIVE GIBBONS

Hylobatids aged 4 – 6 (here defined as adolescents) spent a smaller proportion of time in solo and social play compared to juveniles aged 2 – 4 (Table 4.4). There was a trend for adolescents to initiate play with others less often than juveniles did. Adolescents attempted food transfer less frequently than did juveniles (Table 4.4). Adolescents were neither more aggressive towards other group members compared to juveniles, nor did they receive more aggression from group members (Table 4.4). There were trends for adolescents to be found further away from parents compared to juveniles; but adolescents spent the same proportion of time within arm's reach of both parents (Table 4.4).

Table 4.4 Differences in behaviour between juveniles, adolescents and subadults

Behaviour	Adolescents compared to juveniles ¹			Subadults compared to adolescents ²			N (individuals) Juveniles, adolescents, subadults	N (10-day samples) Juveniles, adolescents, subadults
	Estimate ± S.E.	t	p	Estimate ± S.E.	t	p		
Social play	-0.04 ± 0.02	-2.2	0.03*	-0.04 ± 0.02	-2.1	0.04*	9, 6, 5	109, 77, 56
Solo play	-0.14 ± 0.01	-13.7	< 0.001***	-0.05 ± 0.01	-4.4	< 0.001***	6, 4, 4	63, 45, 42
Play initiation	-0.47 ± 0.28	-1.7	0.10	-1.19 ± 0.29	-4.1	< 0.001***	8, 5, 5	91, 59, 56
Food transfer attempts	-0.23 ± 0.05	-4.7	< 0.001***	-0.10 ± 0.06	-1.7	0.09	8, 5, 5	85, 57, 56
Aggression to others	+0.02 ± 0.06	0.37	0.711	+0.05 ± 0.07	0.67	0.472	8, 5, 5	90, 57, 56
Aggression received	+0.08 ± 0.06	1.3	0.203	+0.008 ± 0.07	0.102	0.917	6, 4, 4	59, 46, 42
Distance from father	+0.15 ± 0.08	1.98	0.05	+0.13 ± 0.09	1.4	0.147	6, 4, 4	64, 46, 42
Distance from mother	+0.12 ± 0.08	1.54	0.10	+0.03 ± 0.10	0.32	0.502		
Time in proximity to father	-0.02 ± 0.07	-0.33	0.63	+0.04 ± 0.06	0.62	0.713		
Time in proximity to mother	-0.01 ± 0.06	-0.22	0.75	-0.09 ± 0.06	-1.4	0.154		

¹Juveniles are the reference category

²Adolescents are the reference category

* p < 0.05, ** p < 0.01, *** p < 0.001, bold p values indicate a trend (0.05 ≤ p ≤ 0.10)

Subadults (6 – 9 years old) spent even less time in solo and social play than adolescents (Table 4.4). In addition, subadults initiated play with others less frequently than did adolescents. There was a trend for subadults to attempt food transfers less frequently compared to adolescents (Table 4.4). Subadults were not more aggressive than younger offspring and did not receive more frequent aggression from group members overall (Table 4.4). Subadults were no different from adolescents in their distance from parents, and spent the same proportion of time in close proximity to parents (Table 4.4).

SOCIOSEXUAL BEHAVIOUR OF IMMATURES

Sexual behaviour in the natal group

Sexual behaviour was extremely rare in these immature gibbons; however, there were some instances worth noting (Table 4.5). Only two instances involved one of the breeding adults (i.e. a parent). One of those was an attempted copulation by a subadult male (7.3 years old) towards his mother, however, the attempt was not obvious. The second observation involved a father mounting and thrusting towards his adolescent daughter (5.1 years old) during a play bout. The remaining 3 observations involved a subadult and juvenile; only one of which involved opposite-sex immatures (Table 4.5).

Table 4.5 Observations of mounting behaviour involving immatures

Case	Species	Individual A	Individual B	Details
1	<i>S. syndactylus</i>	Subadult male (son, Jambi)	Adult female (mother, Fern)	Possible attempted copulation.
2	<i>S. syndactylus</i>	Adult male (father, Armstrong)	Adolescent female (daughter, Tunku)	Dorso-ventral mounting and thrusting by adult male during play bout.
3	<i>S. syndactylus</i>	Subadult male (brother, Jambi)	Juvenile female (sister, Tunku)	Dorso-ventral mounting attempt while walking (juvenile female appears to lean forward in presentation).
4	<i>S. syndactylus</i>	Subadult male (brother, Jambi)	Juvenile male (brother, Figaro)	Juvenile male presenting (as female) and dorso-ventral mounting and thrusting by subadult during wrestling bouts. Observed multiple times during a play bout and observed a second time the following day, also during play.
5	<i>H. moloch</i>	Subadult male (brother, Arjuna)	Juvenile male (brother, Nakula)	Dorso-ventral mounting and thrusting by the subadult male. Juvenile tried to initiate play in response.

Contrast in sexual behaviour between the natal group and pairing

During the course of this study one male *H. moloch* (Arjuna) was removed from his natal group at 7.7 years of age (28/09/2008), and introduced to a 6.4 year old female (Layar). During 23 hours of observation on Arjuna in his natal group (from 14/02/2008 to 02/06/2008), he never attempted to copulate with his mother. In contrast, during the first 5 hours following his introduction to Layar (29/09/2008), there were 17 copulation attempts (~3.4 attempts per hour).

OBSERVATIONS ON DEVELOPMENT IN A STEP-FAMILY

One subject, a subadult female (Jermei, ~ 6.5 years) was removed from her natal group and housed with an unrelated juvenile female (Li-Lian, ~1.5 years) until an unrelated young adult male was introduced to both females (Tao, ~8 years). Jermei went through the colour change between ~6.5 – 7 years of age and displayed irregular sexual

swellings, genital and nipple grooming behaviour, and sexually solicitous “bobbing” behaviour typical of *N. leucogenys* females (Lukas et al. 2002), before the arrival of the male. During this period her bobbing behaviour was directed towards humans of both sexes. After Tao was introduced, (Jermei then ~8 years old, Li-Lian ~3 years old) Jermei continued to display sexual swellings, frequent genital grooming behaviour, and directed bobbing towards Tao. In addition to the bobbing behaviour, Jermei sometimes presented her genital area at the male’s face. Li-Lian was also observed “presenting” her genital area at the male in the same way, but this occurred < 5 times. Possibly Li-Lian was simply copying Jermei’s behaviour, as Li-Lian showed no evidence of colour change, sexual swellings, genital/nipple grooming or bobbing behaviour. The male eventually responded to Jermei’s advances by mounting and thrusting; but never mounted Li-Lian. During these copulation attempts, Li-Lian would frequently attempt to play with either Jermei or Tao and attempt to force herself in between the two adults. This behaviour was performed by another juvenile female towards her parents during the study.

AGGRESSION BY PARENTS

Mothers directed more frequent aggression towards adolescent offspring, than towards juvenile offspring (Table 4.6). In contrast, fathers were no more frequently aggressive towards adolescent than towards juvenile offspring (Table 4.6). There was a trend for adult females to be less frequently aggressive towards subadults than towards adolescents (Table 4.6). In contrast, adult males were significantly more frequently aggressive towards subadults than towards adolescents (Table 4.6).

Table 4.6 Aggression by parents towards adolescents relative to juveniles (reference category), and aggression by parents towards subadults relative to adolescents (reference category). Significant differences in bold

Behaviour	Adolescents compared to juveniles ¹			Subadults compared to adolescents ²			N (individuals) Juveniles, adolescents, subadults	N (10-day samples) Juveniles, adolescents
	Estimate ± S.E.	t	p	Estimate ± S.E.	t	p		
Aggression by father towards offspring	-0.004 ± 0.04	-0.1	0.918	+0.17 ± 0.05	3.29	< 0.001***	6, 4, 4	84, 56, 55
Aggression by mother towards offspring	+0.16 ± 0.06	2.63	0.009**	-0.11 ± 0.07	-1.66	0.08	6, 4, 4	86, 57, 55

¹Juveniles are the reference category
²Adolescents are the reference category
* p < 0.05, ** p < 0.01, *** p < 0.001, bold p values indicate a trend (0.05 ≤ p ≤ 0.10)

DISCUSSION

In this chapter I review the available data on developmental markers in hylobatids, and quantify changes in the frequencies of social interaction in captive immatures with maturation. I provide some of the first longitudinal data on social behaviour in immatures of known age and sex, all of whom were residing in their natal groups at the time of observation. Although captivity influences the activity levels of primates, quantifying changes in social interactions within naturalistic social groupings provides a worthwhile comparison with wild primate behaviour where the latter is available. In addition, many developmental markers are more easily quantified in a captive setting, including physiological measures. Studies of captive hylobatids are particularly useful for measuring within-group social interactions, which are difficult to observe and quantify in the field. I investigated differences in rates of play, food transfer attempts, aggression, sexual behaviour and spatial association with parents, changes in which have been associated with the end of juvenescence, puberty onset and maturation in other primates (Pereira & Altmann 1985; Caine 1986; Hewlett & Hewlett 2013).

Behavioural patterns reminiscent of “adolescent” primates began between 4 – 6 years in these captive individuals and the age at onset of these behavioural changes is similar to that reported for wild individuals. In the current study groups, 4 – 6 year olds living in the natal group spent less time in social and solo play, and initiated play with others less frequently compared to 2 – 4 year olds. Similarly, play decreases at 5 – 6 years of age in wild *H. lar* (Reichard 2003). The frequency of attempting food transfers was also lower in 4 – 6 year olds, and even lower in older immatures, corresponding with previous research on this behaviour in captive hylobatids (Schessler & Nash 1977; Fox 1977). Immatures also began to venture further from parents between 4 – 6 years of age and continued to do so at older ages. Estimates for receipt of parental aggression, exclusion from food sources and spatial peripheralisation are more variable in the wild (range 4 –

9 years of age), but the range overlaps estimates from this study, and other captive groups (onset 5 – 6 years of age, Table 4.2). In contrast to the typically “adolescent” reductions in play, and increases in spatial distancing, the captive immatures in the current study did not show increases in sexual or aggressive behaviour with age. This may be a result of the pooling of male and female immatures, but both aggression and sexual behaviour were infrequent even in adults (see Chapter 2). Similar low rates of aggression within families are reported by Mootnick et al. (2006); thus, it might be difficult to use aggressive or sexual behaviour by immatures as markers of puberty onset in hylobatids.

Later developmental milestones are more difficult to determine using behaviour alone, due to the greater inter-individual variability in behavioural and physiological measures at older ages. At this point it is worth noting that differences in adult body size among species may influence interpretations of developmental timing when hylobatid species are pooled. I controlled for species by including it as a fixed effect in my models, but could not investigate interaction effects. Potential species differences in developmental timing can only be addressed when more data has been accumulated for each species. However, there is variation both within and among genera in estimates of body weight, suggesting overlap in body size between species (Zihlman et al. 2011). In addition, there remains variation in the age of developmental markers among individuals of the same species (see Table 4.2). Species differences therefore cannot explain all of the variation in the age at attainment of later developmental markers. In the following paragraphs, I discuss some other possible proximate causes of variation in later developmental milestones. Due to the paucity of data, this discussion is preliminary and primarily anecdotal, but highlights the importance of further research on variable development in hylobatids.

THE EFFECT OF NUTRITION ON DEVELOPMENTAL RATES

The precise impact of nutrition on early physiological developmental milestones is difficult to estimate, since physiological measures are difficult to obtain in the wild. Behavioural estimates for the age at weaning are similar in captive and wild hylobatids (Table 4.2), indicating minimal impact of nutrition on early development. This is not surprising given that the daily cost of lactation is comparatively low in primates compared to other mammals, and moderate food restriction has a limited impact on milk production (Dufour & Sauther 2002; Lappan 2009). In later development, nutrition in captivity allows earlier onset of puberty and earlier attainment of adult body size. Adult body size is reached 6 months to 2.3 years earlier in captivity than in the wild (Table 4.2). Similarly, in females, the appearance of first sexual swellings and menarche in the natal group occur 6 months to 3 years earlier in captivity than in the wild (Table 4.2). This approximates the influence of nutrition on the age at sexual maturity in human populations (Wyshak & Frisch 1982), and similar reaction norms in many other vertebrates (Day & Rowe 2002). Receipt of parental aggression, exclusion from food sources and the onset of peripheralisation can also be compared using captive and wild data, since immatures must be in the natal group for this to be reported. In contrast to physiological measures, estimates for the timing of these behavioural events overlap in captive and wild immatures (Table 4.2), and thus are unlikely to be nutrition dependent. Thus, nutrition allows earlier onset of some physiological markers of maturity; however, the large range of estimates in captive and wild individuals indicates that other variables (e.g. social group composition) influence the timing of maturation in hylobatids.

THE SOCIOECOLOGICAL CONTEXT OF BEHAVIOURAL MATURITY

Within samples of captive and wild immatures living in their natal groups, there remains a large amount of variability in the earliest age of both behavioural and

physiological markers of maturity (Table 4.2). The remaining variation among individuals is likely to result from differences in the socioecological context. For example, the occurrence and intensity of parental aggression is associated with the sexual behaviour of subadults or the resumption of sexual activity in the breeding pair (Tilson 1981; Leighton 1987, p. 141; Lappan 2005, p. 113; Chivers 1980, p. 245). This context-dependent aggression may contribute to the variation in ages at which parental aggression is reported, or whether it is reported at all. Subadults might alter their behaviour in order to reduce this conflict, either by dispersing (in the wild) or by inhibiting behaviours that signal adulthood or reproductive potential (in captivity or in the wild). Despite many field researchers defining subadults by their peripheral status, other observations suggest that extra adult-sized individuals are not peripheral (Lappan 2005; Dooley & Judge 2014) and in fact are often fully integrated into the group's social network (Guan et al. 2013). Furthermore, some field researchers have noted that social maturity is delayed while immatures remain in the natal group (Chivers 1980, p. 294).

Anecdotal evidence from the subadult male *H. moloch* in the current study suggests a sharp contrast between sexual behaviour displayed in the natal group and sexual behaviour displayed during introduction to an appropriate mate. His behaviour could indicate that physiologically capable males inhibit their sexual behaviour in the natal group, and thus reduce conflict with parents and allow maintenance of positive social contact. Direction of mounting behaviour towards fathers or male siblings may occur in subadult hylobatids before dispersal, allowing males to avoid inbreeding and/or competition with fathers without suppression of sexual behaviour (this study, Table 4.5; Edwards & Todd 1991). A lack of sexual behaviour in the natal group could also simply reflect that males are more stimulated by young and/or unrelated females (i.e.

inbreeding avoidance). Longitudinal observations of this single case indicate the need for further longitudinal research of subadult behaviour. Nevertheless, the general lack of aggressive and sexual behaviour by young hylobatids in the natal group may facilitate delayed dispersal and allow extended exploitation of the parental territory in the face of ecological constraints. This partially explains the low rates of aggressive and sexual behaviour displayed by subadults, and the generally peaceful nature of hylobatid groups.

Similarly, variation in food-related aggression, and associated variation in subadult behaviour may be related to the interaction between territory size/quality and the size of the social group (Emlen 1995). For example, Geissmann (1993) described a captive siamang group in which a second daughter was not peripheralised by her parents, suggesting that it may have been due to a lack of surviving younger siblings. The mother was subsequently peripheralised by the mature daughter and received increased aggression when the father died and a young male was introduced. In the wild, the age at dispersal is highly variable (Table 4.2) and is sometimes noted to coincide with a sibling birth (Aldrich-Blake & Chivers 1973; Leighton 1987). The timing of dispersal appears flexible rather than tied to a particular stage in development (in *S. syndactylus*, Lappan 2005, p.111). Thus, the frequency and intensity of parent-offspring aggression and the age at dispersal appears to depend on the additive influences of group size and reproductive context. Aggression by parents and spatial distancing of immatures could be predicted to vary with territory quality, as in other family-living species (Emlen 1995). Likewise, the variation in age at first reproduction in wild hylobatids is likely to result from ecological constraints on breeding opportunities (e.g. no vacant territories). This is reflected in the narrower range of estimates for independent reproduction in captive compared to wild hylobatids, indicating the influence of keeping staff on age at first reproduction in captivity (Figure 4.1). As long as a suitable mate is available in the

breeding pool, subadults removed from their natal groups in captivity are likely to begin reproducing faster than would be possible in the wild.

THE SOCIOECOLOGICAL CONTEXT OF PHYSIOLOGICAL MATURITY

Hylobatids are generally found in two-adult groups in which a single male and female breed, but many groups also contain additional adults, some of which are mature offspring (Fuentes 2000a; Brockelman et al. 1998; Srikosamatara & Brockelman 1987; Lappan 2007b; Dooley 2015). The physiological evidence from wild hylobatids indicates that independent reproduction is possible by age 8, but many hylobatids remain in their natal groups for longer than this (Srikosamatara & Brockelman 1987; Brockelman et al. 1998; Huang et al. 2013). Breeding by more than one female is rare in hylobatids and possibly restricted to only the genus *Nomascus* (Fan & Jiang 2010). Plastic developmental mechanisms might prevent reproductive competition between parents and offspring that delay dispersal, and this may contribute to the wide variation in timing of reproductive maturity among individual hylobatids.

Prevention of offspring breeding could be achieved through hormonally or behaviourally mediated inhibition of reproduction by parents (French 1997). There is some (albeit limited) evidence that attainment of full reproductive function is delayed for female hylobatids living in their natal group. Although wild female *H. lar* show signs of puberty in the natal group (first sexual swellings), they show no evidence of mature cycling patterns before dispersal (Palombit 1995; Barelli et al. 2007). Similarly, two female siamang reached adult size 2 years before dispersal, but only displayed cyclical changes in genitalia several months leading up to dispersal (Lappan 2005).

Additionally, there are few observations of females reproducing before dispersal. In captivity, females between 4 – 5 years of age are able to reproduce immediately upon removal from the natal group and introduction to a male (Geissmann 1991), while

females remaining in the natal group do not conceive at these ages. In captivity this may be explained by administration of contraceptives by keeping staff, but this is not reported in the literature. Data on markers of puberty in 4 – 5 year old captive females in the natal group, in the absence of contraceptive use, would therefore be useful. The apparent delay in markers of sexual maturity observed in wild groups suggest that physiological reproductive development is at least slowed in the natal group, perhaps through the presence of a breeding female (e.g. via olfactory cues) or through intra-sexual aggression (French 1997).

Evidence for inhibition of breeding by offspring mediated through aggression-induced stress comes from accounts of same-sex parent-offspring aggression in hylobatids. In the current study, mothers were most aggressive towards 4 – 6 year olds, and this may be because most of the offspring in this age bracket were females. These offspring were not yet adult sized, and none exhibited obvious signs of menarche so it is unclear what cues stimulated an increase in aggression in these mother-daughter pairs. However, given that puberty onset can occur at 5 years of age in captivity (Table 4.2), maternal aggression towards 4 – 6 year old daughters in captivity could function to successfully prevent breeding after puberty onset. There have been six other studies in which groups have contained reproducing females and their (putative) subadult daughters, and authors have noted the social relationships between them (Crandall 1964; Fox 1977; Schessler & Nash 1977; Tilson 1981; Leighton 1987; Geissmann 1993). In all but one of these studies (Fox 1977), mother-daughter aggression was observed in association with either presumed sexual maturation, sexual behaviour of the subadult daughter or introduction of a novel male. In contrast, some females are clearly able to co-exist in the same groups (Bleisch & Chen 1991; Jiang et al. 1999; Dooley 2015). These observations indicate that 1) mothers recognize their subadult daughters as reproductive competitors at some point and 2) mother-daughter or female-female aggression may be transient and

depend on the social and ecological context. More detailed studies in this area could be useful, linking the physiological and behavioural data of mother-daughter co-residents.

Alternatively, the delay in reproductive maturity in the natal group may not be a consequence of inhibition, but of activation in the presence of an appropriate mate, although the two mechanisms may operate simultaneously (Geissmann 1991). Evidence for stimulation by novel males comes from the sexual behaviour of adolescent and subadult females. In the current study, neither 6.4 year old *N. leucogenys* Jermei, nor (later) her 6.4 year old sister Kit were observed soliciting copulation from their father, nor was their father observed attempting to copulate with them. In contrast, during the 3 months of observation that followed Jermei's introduction to 8 year old Tao, the mean frequency of copulation attempts was 2.5 (\pm 2.7) attempts per hour of focal sampling. Similarly, copulation has been observed rarely in the wild for maturing females in the natal group. Only one *S. syndactylus* female was observed copulating before dispersal (Lappan 2005) and two *H. lar* females copulated for the first time with immigrant males while still in their natal groups (Reichard 2009). Parental aggression may hinder copulation attempts in the natal group, but the low frequency of copulation attempts by females with fathers (or other familiar males) could also indicate that fathers generally do not stimulate sexual behaviour in daughters (as in cotton-top tamarins, Widowski et al. 1990; humans, Schneider & Hendrix 2000; but see Mootnick et al. 2005).

Further evidence for reproductive inhibition in the natal group or stimulation by novel males comes from observations of sexual swellings in females as young as two years of age who were housed with males in pairs (Cheyne & Chivers 2006). In the step-family in the current study, the three year old juvenile female did not show any evidence of physiological puberty (e.g. sexual swellings, colour change) when introduced to her step-father. This could indicate that both the absence of a dominant breeding female (in

this case eight year old Jermei) *and* the stimulation of a novel male are required for full reproductive maturity. These two requirements for reproductive function may be beneficial in territorial, family-living taxa in which unoccupied territories and available mates are required for successful independent reproduction. It is currently difficult to tease apart the influence of breeding females and novel males on the reproductive function of captive hylobatid females, because removal from the natal group and pairing with an appropriate mate often occur simultaneously in captivity. Close monitoring of female behaviour and hormone levels before, during and after removal from their natal group and introduction to males would be worthwhile in order to isolate the impact of each social stimulus.

CONCLUSIONS

The total range of estimates for the transition from infant to juvenile is small and indicators are well defined and comparable for wild and captive hylobatid groups. In comparison, estimates of puberty, sexual maturity and adulthood vary, both within and between captive and wild groups. Behaviour indicative of adolescence begins between 4 – 6 years in captivity and the age at onset is similar to earliest behavioural estimates of puberty in wild groups (range 4 – 9 years). The similarity between these behavioural measures in captive and wild hylobatids contrasts with the sometimes large discrepancies in physiological markers of puberty between captive and wild hylobatids. For females, adult body size and markers of physiological puberty onset can appear 2 -3 years earlier in captivity than in the wild. These results support the use of a juvenile age class between 2 – 4 years of age, and onset of the adolescent phase at ~5 years. After behavioural onset of puberty, the relative timing of physiological puberty, sexual, and social maturity are more variable, such that definition of age classes in individuals older than 5 years depends on the physical and social environment.

The persistence of large age ranges for puberty and sexual maturity in captive gibbons indicate that nutrition may *allow* earlier maturity, but it is also conditional on the social environment. Preliminary evidence suggests that some aspects of physiological and behavioural maturation are slowed in the natal group, compared to same-aged individuals that have been removed from the natal group and housed with opposite-sex adults. If there is considerable variation in the availability of breeding opportunities in the wild, then reproductive success might be improved for individuals that are able to mature faster to take advantage of breeding vacancies. Likewise, slowing maturation while still in the natal group allows longer exploitation of the parental territory and social support. In this context, a flexible mechanism of sexual and social maturation would be adaptive for hylobatids and explains the wide range and progressions of sexual and behavioural development in this taxon.

CHAPTER 5 THE BENEFITS OF SLOW MATURATION

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INTRODUCTION

Primates exhibit some of the longest dependent periods and slowest growth rates of all mammals (Case 1978; Charnov & Berrigan 1993; Pereira & Fairbanks 2002). The period between weaning and sexual maturation is particularly long in primates (Pereira & Fairbanks 2002). In the previous chapter I showed that in hylobatids, like in many other primates, the transition to adulthood is multifactorial, with social and physiological aspects developing asynchronously with age, as well as variably among individuals. This mosaic and highly variable process makes it difficult to define the end of the dependent period, because the physiological and behavioural changes that allow independent reproduction (the ultimate definition of adulthood) can take many years, and may be contingent on the social context. This pattern is taken to the extreme in humans, necessitating the addition of the “adolescent” period of life history that some researchers believe to be unique to humans (Bogin & Smith 1996), but which has been increasingly applied to other primates (Lancaster 1986; Watts & Pusey 1993; Setchell & Lee 2004; Chapter 4).

Hylobatids live in nuclear families and display dependent periods as long as 11.5 years in the wild (Reichard & Barelli 2008). Interestingly, the length of the juvenile/adolescent period, is identical to that of the other nonhuman apes (Table 5.1), despite the fact that hylobatids are between 5 and 15 times smaller in body mass. This may partially result from slow growth velocities in hylobatids (< 2kg/year, Leigh & Shea 1995; Mumby & Vinicius 2008; but see Vinicius & Mumby 2013). In contrast to the increasing postnatal growth velocities in other apes, postnatal growth rates in

hylobatids plateau (*S. Syndactylus*) or decline (*Hylobates* spp.), and continue to decrease across development (Leigh & Shea 1995).

Table 5.1 Comparison of the length of developmental life history stages in apes

Species	Lactational period (years) ¹	Juvenile/adolescent period (years) ¹	Age at first reproduction (years) ¹
<i>Hylobates lar</i>	2.9	7.1	10
<i>Homo sapiens</i>	2.5	17	19.5
<i>Gorilla gorilla</i>	3.2	6.8	10
<i>Pongo pygmaeus</i>	6.3	7.2	13.5
<i>Pan troglodytes</i>	5.4	7.7	13.1

There are several hypotheses for delayed maturation in primates (Ross 2004), including that slow brain maturation processes (van Schaik et al. 2006) or ecological pressures (Janson et al. 1993; Deaner et al. 2003) select for slow growth. One hypothesis that relates specifically to extension of the juvenile/adolescent period is the “needing to learn” hypothesis, in which immatures require time to learn complex skills required in adulthood (Joffe 1997; Ross & Jones 1999; Schuppli et al. 2012). This hypothesis predicts that immature primates should engage in activities that promote learning throughout their dependence. This chapter investigates the possible benefits of delayed maturation in hylobatids by first exploring how activity levels change across development in captive hylobatids, relative to the timing of growth completion and adult activity levels. I then discuss how the pattern of behaviour across development may promote skill development and provide potential reasons for the slow maturation so characteristic of hylobatids.

In addition to slow growth, hylobatid offspring also spend time associating with parents beyond growth completion. The physiological evidence from wild hylobatids indicates that independent reproduction is possible by age 8, but many hylobatids remain in their natal groups for longer than this (Srikosamatara & Brockelman 1987; Brockelman et al. 1998; Huang et al. 2013). The timing of dispersal appears flexible rather than tied to a

particular stage in development (in *S. syndactylus*, Lappan 2005, p.111). This means that some hylobatid offspring remain with parents despite having completed growth, and this varies among individuals, even within the same family (Srikosamatara & Brockelman 1987). This aspect of hylobatid life history cannot be associated with growth-related constraints. Although the need for slow growth and learning may explain the general protraction of the maturation process in hylobatids, they do not necessarily explain the variation among individuals in developmental timing, such as the age at dispersal. The evolution of any developmental process that delays independent reproduction for some individuals but not for others must have a fitness payoff later in life, otherwise individuals engaging in that behaviour will be outcompeted by early reproducers. Cooperatively breeding species (including birds and mammals), also show a delay between sexual maturity and reproduction for many individuals, and the age of independent reproduction can be extremely variable (Emlen 1995; Langen 2000).

Delayed dispersal has therefore received significant attention in birds (for a detailed review, see Kokko & Ekman 2002) and in cooperatively breeding mammals (Koenig et al. 1992). Ultimate explanations for the evolution of delayed dispersal reflect the balance of costs and benefits of philopatry to offspring, and parents, relative to all other breeding options (Koenig et al. 1992; Ekman et al. 2001). These costs and benefits encompass ecological and demographic constraints (i.e. external pressures prevent dispersal, Emlen 1982a), including selection for slow life histories (Hatchwell & Komdeur 2000) and the benefits of philopatry (Zack & Stutchbury 1992; Cockburn 1998). The benefits of prolonging dependence to individual gibbons may therefore vary depending on the ecological context (i.e. territory quality and availability of breeding vacancies, Emlen 1995). The behaviour of adult-sized offspring (here termed subadults) in the natal group could reveal the plausibility of potential reasons to delay dispersal.

For example, there might be no benefits to delayed dispersal in hylobatids, and the range in dispersal ages could simply be a sub-optimal outcome of human encroachment on rainforest area, and the resulting decline in the number and quality of territories (Malone & Fuentes 2009). If this is the case, the behaviour of subadult offspring should reflect a lack of benefits to staying with parents. This hypothesis predicts that subadult offspring should be socially distant, and their behaviour should reflect only the drive to leave the group. Evidence for this might include deteriorating or irreparable social relationships with parents, adult-like behaviour and a lack of contribution to the social group.

Alternatively, although recent increases in ecological constraints may prevent easy establishment of a territory for maturing hylobatids, ecological constraints have been historically important for group formation throughout hylobatid evolution (Brockelman & Srikosamatara 1984). Baseline variations in territory quality alter the current cost-benefit ratio of dispersal options, particularly if the natal territory is of high quality and potential vacancies are much lower in quality (Emlen 1982a). Furthermore, the long lifespan of hylobatids creates temporal plugs in the availability of vacant territories; once a territory is occupied, it is likely to remain so for up to 14 years or longer (Reichard 2009). The “safe haven” hypothesis for philopatry predicts that offspring may delay dispersal if dispersal costs are higher than the cost of remaining at home (Kokko & Ekman 2002). The natal territory may be a “safe haven” in hylobatids for several reasons: firstly, the territory is familiar, and secondly, parents may be more tolerant towards offspring than unrelated individuals are towards unrelated young adults. For example, in some birds, parents are more tolerant of philopatric offspring than they are of immigrant or unrelated adults (Ekman et al. 2001; Chiarati et al. 2011).

In addition, subadults at home might benefit from vigilance or alarm calling by parents and/or cooperative defence while waiting for a breeding opportunity to arise in a

neighbouring territory (Gaston 1978). The benefits of remaining at home could be even greater for males, who have the opportunity to achieve copulations with extra-group individuals during encounters on the boundary (Palombit 1994b; Reichard 1995; Brockelman 2009), or during exploratory forays. Lastly, continued association with parents beyond growth cessation may also allow subadults to forge long term relationships with parents that promote nepotism at a later time (Tenaza 1975; Tilson 1981; Komdeur & Edelaar 2001). In addition to describing patterns of behaviour during the growth period, this chapter investigates the social benefits of philopatry for subadult offspring by quantifying and describing the behaviour and social relationships of four captive subadults in their natal groups. I explore how the behaviour of subadult offspring differs from the behaviour of breeding adults and how subadult social preferences reflect the benefits of delayed dispersal for individual hylobatids.

METHODS

STUDY ANIMALS

In total, data were collected for 14 immatures (five *H. moloch*, three *N. leucogenys* and six *S. syndactylus*), including longitudinal data for 10 of these immatures (Table 5.2, Figure 5.1). I used 1.5 years as the cut-off between infants and juveniles; there were 6 *infants* ranging from 0.47 to 0.98 years of age ($\bar{x} = 0.63$ years). The oldest infant was still nursing and occasionally carried by her mother ($5.8 \pm 5.8\%$ of the activity budget, range: 0 – 17%, $N = 11$ 10-day samples). Nine *juveniles* ranged from 1.8 – 3.3 years of age ($\mu = 2.8$ years). The youngest juvenile was never observed nursing and was not carried. Six *adolescents* ranged from 4.1 to 5.9 years of age ($\bar{x} = 5.1$ years), and six *subadults* ranged from 6.1 to 9.5 years of age ($\bar{x} = 7.7$ years). Adults were defined as being potentially sexually mature, removed from their natal groups and housed with an

opposite sex adult. Adults ranged in age from 6.1 to 38.5 years ($\bar{x} = 19.5$ years) and included adults both with and without offspring.

Table 5.2 Characteristics of immatures in the study

Species	Individual (sex, studbook #)	Date of birth	Age classes (year observed)	Age (years)	Parents (studbook #) ¹	Location	
<i>H. moloch</i>	Arjuna (♂, #66)	24/11/2000	Adolescent (2005)	4.9	F: Jury (#36), M: Hecla (#32)	Perth	
			Subadult (2008)	7.5			
			Adult (2010, 2012)	9.4			
	Nakula (♂, #137)	30/05/2005	Infant (2005)	0.5		F: Jury (#36), M: Hecla (#32)	Perth
			Juvenile (2008)	3.0			
			Adolescent (2010)	5.1			
			Subadult (2011)	6.1			
Cahaya (♀, #146)	26/05/2008	Juvenile (2010, 2011)	2.11	F: Arjuna (#66), M: Layar (#75)	Mogo		
Sunda (♀)	12/07/2010	Infant (2011)	0.98				
Cinta (♀)	06/09/2009	Infant (2010)	0.47				
<i>N. leucogenys</i>	Jermei (♀, #28)	05/07/2002	Juvenile (2005)	3.3	F: Phillip (#2), M: Viann (#13)	Perth	
			Adolescent (2008)	5.9			
			Adult (2010, 2011)	8.1			
	Kit (♀, #29)	16/01/2005	Infant (2005)	0.74			
			Juvenile (2008)	3.3			
Li-Lian (♀, #44)	02/06/2007	Juvenile (2010)	3.1	F: Kayak (#21), M: Nelly (#16) SF: Tao (#147) ² , SM: Jermei (#28)			
		Adolescent (2011)	4.06				
<i>S. syndactylus</i>	Jambi (♂, #72)	13/09/2002	Subadult (2010, 2012)	7.6	F: Armstrong (#70), M: Fern (#65)	Mogo	
	Tunku (♀, #79)	22/01/2007	Juvenile (2010)	3.1			
			Adolescent (2012)	5.1			
	Figaro (♂, #82)	13/07/2009	Infant (2010)	0.61			
			Juvenile (2012)	2.7			
	Batak (♂, #86)	22/09/2011	Infant (2012)	0.47			F: Niran (#43), M: Mang (#41)
Jars (♂, #59)	26/10/2001	Subadult (2010)	9.1				
Zain (♂, #84)	06/01/2009	Juvenile (2010)	1.8	F: Irian (#58), M: Suli (#71)			

¹Studbook numbers obtained from the International Studbook for Javan Silvery Gibbons (2009), the Australasian Regional Studbook for White-Cheeked Gibbons (2009), and the Australasian Regional Studbook for Siamang (2011). SF = step-father, SM = step-mother.

²Studbook number for this individual obtained from the European Studbook (2008)

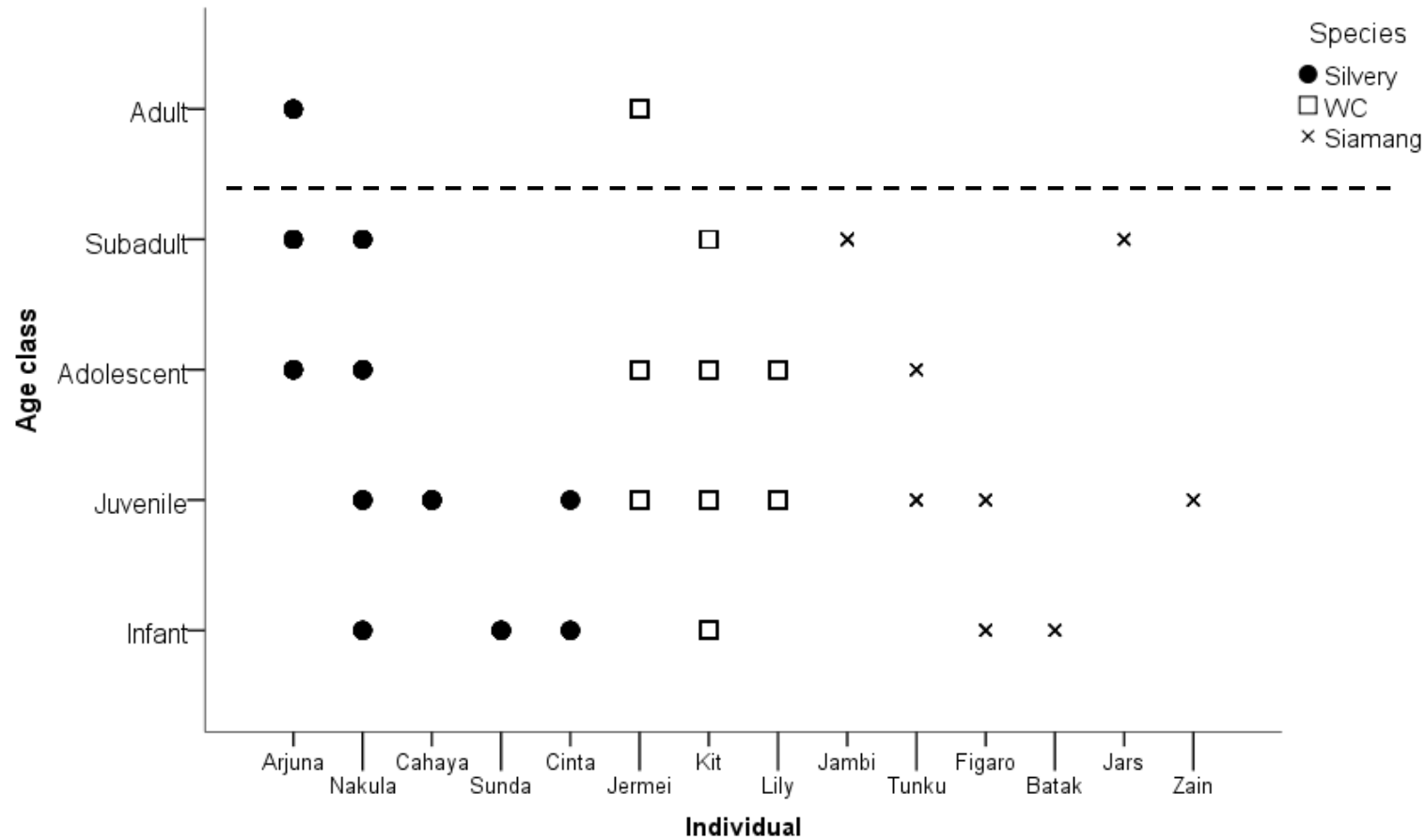


Figure 5.1 Distribution of immature gibbons sampled by age class and species. Two of the immatures were also sampled as adults after they were removed from their natal groups and started their own families. Other adults not shown.

BEHAVIOURAL OBSERVATIONS

Behaviour of individuals was recorded using continuous focal animal sampling (see methods in Chapter 2).

STATISTICAL ANALYSES

Behavioural variables were prepared as in Chapter 2. All behaviours were compared across age class categories, with ‘species’ as a control variable, with generalised linear mixed models (GLMM) as outlined in Chapter 4.

RESULTS

NON-SOCIAL BEHAVIOUR

The proportion of time spent resting was highest in adults and subadults, intermediate in juveniles and adolescents and lowest in infants (Table 5.3). The proportion of time spent moving decreased with age; infants spent the most time moving, followed by juveniles. Adolescents and subadults spent less time moving than did juveniles, but more time moving than did adults (Table 5.3). The proportion of the activity budget spent feeding was highest in juveniles and adolescents, intermediate in subadults and adults, and lowest in infants (nursing was not included in feeding time for infants, Table 5.3). The proportion of the activity budget spent in solo play was highest in juveniles, followed by infants (Table 5.3). Adolescents spent less time solo playing than infants, but more time solo playing than subadults (Table 5.3). Subadults and adults were identical in the proportion of time devoted to solo play (Table 5.3). The proportion of time spent on self-grooming was equally low for all age classes except infants, who spent significantly less time self-grooming compared to individuals older than 2 years of age (Table 5.3).

Table 5.3 Influence of age class on non-social behaviours

Behaviour	Infant	Juvenile	Adolescent	Subadult	Adult (ref)	p
Rest	-0.23	-0.15	-0.13	-0.05	0	< 0.001***
Movement	0.31	0.12	0.06	0.06	0	< 0.001***
Feeding	-0.07	0.09	0.08	0.006	0	< 0.001***
Solo play	0.11	0.18	0.05	-0.003	0	< 0.001***
Self-groom	-0.08	0.007	-0.005	-0.004	0	< 0.001***

Values displayed are coefficients for generalised linear mixed models, with adults as the reference category. Shading represents significant differences, where age classes with the same shading were not different. Lighter colours indicate higher proportions/frequencies of behaviour relative to darker colours. Sample size for all behaviours = 36 individuals, 716 10-day samples.

SOCIAL PLAY

Juveniles spent more time participating in social play compared to any other age class (Table 5.4). Infants and adolescents spent less time participating in social play compared to juveniles, but more time compared to subadults and adults (Table 5.4). Subadults spent more time in social play than did adults (Table 5.4). The frequency of initiating play with others was highest in juveniles and adolescents, with infants and subadults being intermediate, and adults initiating play the least frequently (Table 5.4).

Table 5.4 Influence of age class on social play

Behaviour (# individuals, # samples)	Infant	Juvenile	Adolescent	Subadult	Adult (ref)	p
Social play (36, 716)	0.11	0.17	0.13	0.09	0	< 0.001***
Frequency/hr initiates play (34, 429)	0.74	3	2.5	1.3	0	< 0.001***

Values displayed are coefficients for generalised linear mixed models, with adults as the reference category. Shading represents significant differences, where age classes with the same shading were not different. Age classes showing two colours were not different from the age class(es) sharing either colour. Lighter colours indicate higher proportions/frequencies of behaviour relative to darker colours.

ALLOGROOMING

Infants spent the lowest proportion of time grooming others (Table 5.5), but time spent grooming was the same for all other immatures (aged 2 – 9) (Table 5.5). Adults spent more time grooming compared to all immature age classes (Table 5.5). Grooming frequency (per hour of in sight time) was lowest in infants, but identical in all other age classes (Table 5.5). Infants and subadults were groomed for the lowest proportion of

time, compared to juveniles, adolescents and adults (Table 5.5). Grooming solicitation was infrequent overall, but was lower in infants compared to older individuals and higher in adults and subadults compared to juveniles and infants (Table 5.5).

Table 5.5 Influence of age class on allogrooming

Behaviour (# individuals, # samples)	Infant	Juvenile	Adolescent	Subadult	Adult (ref)	p
Proportion of time grooms others (36, 716)	-0.17	-0.08	-0.07	-0.07	0	< 0.001***
Frequency/hr grooms others (34, 430)	-0.88	-0.02	-0.39 ¹	-0.29	0	< 0.001***
Groomed (36, 716)	-0.06	-0.01 ²	0.009	-0.09	0	0.001**
Frequency/hr grooming solicitation (36, 560)	-0.36	-0.15	-0.11	-0.08	0	0.003**

Values displayed are coefficients for generalised linear mixed models, with adults as the reference category. Shading represents significant differences, where age classes with the same shading were not different. Age classes showing two colours were not different from the age class(es) sharing either colour. Lighter colours indicate higher proportions/frequencies of behaviour relative to darker colours.

¹There was a trend ($p = 0.05$) for adolescents to groom less frequently than adults

²There was a trend ($p = 0.08$) for juveniles to be groomed for a greater proportion of time compared to infants

FOOD TRANSFER ATTEMPTS

Attempts to steal food from others were infrequent in all age classes except juveniles (Table 5.6). When juveniles attempted to take food from other group members, 73% of attempts were for browse items (leaves), with the remaining 27% of attempts for more desirable and difficult to share items such as vegetables, fruits and enrichment items.

All juveniles with older siblings directed some food transfer attempts at siblings as well as parents. Parents apparently continue to tolerate food transfer by immatures older than 4 years of age (Figure 5.2); however, the low frequencies of food transfer attempts in non-juvenile individuals limited formal analysis of parental tolerance across age classes.

Tolerance by parents of food transfer attempts by offspring

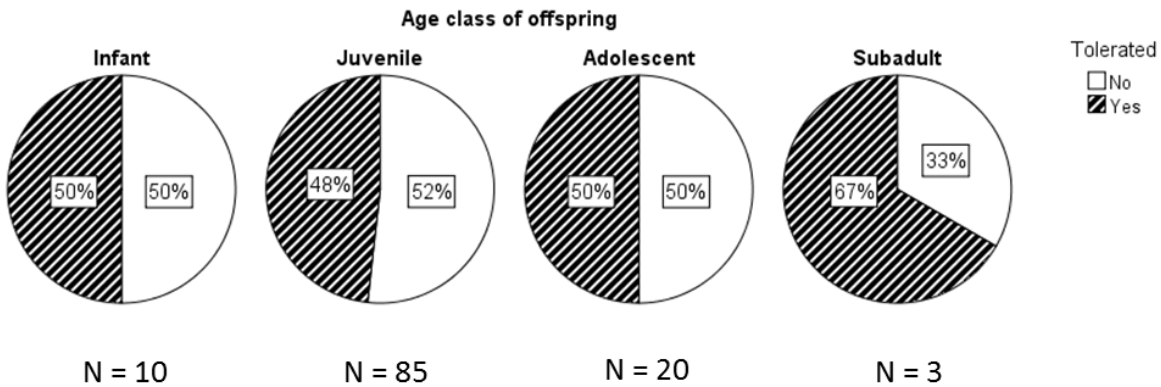


Figure 5.2 Tolerance by parents of food transfer attempts by offspring of different ages. Sample sizes represent counts of food transfer attempts by immatures towards parents, recorded during any group member's focal sample.

AGGRESSION

The frequency of aggression towards others was highest in adults, lowest in infants, and intermediate for all other immature age classes (Table 5.6). The frequency of aggression received by the focal animal (from any other group member) was equally high in non-infant immatures, intermediate in adults and lowest in infants (Table 5.6).

Table 5.6 Influence of age class on frequency of food transfer attempts and aggression

Behaviour (# individuals, # samples)	Infant	Juvenile	Adolescent	Subadult	Adult (ref)	p
Frequency/hr food transfer attempts (36, 560)	-0.02	0.33	0.10 ¹	-0.006	0	< 0.001***
Frequency/hr aggression to others (36, 560)	-0.46	-0.28	-0.26	-0.21	0	< 0.001***
Frequency/hr aggression received (36, 560)	-0.19	0.14	0.22	0.22	0	< 0.001***

Values displayed are coefficients for generalised linear mixed models, with adults as the reference category. Shading represents significant differences, where age classes with the same shading were not different. Lighter colours indicate higher proportions/frequencies of behaviour relative to darker colours.
¹There was a trend for adolescents to steal food more frequently than subadults ($p = 0.09$) and adults ($p = 0.07$)

SPATIAL RELATIONSHIPS WITH PARENTS

Distance from adult male and adult female

Adolescents and subadults were found at greater distances from both the adult male and the adult female compared to other age classes (Table 5.7). Juveniles were intermediate in their distances from the adult male and the adult female (Table 5.7); they were closer than adolescents (trend) and subadults, but further than the other parent, and infants (trend). Infants were closer to the adult female than the adult male was (Table 5.7).

Proportion of time in proximity to adult male and adult female

Immatures of all age classes spent the same proportion of time within arm's reach of the adult male (Table 5.7). Adult females spent more time in close proximity to adult males than juveniles, adolescents, and subadults did (trend, Table 5.7). Infants spent more time in close proximity to the adult female than did the adult male (Table 5.7). Juveniles, adolescents and subadults spent the same proportions of time within arm's reach of the adult female, while adult males were intermediate between older immatures and infants in the time they spent in proximity to the adult female (Table 5.7).

Frequency of approaching the adult male and adult female

Juveniles approached the adult male more frequently than any other age class (Table 5.7); all other age classes were identical in their frequency of approaching the adult male. Infants and juveniles approached the adult female the most frequently (Table 5.7). Adolescents approached the adult female less frequently than infants and juveniles did, and there was a trend for them to approach more frequently than subadults did (Table 5.7). Subadults did not differ from adult males in their frequency of approaching the adult female (Table 5.7).

Responsibility for maintaining proximity to the adult male and adult female

Immatures in all age classes showed the same degree of responsibility for approaching their father (Table 5.7). Hinde's index for the adult pair was higher than that for any father-offspring dyad (Table 5.7). A more positive Hinde's index (calculated from adult male's perspective) suggests greater male responsibility for maintaining proximity; thus, offspring were more responsible for maintaining proximity to adult males than were adult females. Similarly, adult females were more responsible for maintaining proximity to infants and adult males than they were for maintaining proximity to older offspring (Table 5.7). There was no difference among juveniles, adolescents and subadults in the responsibility for maintaining proximity to the mother (Table 5.7).

Table 5.7 Spatial relationships between parents and offspring

Behaviour (# individuals, # samples)	Infant	Juvenile	Adolescent	Subadult	Adult (ref)	p
Distance from adult male (24, 377)	0.05	0.25 ¹	0.40	0.53	0	< 0.001 ***
Distance from adult female (24, 381)	-1.04	0.23	0.35	0.38	0	< 0.001 ***
Proximity to adult male (23, 301)	-0.02	-0.14	-0.16	-0.12	0 ²	0.08
Proximity to adult female (23, 305)	0.53	-0.14	-0.15	-0.23	0	< 0.001 ***
Approach AM (23, 297)	0.13	1.07	0.47	0.33	0	< 0.001 ***
Approach AF (23, 302)	1.59	1.6	0.4 ³	-0.009	0	< 0.001 ***
Hinde's index with adult male (23, 219)	-0.10	-0.21	-0.14	-0.31	0	0.04 *
Hinde's index with adult female (23, 235)	0.16	-0.26	-0.12	-0.21	0	0.002 **

Values displayed are coefficients for generalised linear mixed models, with adults as the reference category. Shading represents significant differences, where age classes with the same shading were not different. Age classes showing two colours were not different from the age class(es) sharing either colour. Lighter colours indicate higher proportions/frequencies of behaviour relative to darker colours.

¹ There was a trend for juveniles to be closer than adolescents ($p = 0.05$) and further away than infants ($p = 0.06$)

² There was a trend for adult females to spend more time in proximity to adult males compared to subadults ($p = 0.07$)

³ There was a trend for adolescents to approach the adult female more frequently than subadults ($p = 0.06$)

TIMING OF TRANSITIONS RELATIVE TO ADULT BEHAVIOUR PATTERNS

Transitions in behaviour between each age class are shown in Table 5.8. All behaviours differed between infants and juveniles, except proximity to the adult male, frequency of approaching the adult female and Hinde's index with the adult male. Only the frequency of grooming solicitation was the same between juveniles and adults. The frequency of food transfer attempts, and the frequencies of approaching the adult male and adult female respectively, transitioned to adult levels in 4-6 year olds. The proportion of time spent resting, feeding and in solo play did not reach adult levels until the subadult category (6+ year olds). Movement, play, grooming, aggression, distance, time in proximity and Hinde's index remained different in grown offspring compared to adults.

Table 5.8 Transitions in behaviour between age classes

Behaviour	Infant/Juvenile ¹	Juvenile/ Adolescent ¹	Adolescent/ Subadult ¹	Subadult / Adult ¹
Rest	↑	-	↑*	-
Movement	↓	↓	-	↓
Feeding	↑	-	↓*	-
Solo play	↑	↓	↓*	-
Self-groom	↑	-	-	-
Social play	↑	↓	↓	↓
Play initiation frequency	↑	-	↓	↓
Allogroom	↑	-	-	↑
Frequency grooms others	↑*	-	-	-
Groomed	↑	-	↓	↑
Grooming solicitation frequency	↑*	-	-	-
Frequency of food transfer attempts	↑	↓*	-	-
Frequency of aggression	↑	-	-	↑
Frequency of aggression received	↑	-	-	↓
Distance from adult male	↑	↑	-	↓
Distance from adult female	↑	↑	-	↓
Proximity to adult male	-	-	-	↑
Proximity to adult female	↓	-	-	↑
Approach adult male	↓	↓*	-	-
Approach adult female	-	↓*	-	-
Hinde's index with adult male	-	-	-	↑
Hinde's index with adult female	↓	-	-	↑
% behaviours different compared to preceding age class	86	36	27	59

¹ Arrows refer to the direction of change in that behaviour in the second age class relative to the preceding age class

* = same as adult level for individuals in the second age class

DESCRIPTION OF SUBADULT BEHAVIOUR WITHIN THE FAMILY

Due to the small sample of subadults a quantitative analysis of their behaviour was not possible. Instead, I present some preliminary descriptive data on subadult behaviour and the nature of their relationships with parents and siblings. Of the four subadults in the study, two had younger siblings during the sampling periods, one of which was sampled in two different years. The remaining two subadults had no siblings at all during the sampling period, thus could only interact with their parents.

Ratio of aggressive : affiliative acts in parent-subadult relationships

The frequency of aggression, grooming and play with subadults were combined to examine the overall frequency of interaction between parents and subadult offspring and to assess whether parents were more frequently aggressive or affiliative towards subadult offspring. Mothers and fathers more frequently engaged in affiliative interactions with subadult offspring, compared to their frequency of aggression towards the same subadults (Table 5.9).

Table 5.9 Frequency of affiliative and aggressive interactions with subadult offspring by mothers and fathers

Parent	Test group (N _i , N _o) ¹	Estimate ± S.E.	t	p
Maternal frequency/hr interacting with subadult	Affiliative (4, 41)	0	-5.5	< 0.001 ***
	Aggressive (4, 55)	-0.9 ± 0.16		
Paternal frequency/hr interacting with subadult	Affiliative (4, 41)	0	-2.6	0.01 *
	Aggressive (4, 55)	-0.34 ± 0.14		

¹ Sample sizes for number of individuals (N_i) and number of 10-day samples (N_o)
 * p < 0.05, ** p < 0.01, *** p < 0.001, bold p values indicate a trend (0.05 ≤ p ≤ 0.10)

Grooming preferences of subadults

The grooming preferences of each subadult were highly variable (see Table 5.10). Subadults with younger siblings generally did not direct frequent grooming towards parents, but directed more frequent grooming towards younger siblings, particularly juveniles. The subadults who did not have younger siblings groomed their fathers more

often than they groomed their mothers, and also showed higher overall grooming frequencies than the subadults who had siblings.

Table 5.10 Mean ± S.D. frequency per hour that subadults groomed each family member

Subadult	Grooms infant	Grooms juvenile	Grooms adolescent	Grooms father	Grooms mother	Total grooming frequency
♂Jambi (2010)	0.22 ± 0.63	0.69 ± 0.70	-	0	0	0.91
♂Jambi (2012)	0.07 ± 0.16	0.40 ± 0.50	0.16 ± 0.40	0.36 ± 0.69	0	0.99
♂Nakula (2011)	0	0.42 ± 1.5	-	0.08 ± 0.28	0.08 ± 0.28	0.58
♂Jars (2010)	-	-	-	4.1 ± 3.6	0.21 ± 0.47	4.3
♀Kit (2011)	-	-	-	3.9 ± 4.9	1.8 ± 1.6	5.7

There were no consistent patterns in the grooming preferences of subadults based on the proportion of time that they groomed each family member (see Table 5.11). Even the *S. syndactylus* subadult Jambi, whose behaviour was sampled in two different years, appeared to change his grooming preferences in the second sampling period. Overall he directed most of his grooming efforts towards his juvenile (later adolescent) sister, and towards his father. In contrast, the *H. moloch* subadult Nakula directed most of his small amount of grooming towards his mother. The two subadults without siblings also differed in their distributions of grooming effort. While the *S. syndactylus* male Jars groomed his father more than his mother, the *N. leucogenys* female Kit groomed her parents equally.

Table 5.11 Mean \pm S.D. percentage of the activity budget spent grooming each family member by subadults

Subadult	Grooms infant	Grooms juvenile	Grooms adolescent	Grooms father	Grooms mother	Total % time grooming
♂ Jambi (2010)	0.1 \pm 0.3 4% ¹	2.0 \pm 3.8 74%	-	0.6 \pm 1.7 22%	0	2.7
♂ Jambi (2012)	0.05 \pm 0.1 2%	0.3 \pm 0.6 10%	1.0 \pm 2.6 34%	1.6 \pm 3.9 54%	0	2.95
♂ Nakula (2011)	0	0.07 \pm 0.3 15%	-	0	0.4 \pm 1.3 85%	0.47
♂ Jars (2010)	-	-	-	2.4 \pm 3.7 89%	0.3 \pm 0.7 11%	2.7
♀ Kit (2011)	-	-	-	4.4 \pm 7.8 47%	4.9 \pm 8.7 53%	9.3

¹ Bold values denote the percentage distribution of grooming effort across family members for each subadult

Ratio of grooming others to being groomed

The two subadults that had younger siblings were groomed by other group members for a greater proportion of time than they spent grooming others (see Table 5.12). This was also the case for all except one of the younger immatures in the same families, and for all except one of the adult males. Mothers always groomed others for a longer proportion of time than they were groomed themselves. In contrast, the two subadults who had no younger siblings groomed parents for a slightly greater proportion of time than they were groomed themselves.

Table 5.12 Ratio of the proportion of time individuals spent grooming others compared to being groomed

Family ¹	Individual	Sum of % time grooming others	Sum of % time groomed by others	Ratio grooms/groomed ²
Siam-F1-T1	Father	19.7	5.22	3.77
	Mother	18	11.93	1.51
	Subadult ♂ (Jambi)	2.7	6.5	0.43
	Juvenile ♀	1.9	13.6	0.14
	Infant ♂	0.05	5.3	0.009
Siam-F1-T2	Father	7.02	10.9	0.64
	Mother	19.1	4.6	4.15
	Subadult ♂ (Jambi)	2.95	5.61	0.53
	Adolescent ♀	2.8	5.8	0.48
	Juvenile ♂	2.11	3.02	0.70
	Infant ♂	0	4.25	0
Silv-F1-T6	Father	0.4	0.6	0.67
	Mother	7.03	0.6	11.7
	Subadult ♂ (Nakula)	0.47	3.23	0.15
	Juvenile ♀	0.80	0.1	8
	Infant ♀	0.03	4.2	0.007
Siam-F2	Father	0.7	2.6	0.27
	Mother	1.5	0.8	1.88
	Subadult ♂ (Jars)	2.7	1.5	1.8
WC-F1-T4	Father	9.7	15.7	0.62
	Mother	14.7	9.3	1.6
	Subadult ♀ (Kit)	9.3	8.6	1.1

¹Families labelled with a code that denotes the species (WC = white-cheeked gibbons, *N. leucogenys*, Silv = silvery gibbons, *H. moloch*, Siam = siamang, *S. syndactylus*), composition (F = family with offspring), and sampling period (T1-6) for pairs that were sampled longitudinally, more detail on each family available in Table 3.3

²Calculated from the total mean proportions of time that each individual groomed each family member. Subadults are highlighted in grey.

Play partners

The frequency of initiating social play with family members varied among subadults from less than once per hour to 12 times per hour of focal sampling (Table 5.13). The subadults with younger siblings most often initiated social play with juvenile siblings rather than with parents. The two subadults without siblings varied in their initiation of play with parents; the *S. syndactylus* subadult Jars attempted to initiate play equally often with both parents, while the *N. leucogenys* subadult Kit initiated play more frequently with her father than with her mother.

Table 5.13 Mean \pm S.D. frequency per hour that subadults initiated play with each family member

Subadult	Play with infant	Play with juvenile	Play with adolescent	Play with father	Play with mother	Total play initiation frequency
♂ Jambi (2010)	0	0.62 \pm 0.92	-	0.05 \pm 0.15	0	0.67
♂ Jambi (2012)	0	1.8 \pm 2.9	2.0 \pm 1.8	0.21 \pm 0.52	0	4.01
♂ Nakula (2011)	2.1 \pm 2.6	8.7 \pm 6.3	-	0.78 \pm 1.4	0.65 \pm 1.5	12.2
♂ Jars (2010)	-	-	-	0.09 \pm 0.19	0.09 \pm 0.19	0.18
♀ Kit (2011)	-	-	-	8.2 \pm 18.4	2.5 \pm 4.7	10.7

For the subadults with younger siblings, 76 – 98% of their social play was with younger siblings, rather than with parents (Table 5.14). The *S. syndactylus* subadult without siblings (Jars) was observed to play with his parents on several occasions, but this was not frequent enough to be recorded in focal samples. The *N. leucogenys* subadult Kit spent more time playing with her father than with her mother.

Table 5.14 Mean \pm S.D. percentage of the activity budget spent playing with each family member by subadults

Subadult	Play with infant	Play with juvenile	Play with adolescent	Play with father	Play with mother	Total % time playing
Jambi (2010)	0	0.6 \pm 0.8 98%	-	0.01 \pm 0.02 2%	0	0.61
Jambi (2012)	0	1.3 \pm 1.9 81%	0.3 \pm 0.4 19%	0	0	1.6
Nakula (2011)	0.3 \pm 0.6 14%¹	1.3 \pm 1.4 62%	-	0.5 \pm 1.4 24%	0	2.1
Jars (2010)	-	-	-	0	0	0
Kit (2011)	-	-	-	0.06 \pm 0.1 75%	0.02 \pm 0.07 25%	0.08

¹ Bold values denote the percentage distribution of social play across family members for each subadult

DISCUSSION

Differences in behaviour across age classes showed a gradation from infants to adults with other immatures being intermediate (Table 5.15). The greatest number of behavioural transitions occurred between infants and juveniles (Table 5.8) and infants were unique in the proportions of time that they devoted to many activities compared to all other age classes (Table 5.15). It is no surprise that this is a significant behavioural

transition in hylobatids, given that it is associated with known changes in diet, locomotion and social interactions (see Chapter 4). These results confirm that 1.5 - 2 years is an appropriate cut-off in captivity for the transition from infant to juvenile. The end of the juvenile phase is less obvious using these behavioural measures.

Table 5.15 Behavioural patterns unique to each age class

Infant	Least resting Most movement Least feeding Least self-grooming Least grooming solicitation Closest to adult female Least aggressive Least aggression received
Juvenile	Most solo play Most social play Most approaches to adult male Most food transfer attempts
Adolescent	-
Subadult	Least groomed by others
Adult	Least movement Least social play Least play initiation Most allogrooming Most aggressive

The pattern of change in activity across development reflects that seen in other primates, in which activity levels peak during and immediately following weaning, declining thereafter until growth completion (Fagen 1993; Prates & Bicca-Marques 2008).

Juveniles in the current study showed a distinctive behavioural pattern (Table 5.15), spending the most time playing, approaching the adult male most frequently and attempting food transfers more frequently than all other age classes. Rates of behaviour began to approach adult levels between the ages of 4 and 6, including declines in the proportion of time spent in movement, solo play and social play, declines in the frequency of food transfer attempts and the frequency of approaching parents. These changes and the additional increase in distance between 4 – 6 year olds and their

parents, signal the end of juvenile behaviour and the onset of maturation. This corresponds closely with the ages suggested for other behavioural indicators of puberty in captive and wild hylobatids (for more detail, see Chapter 4).

Growing at a slower rate may be a life history adaptation that buffers immature hylobatids against fluctuations in food availability and requires that the dependent period is extended in order to reach adult brain and body size without risking starvation (Janson et al. 1993; van Schaik et al. 2006). It is plausible then that delayed maturation is simply a by-product of selection for slow growth in hylobatids, given the fluctuation in fruit availability associated with masting events in Southeast Asian rainforests (van Schaik et al. 1993; Bartlett 2009b), and the additional metabolic cost of brain tissue (Isler & van Schaik 2009). This would predict that activity levels should approach adult values as soon as possible during the growth period, in order to minimise energy expenditure.

This could be argued to be the case for the time spent resting, solo playing, and approach rates in the current study (Table 5.8), which are all general indicators of activity levels and thus energy expenditure, and which reached adult levels before growth completion. However, some behavioural patterns in these captive immatures did not reach adult levels until after growth completion, or did not reach adult levels at all in the natal group. Social behaviour (time in close proximity to parents, participation in and initiation of social play) continued throughout development and beyond growth completion, remaining different from adult levels (Table 5.8). The nature of this social behaviour in immatures may indicate further benefits of slow maturation beyond ecological risk aversion, and may also indicate the benefits of delayed dispersal for fully grown offspring. In the following paragraphs, I outline some potential social benefits of slow maturation in hylobatids.

DEVELOPMENT OF SOCIAL SKILLS

Arguments for delayed maturation as an adaptive strategy to maximise skill-acquisition incorporate many potential areas of skill development. Hylobatid immatures could learn general social skills, territorial defence and parenting skills during their long developmental period. The continued participation in social play (compared to adults) in older offspring in the current study could indicate that small amounts of social play are still beneficial for development of locomotor and social skills, even in adult-sized immatures. Both chasing and wrestling may be beneficial for learning skills required in territorial defence altercations. This benefit might be more important for males, but observations of female participation in inter-group conflict (Tilson 1981; Bartlett 2003; Reichard & Sommer 1997) might require that females also develop defensive skills. The evidence so far suggests that this may not be the case. Presumably subadults (which are adult size) would benefit more from play with other adults (Biben 1989; Watts & Pusey 1993; Thompson 1996; Fairbanks 1993). Subadults in the current study groups who were able to choose between parents and younger siblings as play partners invariably played more with siblings than with adults. An alternative benefit of participation in social play with mostly younger individuals is the development of parental skills. Adult hylobatids exercising their full strength in play bouts with smaller individuals have the potential to inflict serious injuries. For this reason, continued play with smaller siblings might allow older offspring to practice restrained play that might improve parental behaviour later on and/or improve the development of younger siblings (Spinka et al. 2001).

DEVELOPMENT OF FORAGING SKILLS

Some foraging skills require observational learning or practice in order to be both effective and efficient (Janson et al. 1993). Unlike great apes, hylobatids do not display extractive foraging or other complex foraging skills (Reichard & Barelli 2008),

although Ellefson (1974) describes some simple insect foraging techniques used by *H.lar* individuals that would require some learning and skill acquisition. This hypothesis is difficult to test in captivity since foraging behaviour is altered by the nature of food provisioning. The high proportion of time spent feeding by growing immatures in the current study could reflect a greater interest in food-related activities that would promote learning in the wild. However, this age-specific behaviour is more likely to reflect the cost of growth considering that 75% of the total feeding time for 2 – 6 year olds consisted of eating rather than foraging behaviour.

Similarly, the variation in inter-annual masting of fruit trees in South-East Asian rainforests (Ashton et al. 1988) may require that offspring remain with their parents for longer in order to learn all of the appropriate food items required for survival (Schessler & Nash 1977). This would require that immatures pay close attention to the feeding behaviour of parents; indeed immature hylobatids feed close to parents as they develop independence (Kleiman 1977), and affiliative contact with parents during feeding is described in detail for captive juvenile *S. syndactylus* (Fox 1977, p. 206). This could be one reason why immatures in the current study spent time in close proximity to parents despite increasing exploratory behaviour. However, I did not record the context of proximity bouts so it is unknown how much of this time in proximity occurs during feeding bouts.

Given that parents become intolerant of immatures in feeding contexts as early as 4 years of age, and that this increases in intensity as offspring reach adult size, older offspring are likely to avoid parents in feeding contexts (Ellefson 1974; Bartlett 2009a). In addition, solitary feeding (away from the parents) in wild *H.lar* occurs by about 5 years of age (Ellefson 1974; Gittins & Raemaekers 1980), yet offspring do not stop growing and disperse for at least another 2 - 3 years (Srikosamatara & Brockelman 1987; Brockelman et al. 1998; Barelli et al. 2007; Zhou et al. 2008; Reichard et al.

2012). Thus, social learning of food items cannot wholly explain the delay in maturity unless immatures are able to gain this information from a distance. Hylobatids in the wild might spend this time learning travel routes and the spatiotemporal distribution of fruiting trees and other resources (Asensio et al. 2011), but both sexes tend to disperse from their natal territory so this knowledge is not transferable to other territories.

DELAYING MATURATION BEYOND GROWTH COMPLETION

Subadults in the current study continued interacting with parents, despite receiving aggression and exploring independently, spending the same proportion of time in close proximity to parents as younger offspring did. Notably, subadults were groomed for the smallest proportion of time, compared to all other age classes. Subadults were therefore gaining little direct parental care by continuing to spend time near parents, in comparison to younger offspring. This raises the question: what are subadults gaining from continuing to interact with parents? Subadults may actively contribute to the social group to directly benefit from continuing long-term relationships with parents beyond sexual maturity. This strategy is particularly advantageous if the resulting nepotism by parents allows delayed dispersal or reduces the cost of dispersal through other means, e.g. budding off of parental territory (Tenaza 1975; Komdeur & Edelaar 2001) or assistance in defending neighbouring territory from unrelated conspecifics (Tilson 1981).

The short dispersal distances of many gibbons suggest that this is an attractive option for maturing offspring (Brockelman et al. 1998), perhaps more so for males, as in *S. syndactylus* (Aldrich-Blake & Chivers 1973; Lappan 2007a). Chivers' (1974, p.206) description of two subadult male *S. syndactylus* suggests that both were active in maintaining proximity to parents and initiating grooming bouts with them; although, variable observations of grooming by subadult male *N. concolor* (Guan et al. 2013) suggest individual differences. If grooming by subadults encourages nepotism then I

would expect subadults to preferentially groom parents more than they groomed siblings. I found little evidence of this. The subadults in the current study varied in their grooming behaviour; only those subadults without younger siblings directed substantial grooming towards their parents.

SUBADULT CONTRIBUTIONS TO INCLUSIVE FITNESS

Individuals that delay dispersal (and therefore independent breeding) can counteract the initial cost to their lifetime reproductive success by contributing to their natal group in a way which increases the fitness of parents or siblings (Emlen 1982a; Koenig et al. 1992; Ekman et al. 2004). One aspect of these inclusive fitness benefits might include grooming parents and younger siblings. Subadults in the current study did not spend a greater proportion of time grooming other group members compared to younger offspring. However, the two subadults with younger siblings did direct more frequent grooming towards siblings than towards parents, suggesting that the presence of subadults may contribute to allocare of younger siblings. Nonetheless, in Chapter 3, I showed that the presence of multiple offspring in a group does not influence parental grooming behaviour, suggesting that subadult contributions to grooming do not decrease the parental grooming workload.

Subadults spent more time in social play than did adults, despite initiating play and engaging in solo play less often than younger offspring did. Interestingly, older offspring were sometimes subject to aggression from the mother during play bouts with younger siblings (pers. obs), suggesting that older siblings have to adjust the level of play to that of younger playmates to avoid conflict. Additionally, this suggests that subadults are not merely responding to the solicitations of younger siblings, since enduring parental aggression whilst receiving no benefit should discourage subadults from participating in play with siblings. Thus, this behaviour might function

simultaneously as an inclusive fitness benefit as well as skill development, increasing the benefits of such behaviour to mature offspring.

In the wild, subadults may also increase their inclusive fitness through vigilance or territorial defence (Srikosamatara & Brockelman 1987). I did not measure vigilance specifically, but subadults in the current study spent the same proportion of time resting as did adults. This suggests that subadults no longer receive subsidised vigilance from parents and thus may be contributors to vigilance efforts for the group; however, resting time is a crude proxy since it is influenced by the time spent in other behaviours (see Appendix C). If subadults are as vigilant as parents, then the presence of subadults in a group could increase inclusive fitness through decreased mortality risk from predation (Dooley 2015) or infanticide (Borries et al. 2011). This would have to be measured more specifically and ideally matched with measures of mortality risk or reproductive success for parents and siblings of subadults who help. Subadults may also play a more active role in defence of siblings by accompanying younger siblings during group fission (Dooley & Judge 2014). In addition, subadults can contribute to parents' territorial defence by participating in encounters with neighbours and chasing intruders (MacKinnon & MacKinnon 1977; Reichard & Sommer 1997; Brockelman et al. 1998; Fan & Jiang 2010).

CONCLUSION

The pattern of change in activity levels across development is similar to the pattern seen in other nonhuman primates, with activity levels peaking around weaning age and decreasing thereafter. Some behaviours indicative of activity levels (resting, solo play, approach frequency) reach adult levels before growth completion. However, adolescents (still growing) and subadults (fully grown) are both active members of social groups despite showing increased independence and decreased activity compared to juveniles. This suggests that older immatures benefit from social interactions in their natal groups

and this social behaviour may improve the development of social skills or function to increase inclusive fitness. Participation in social play with younger siblings indicates potential benefits to inclusive fitness through allocare that improves the development of younger siblings, or through skill development in handicapped play that may improve parenting skills after dispersal.

CHAPTER 6 SIBSHIP COMPOSITION AND SOCIAL RELATIONSHIPS

CHAPTER 6 SIBSHIP COMPOSITION AND SOCIAL RELATIONSHIPS

INTRODUCTION

Conflict between parents and offspring can arise in response to the difference in relatedness between offspring and themselves (related by 100%) and offspring and their siblings (related by 50% on average, Trivers 1974). This difference in relatedness means that parents and current offspring have divergent optima for the amount of parental care given to each offspring. The small apes (family Hylobatidae) tend to live in small territorial social groups, the majority of which are composed of a single breeding pair and their offspring. This social organisation is best described as a simple family structure, in which grown offspring do not breed in the natal group but may delay dispersal (Emlen 1995). Hylobatids have long maturation periods (≥ 8 years) in which offspring remain with parents (Reichard et al. 2012), but inter-birth intervals range from 2 – 5 years, producing overlapping dependent offspring (Palombit 1995).

This accumulation of dependent offspring in the same group provides an avenue for observable behavioural conflict to occur between parents and older offspring over the care of new siblings, and between siblings directly. For example, parent-offspring conflict occurs simultaneous with renewed reproductive efforts of mothers in other nonhuman primates (e.g. around conception of her next offspring, Maestriperi 2002). In humans, where there is also an accumulation of dependent offspring, the birth of a sibling can produce changes in parent-offspring relationships that create conflict (Kowaleski-Jones & Dunifon 2004). The variation in inter-birth intervals in hylobatids means that some offspring experience the birth of a sibling soon after nutritional weaning, while others do not, but the prolonged development period means that most offspring will experience the birth of a sibling at least once. Offspring that are still

growing may therefore be predicted to compete with younger siblings for parental care (e.g. thermoregulatory care, play and grooming) when the mother conceives again. This could contribute to variation in behaviour among individuals of a similar age in families of different compositions.

Sibling birth is not the only change in family composition that may increase conflict between parents and offspring. The dynamic of parent-offspring relationships should also change when offspring reach maturity due to changes in the costs and benefits of philopatry to both parties (Emlen 1995). Offspring that have completed growth (here termed subadults) should no longer require parental care and should be reproducing independently. From the parental perspective, fully grown offspring become resource and breeding competitors, so more serious conflict can arise between parents and grown offspring that may result in dispersal of those offspring (Kleiman 1979). Hylobatid offspring are believed to disperse as a result of both self-motivation and parent-offspring aggression in the context of a) resource competition and/or b) sexual activity (Aldrich-Blake & Chivers 1973). Intra-group resource competition might reduce the benefits of mature offspring remaining at home, if ecological constraints (resource competition) limit group size in hylobatids (Brockelman 2009). As more offspring are born, parents could become less tolerant of older offspring because of their shifting investment towards younger, more dependent offspring. In the absence of younger offspring, parents may be more tolerant (Geissmann 1993, p. 147). Observations of feeding-related aggression in hylobatids older than 4 years of age (Ellefson 1974) suggest that adolescents (still growing) and subadults (adult-sized) are perceived as resource competitors by parents.

Furthermore, parental tolerance of subadults varies with the reproductive state of the breeding female, or the sexual behaviour of subadults. For example, aggression between father and son in a wild group of *S. syndactylus* increased following the resumption of

sexual activity between the adult pair (Aldrich-Blake & Chivers 1973). Similarly, aggression between mother and daughter *S. Syndactylus* (Lappan 2005) and *H. klossii* (Tilson 1981) increased following sexual activity by the daughters. The social context thus influences parent-offspring relationships and increases the benefits of dispersal to both parents and offspring. However, many subadult hylobatids delay dispersal and continue to associate with their parents (Srikosamatara & Brockelman 1987; Brockelman et al. 1998; Huang et al. 2013; Dooley 2015).

Species that tend to live in family groups are usually also territorial, cooperative breeders, in which older offspring or grown offspring that delay dispersal contribute to parental breeding efforts, or to group territorial defence (Emlen 1995). Older immatures may therefore improve parental reproductive success (and thus inclusive fitness) while continuing to develop social skills that improve individual competitive ability (Emlen 1995; Chapter 5). If subadult offspring are able to contribute to parental breeding efforts, then the benefits (for parents) of delayed dispersal by subadult offspring may outweigh the costs. On the other hand, if delayed dispersal of older offspring is only a result of ecological constraints on breeding opportunities *and* resources within the natal group are limiting, then the birth of siblings, or the presence of younger siblings should increase conflict within the family and increase the benefits of dispersal to both subadults and parents (Mitchell et al. 1989). Families such as those produced when offspring delay dispersal are therefore predicted to be unstable groupings, since the costs and benefits to parents and offspring depend on multiple social and ecological factors (Emlen 1995).

The impact of sibling births and increasing family size on behavioural development and parent-offspring relationships has not been explored in hylobatids, partially because observations of sibling births and their impact on family dynamics are limited. In the only two observations of births in wild hylobatids, a juvenile male siamang (Aldrich-

Blake & Chivers 1973) and a subadult male siamang (Chivers & Chivers 1975) dispersed on the day of birth of a sibling. Aldrich-Blake and Chivers (1973) suggested that these responses were possibly due to increased aggression by the mother or the father, but did not actually observe this. Similarly, 3 of 4 *Nomascus nasutus* subadults who dispersed, did so within 1 – 5 months of the birth of infants (Fan et al. 2015). The presence of many stable family groups containing adolescent and subadult offspring indicates that dispersal is not always triggered by increasing group size (Ellefson 1974; Chivers 1974; Brockelman et al. 1998; Bartlett 2009a), but the birth of new siblings may create additional tension that increases the cost of remaining at home after growth completion. The opposing selective pressures of intra-group resource/breeding competition and dispersal risk may then have an effect at the individual level and determine the observed ratio of affiliation and aggression within the family (Figure 6.1).

In this chapter, I add to accumulating data on how family composition influences hylobatid social behaviour. The captive groups in the current study varied in their family compositions, allowing a comparison of the behaviour of older offspring and their relationships with parents depending on the presence or absence of younger siblings. In captivity, the dispersal behaviour of maturing offspring is clearly limited; however, the captive environment provides an opportunity to observe parent-offspring interactions in detail during the developmental process. In addition, the influence of territory quality and ecological fluctuation in resource availability is controlled, especially since management protocols are similar across institutions. This allows observation of the influence of family composition and social events (like sibling births) whilst controlling for differences in “ecology” between groups. In this chapter I provide a longitudinal comparison of a silvery gibbon (*H. moloch*) social group before and after a birth. I then examine the influence of increased group size (birth of infants, presence of younger siblings) on parent-offspring relationships, and on the timeline of

behavioural development in immature hylobatids (Figure 6.1). I control for the influence of age on behaviour by comparing similarly aged immatures with and without younger siblings.

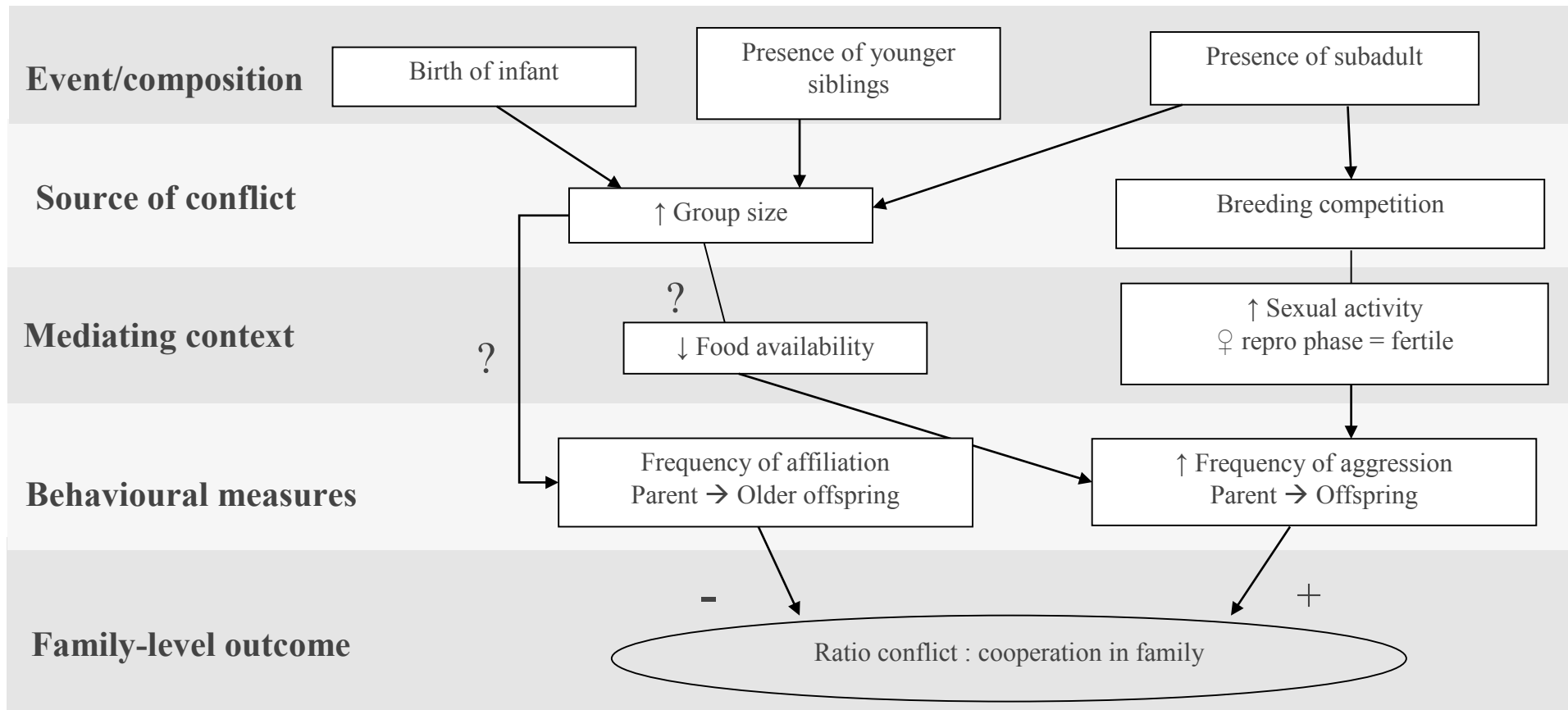


Figure 6.1 Schematic of the possible influence of social events/family composition on older offspring's behavioural development and family dynamics.

The impact of increased group size on affiliative and aggressive behaviour by parents towards older offspring is currently unknown (indicated by question marks). It is hypothesised that increases in group size may alter food availability and increase conflict between parents and older offspring, or decrease affiliative parental care of older offspring, due to a shift in focus towards new offspring.

METHODS

STUDY ANIMALS

Data were collected for 12 non-infant immatures (four *H. moloch*, three *N. leucogenys* and five *S. syndactylus*), and longitudinal data were collected for 8 of these immatures. All subadults lived in their natal groups at the time of observation and were adult size. Not all immatures were completely mother-reared; details on the rearing status of adolescents and subadults can be found in Chapter 4.

BEHAVIOURAL OBSERVATIONS

Behaviour of individuals was recorded using continuous focal animal sampling (see methods in Chapter 2).

STATISTICAL ANALYSES

Behavioural variables were prepared as in Chapter 2. To look at the influence of sibling composition on parent-offspring relationships, I compared parent-offspring interactions and activity of immatures with and without younger siblings using generalised linear mixed models (GLMM) via the function “lmer” in the R (v.2.15.2) package lme4 (version 0.999999-0) (Bates et al. 2012; R-Core-Team 2012). The details of each model are outlined in Table 6.1. For all models, residuals and fitted values were plotted and visually checked for normality of residuals and homoscedasticity across the fitted values (Zuur et al. 2009). Markov-Chain Monte Carlo (MCMC) p-values were calculated for each fixed effect using the “pvals.fnc” function in the languageR package (v.1.4) (Baayen 2011).

For one of the *H. moloch* groups, observations were conducted during the eight 10-day periods before and five 10-day periods after the birth of an infant. This group contained an adolescent male and juvenile female during the observation period. I compared the behaviour of siblings and parent-offspring relationships before and after the birth using

t-tests. Appropriate p-values are displayed where Levene's tests showed unequal variances between the test groups. The influence of younger siblings on older offspring behaviour and parent-offspring relationships was analysed cross-sectionally (analyses 1 and 2, Table 6.1). 'Individual ID' nested in 'group ID' were used as a random variables to account for repeated measures for some individuals in different age classes and for nesting of related individuals within the same family. Due to the small sample size, I pooled adolescents and subadults to look at the influence of younger siblings on older offspring behaviour. If there was a difference in behaviour between adolescents and subadults in Chapter 5, age class (categorical: adolescent or subadult) was included as a fixed effect. To look at the influence of younger siblings on maternal aggression towards offspring I analysed the frequency of aggression by mothers towards offspring of each age class (analysis 3, Table 6.1). 'Mother ID' was included as a random effect and 'species' as a fixed effect in analysis 3. To limit the number of fixed effects, 'species' was only included in some models, based on potential species differences identified in Chapter 5 analyses. Behaviours for which 'species' or 'age class' were included as a fixed effect are identified in the results. Significance was set at $\alpha = 0.05$ but I also report trends where $0.05 \leq p \leq 0.1$.

Table 6.1 Details (fixed and random effects) for generalised linear mixed models

Analysis	Age class and behaviour tested	Fixed effects	Random effects
1	Juvenile behaviour and relationships with parents	Presence of infant Species ¹	Individual ID nested in group ID
2	Adolescent and subadult behaviour and relationships with parents	Presence of younger siblings Species ¹ Age Class ¹	Individual ID nested in group ID
3	Maternal aggression towards offspring	Presence of infant/Presence of younger siblings Species ¹	Individual ID

¹Species and age class only included for some behaviours, identified in the results

SAMPLE

Table 6.2 shows the distribution of 10-day focal samples within each age class that represent individuals from different sibling composition categories.

Table 6.2 Distribution of individuals (# 10-day focal samples) in each age class with differing sibling compositions

Age class	Younger sibling(s) present		Younger sibling(s) absent	
	Younger sibs only	Younger and older sibs	Older sibs only	No sibs at all
Juvenile (2 – 4)	1 (18)	4 (35)	3 (32)	3 (24)
Adolescent (4 – 6)	3 (45)	1 (6)	0	2 (26)
Subadult (6 – 9)	3 (41)	0	0	2 (15)

RESULTS

IMPACT OF SIBLING BIRTH ON A SILVERY GIBBON FAMILY

There were no differences in the adult pair relationship before and after the birth of the infant, and only limited differences in parent-offspring relationships. The juvenile female was closer to her father on average following the birth than she was before the birth (before: $\bar{x} = 5.6\text{m} \pm 2.8$, after: $\bar{x} = 2.9\text{m} \pm 1$, $t_{11} = 2.3$, $p = 0.047$). Despite this closer distance, there was a trend for her to approach her father less frequently after the birth (before: $\bar{x} = 7.3 \pm 2$ approaches/hr, after: $\bar{x} = 4.8 \pm 2.8$ approaches/hr, $t_{11} = 2$, $p = 0.07$). There were no other differences in her behaviour following the birth of the infant, including the proportion of time spent in close proximity or physical contact with either parent. There was no difference in parental behaviour towards the juvenile before and after the birth. Likewise there was no change in the relationship between the adult male and the adolescent male. After the birth, the mother retreated from her adolescent son

more often than before the birth (before: $\bar{x} = 0.23 \pm 0.44$ retreats/hr, after: $\bar{x} = 1.4 \pm 1.2$ retreats/hr, $t_{11} = -2.5$, $p = 0.03$).

IS JUVENILE BEHAVIOUR DIFFERENT WHEN THERE IS AN INFANT SIBLING?

Juveniles with infant siblings approached their mothers less frequently compared to juveniles without infant siblings (Table 6.3), but there were no other differences in mother-juvenile relationships between groups with and without infants (Table 6.3).

Juveniles who had an infant sibling spent less time engaged in solo play and approached the adult male less frequently, compared to juveniles without an infant sibling (Table 6.3). There was a trend for juveniles with an infant sibling to spend a greater proportion of time grooming others compared to juveniles without an infant sibling (Table 6.3).

There were no other differences in behaviour between juveniles with and without an infant sibling (Table 6.3).

Table 6.3 Differences in juvenile behaviour across sibling composition (presence/absence of infant sibling)

Behaviour ¹		Estimate \pm S.E. (Infant present) ²	t	p	N individuals (10-day samples) ³
Approach adult female	↓	-0.98 \pm 0.28	-3.5	0.002**	IP: 3 (31) IA: 4 (32)
Approach adult male	↓	-1.2 \pm 0.27	-4.1	< 0.001***	IP: 3 (31) IA: 4 (27)
% Solo play	↓	-0.06 \pm 0.02	-2.5	0.016*	IP: 5 (53) IA: 6 (56)
% Allogroom	↑	+0.05 \pm 0.02	2.3	0.10	IP: 5 (53) IA: 6 (56)

¹Infant presence had no influence on time spent in social play ($p = 0.90$), being groomed ($p = 0.22$), in proximity to adult female ($p = 0.47$), in proximity to adult male ($p = 0.66$), frequency of play initiation ($p = 0.86$), frequency of allogrooming ($p = 0.23$), frequency of grooming solicitation ($p = 0.61$), distance from adult female ($p = 0.99$), distance from adult male ($p = 0.46$), Hinde's index with adult female ($p = 0.61$), Hinde's index with adult male ($p = 0.31$), frequency of food transfer attempts ($p = 0.75$), frequency of aggression to others ($p = 0.98$), frequency of aggression received (total, $p = 0.50$), and frequency of aggression received from adult female ($p = 0.39$) by juveniles

²Estimate for infant-present compared to infant-absent (reference category)

³IP = infant-present, IA = infant-absent

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, bold p values indicate a trend ($0.05 \leq p \leq 0.10$)

DO YOUNGER SIBLINGS INFLUENCE PARENT-ADOLESCENT AND PARENT-SUBADULT RELATIONSHIPS?

Subadults and adolescents with younger siblings were more distant from their mothers compared to same-aged individuals without younger siblings (Table 6.4). There was a trend for older offspring with younger siblings to approach their father less frequently than those without younger siblings (Table 6.4). Mothers were less frequently aggressive towards their adolescent offspring when younger siblings were present in the group (Table 6.4). There were no other differences in parent-adolescent and parent-subadult relationships associated with the presence of younger siblings.

Table 6.4 Influence of sibling composition (presence/absence of younger siblings) on adolescent and subadult relationships with parents

Behaviour ¹	Estimate ± S.E. Younger sibling(s) present ²	t	p	N individuals (10-day samples) ³
Distance from adult female	↑ +0.51 ± 0.19	2.7	0.04*	SP: 5 (73) SA: 3 (40)
Approach adult male	↓ -0.80 ± 0.18	-4.6	0.07	SP: 3 (46) SA: 3 (40)
Maternal aggression received by adolescents ⁴	↓ -0.38 ± 0.21	-1.7	0.006**	SP: 3 (32) SA: 2 (25)

¹Presence of younger sibling(s) did not influence time in proximity to adult female ($p = 0.58$), proximity to adult male ($p = 0.36$), distance from adult male ($p = 0.11$), frequency of approaching adult female ($p = 0.18$), Hinde's index with adult male ($p = 0.43$), Hinde's index with adult female ($p = 0.93$) by adolescents and subadults, and did not influence the frequency of maternal aggression received by subadults ($p = 0.15$)

² Estimate for sibling(s)-present compared to sibling(s)-absent (reference category)

³SP = sibling(s) present, SA = sibling(s) absent

⁴Species included as an additional fixed effect only for this behaviour

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, bold p values indicate a trend ($0.05 \leq p \leq 0.10$)

DOES ADOLESCENT/SUBADULT BEHAVIOUR DIFFER WITH THE PRESENCE OF YOUNGER SIBLINGS?

There was a trend for adolescents and subadults with younger siblings to receive less aggression from group members, compared to adolescents and subadults without younger siblings (Table 6.5). There was a trend for adolescents and subadults to spend

less time playing with parents when younger siblings were present, despite spending the same proportion of time in total social play (Table 6.5). There were no other differences in adolescent or subadult behaviour associated with the presence of younger siblings (Table 6.5).

Table 6.5 Influence of sibling composition (presence/absence of younger siblings) on adolescent/subadult behaviour

Behaviour ¹		Estimate ± S.E. Younger sibling(s) present ²	t	p	N individuals (10-day samples) ³
Aggression received ⁴	↓	-0.34 ± 0.11	-3.0	0.06	SP: 5 (74) SA: 3 (41)
% Play with parents ⁴	↓	-0.10 ± 0.02	-4.3	0.08	SP: 3 (47) SA: 3 (41)

¹Presence of younger sibling(s) did not influence time spent in solo play (p = 0.87), in total social play (p = 0.17), total allogrooming (p = 0.38), allogrooming parents (p = 0.79), being groomed (p = 0.78), total frequency of play initiation (p = 0.47), frequency of play initiation with parents (p = 0.88), total frequency of allogrooming (p = 0.31), frequency of grooming parents (p = 0.12), frequency of grooming solicitation (p = 0.54) and frequency of aggression (p = 0.19) by adolescents and subadults

² Estimate for sibling(s)-present compared to sibling(s)-absent (reference category)

³SP = sibling(s) present, SA = sibling(s) absent

⁴Species included as an additional fixed effect for these behaviours

* p < 0.05, ** p < 0.01, *** p < 0.001, bold p values indicate a trend (0.05 ≤ p ≤ 0.10)

PRELIMINARY OBSERVATIONS ON PARENT-SUBADULT RELATIONSHIPS

Only the mother of one subadult (male *S. syndactylus* Jars) was cycling during the observation period. Jars received the highest frequency of aggression compared to other subadults (mean frequency of aggression/hr received by Jars [N = 5 10-day samples] = 1.9, mean frequency received by other subadults [N = 51 10-day samples] = 0.43, t = 6.3, p < 0.001). Both parents contributed to this aggression (Figure 6.2). Sexual behaviour of subadults was extremely rare (Chapter 4), so I could not measure the impact of sexual behaviour by subadults on parent-subadult conflict.

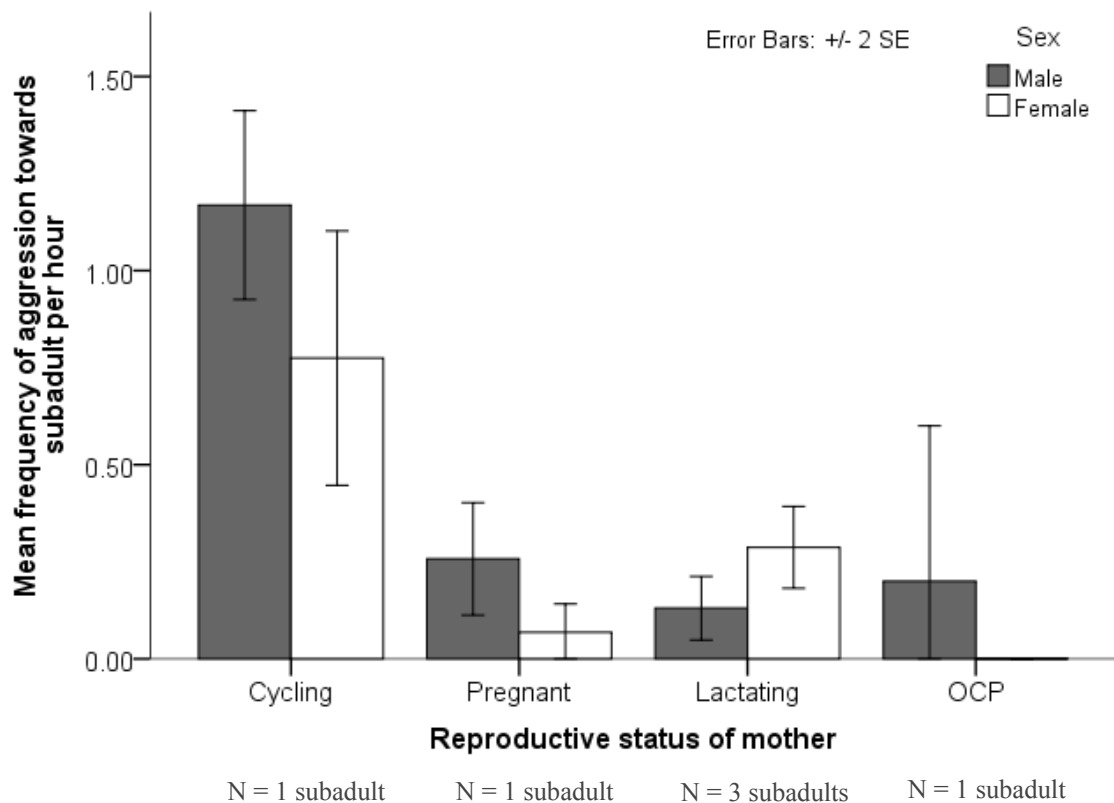


Figure 6.2 Frequency of aggression received by male and female subadults according to the reproductive status of the mother (OCP = oral contraceptive pill). Sample sizes refer to the number of subadults in each category. No aggression towards the subadult was recorded for the mother who was on oral contraceptives.

PRELIMINARY OBSERVATIONS ON SUBADULT CO-SLEEPING

Limited anecdotal observations of the sleeping patterns of one *S. syndactylus* family were possible due to their habit of sleeping outside on top of the large poles in their outdoor enclosure. Only 2 individuals could fit on the top of each pole (not unlike some descriptions of sleeping spots in wild hylobatids). On a few occasions when observations on this group finished at the end of the afternoon, I watched them settle into their (presumed) sleeping positions. During the first set of observations on this family (2010), the infant was always with the mother on one pole, and the juvenile female embraced with her father on another pole. The subadult son was alone on his own pole. In the following observation year (2012), the new infant was with the mother,

and the new juvenile would often be embraced with his subadult brother, whilst the female adolescent still embraced with her father.

DISCUSSION

MINIMAL IMPACT OF SIBLING BIRTHS ON SOCIAL DYNAMICS IN CAPTIVITY

The birth of siblings is not disruptive to juvenile hylobatids; neither mothers nor juveniles were more aggressive when an infant was present. In addition, there was no difference in parental care received by juveniles with and without younger siblings: juveniles with infant siblings were groomed for the same proportion of time, spent the same proportion of time playing and spent the same proportion of time within arm's reach of both parents as did juveniles without younger siblings. Additionally, maternal responsibility for maintaining proximity to their juvenile offspring did not differ in groups with infants. These results are also reflected in the dearth of changes in behaviour in the silvery gibbon family surrounding the birth. The minimal impact of sibling births on juvenile behaviour, and the trend for older immatures to receive less aggression when younger siblings were present, do not provide support for increased conflict in larger families.

It is possible that this minimal impact of sibling births is reflective of the provisioned diet in captivity; as group size increases and offspring mature, diets are adjusted accordingly so that all individuals can obtain sufficient food. In the wild, there may be a greater influence of family size on family conflict, due to variation in territory quality between families, and seasonal availability of resources (Figure 6.1). This could explain the dispersal response of the two wild *S. syndactylus* immatures to sibling births, contrasting with the minimal impact observed here in captivity (Aldrich-Blake & Chivers 1973; Chivers & Chivers 1975). Whether the dispersal response is triggered by greater aggression in the wild is yet to be seen; however, older offspring in captivity

still showed spatial distancing from parents in the absence of an increase in parental aggression. In addition to the observations of delayed dispersal in other wild groups, this indicates that there are additional mechanisms involved in dispersal timing for grown offspring. Also, larger groups tend to have larger territories (Brockelman 2009), suggesting that wild groups are able to adjust their resource base by defending a larger area. So the influence of contest competition on intra-group conflict may be minimal in wild groups also (Fan et al. 2015). This may arise because more individuals are needed on larger territories for successful monopolisation of resources, as suggested by the increased presence of polyandry in large, low quality territories in *H. lar* (Savini et al. 2009). Thus social tolerance of additional adults (and subadult offspring) may depend on the size and quality of the territory in wild groups.

YOUNGER SIBLINGS ACCELERATE INDEPENDENCE AND MATURATION IN JUVENILES

The behaviour of juveniles (2 – 4 years) with infant siblings indicates that the birth of a sibling encourages more independent and mature behaviour. Juveniles with younger siblings were more distant from their mother, spent less time engaged in solo play and tended to spend more time grooming than did juveniles without younger siblings.

However, since 4 of the 5 juveniles with infant siblings also had older siblings, it is possible that these results instead reflect the availability of more social partners. The behaviour of older immatures with younger siblings is also reflective of greater independence; however, older individuals with and without younger siblings did not differ in their absolute levels of behaviour. The family composition may therefore contribute to variation in the activity levels of juveniles, but not of older offspring.

FAMILY STABILITY FACILITATED BY FLEXIBLE SOCIAL ROLES

The non-disruptive nature of parent-juvenile relationships following sibling births may be facilitated by the presence of alternative social partners. For example, some juvenile

rhesus macaques respond to sibling births by increasing contact with other group members (Singh & Sachdeva 1977; Holman & Goy 1988). The ability to respond to decreased care by one parent by increasing contact with other group members may be a useful strategy for immatures that are semi-dependent. In humans, research on family dynamics and birth order effects suggests that offspring strategies during development are adaptive and have long-term consequences for adult behaviour and reproductive strategies (Sulloway 2011). In the current study, all groups contained both a father and a mother; however, despite venturing further from their mothers, juveniles with infant siblings did not compensate for this by becoming closer to their fathers. In fact, juveniles with infant siblings approached their fathers less often than juveniles without infant siblings.

This contrasts with some of the observations surrounding a birth within the *H. moloch* family, whereby the juvenile female was closer to her father following the birth. Similarly, during previous observations on this family before and after a birth, a juvenile male was closer to his father (and his mother) following the birth of an infant (Burns et al. 2011). The difference between the longitudinal and cross-sectional data could reflect the mutual interest in newborn infants (a novel stimulus) by all family members. Similar increases in social cohesion have been noted in captive gorillas following a birth (Stoinski et al. 2003; Kurtycz et al. 2014). Furthermore, the difference between the longitudinal and cross-sectional data may result from the timing of the observations relative to the births, with juveniles seeking social contact with other family members (e.g. the father) immediately following a sibling birth, and requiring less substitutive contact over time.

Alternatively, the absence of increased contact with the father for juveniles with infant siblings could result from the sibling composition; in addition to fathers, all but one of the juveniles with an infant sibling also had older siblings. Juveniles with infant siblings

may therefore have sought social interactions with older siblings instead of seeking contact with the father. This is reflected in the behaviour of those older siblings, who associated less with parents when younger siblings were present, including being further from their mother, approaching their father less often (Table 6.4), and playing less with parents (Table 6.5). Since the absolute levels of behaviour did not differ between adolescents and subadults with and without younger siblings, this indicates that older offspring shift their social activities towards younger siblings when younger siblings are present. These sibling relationships may facilitate both a reduction of the impact of sibling births on mother-juvenile relationships and reduced aggression by parents towards older offspring (Table 6.3; Table 6.5). In the absence of older siblings, there may be a greater reliance on the father by semi-dependent juvenile offspring (see Chapter 3). The sleeping positions of the *S. syndactylus* family, while potentially an artefact of the short inter-birth intervals possible in captivity, indicate the potential of subadult offspring as substitute attachment figures for younger siblings. This means that subadults may contribute to inclusive fitness through social and thermoregulatory care of smaller siblings.

BREEDING COMPETITION AND SEXUAL MATURITY

Parent-subadult relationships may be influenced not only by family size, but by breeding competition. I could not assess the impact of sexual maturity and breeding competition on parent-subadult relationships, partially as a result of the low frequency of aggression and sexual behaviour displayed by the subadults themselves (Chapter 4). The variation in maternal reproductive status in groups with subadults also did not allow a comprehensive analysis of the impact of maternal fertility on parent-subadult relationships. The higher frequency of aggression received by the only (male) subadult with a cycling mother suggests that some of the variation in parent-offspring relationships (Figure 6.2) is explained by the reproductive status of the breeding female.

This corresponds with other observations of context-specific aggression associated with the sexual activity of the adult pair or the subadult offspring in wild hylobatids (Aldrich-Blake & Chivers 1973; Lappan 2005).

CONCLUSION

Overall the results of this study suggest that sibling births and increasing family size are not disruptive events in captive hylobatid groups. This may be possible through flexible social relationships, such that semi-dependent offspring can rely on fathers or older siblings for care that would otherwise come from the mother. The presence of younger siblings was associated with more mature behaviour, suggesting that behavioural development is not only age related but is influenced by the family composition. Flexible social roles within the group and long developmental periods may allow hylobatids to produce overlapping dependent offspring without creating conflict. Reduced conflict in the family could also increase success in cooperative resource defence. In the wild, the influence of younger siblings and increased group size may have a more disruptive influence on family stability, due to ecological constraints; however, detailed intra-family interactions are difficult to obtain in the wild. Observing detailed social dynamics in captive groups where ecological factors are somewhat removed, or can be manipulated, can therefore distinguish the more subtle impacts of social and reproductive events on hylobatid behaviour.

CHAPTER 7 CONCLUSIONS AND GLOBAL DISCUSSION

CHAPTER 7 CONCLUSIONS AND GLOBAL DISCUSSION

As a result of this study, I provide three major new contributions to the field of hylobatid social behaviour:

- 1) I offer one of the first quantitative explorations of variation in intra-group behaviour across various social and reproductive contexts in three hylobatid species,
- 2) I quantify behaviour over the entire period of development using a large sample of immatures, which has not been achieved in any previous studies, and
- 3) I contribute to the accumulation of data on intra-group behaviour in hylobatids, which is so far lacking in the literature and difficult to obtain in the wild.

In this final chapter, I raise some of the significant findings for discussion in a broader context. First, I summarise the main findings from each chapter of the thesis. Following this, I propose a theoretical framework drawing on elements from life history theory, female reproductive research and developmental biology that integrates my findings with the existing literature. By unifying approaches from several distinct fields I offer a holistic approach to hylobatid socioecology that provides a novel direction for future research.

SUMMARY OF FINDINGS FROM EACH CHAPTER

The data from Chapter 2 (The social pair bond) suggested that captive pairs maintain close spatial proximity, but vary in the degree to which they spend time within arm's reach of their mate or engage in overt affiliative behaviour, such as grooming or body contact. Similar between-group variation in pair bonding behaviour has been reported in other captive studies of hylobatid pairs (Bricknell 1992; Rosenkranz 2002). The greater

degree of variation in some behaviours (e.g. mate grooming) but not others (spatial proximity) confirms that social bonding does not necessarily accompany spatial bonding in “socially monogamous” mammals (Gowaty 1996). Data from this study and others (Table 2.2; Table 2.5) also indicate no consistent sex-bias in investment into the pair bond. Moreover, variation in pair behaviour is not closely associated with the social or reproductive context in captivity. Male and female investment into the pair bond may change on a more subtle basis within pairs (Barelli et al. 2011). However, an alternative explanation for the variation among groups and the lack of a consistent sex-bias is that the ultimate outcome of individual investment in the mate is a mutual, cooperative bond. This would suggest that hylobatid pair bonds are mutually maintained, rather than being the result of sex-biased reproductive strategies. It must be noted that species differences in sex-biased pair bond maintenance may be clouding this interpretation. Some of the data indicate more male-biased pair bonds in *S. syndactylus* and more female-biased pair bonds (or social bonds in general) in *Nomascus* spp. (Table 2.2; Table 2.5). This should be further investigated when more data for each genus is available. Either way, the variation in sex-biased investment despite the relative homogeneity of the hylobatid socioecological niche indicates that sex-specific explanations for social structure do not apply to all hylobatids.

In Chapter 3 (Parental roles), I showed that adult sex differences in activity are greater when offspring are present in the group, indicating that sex differences in behaviour are associated with reproductive roles. The activity budgets of pregnant and lactating mothers reflect energy-conservation, including increased resting and decreased contribution to play with offspring. Play with offspring by fathers depends on both the maternal contribution to play and the presence of siblings such that fathers play more when other potential contributors are unavailable (no siblings) or not contributing (reproductively active mothers). The activity budgets and parental behaviour of males

and females in captivity thus reflect the significant investment by female hylobatids into reproductive effort. The flexible pattern of parental care could explain variation in individual contributions to offspring care across groups.

In Chapter 4 (The timing of development), I described changes in social behaviour during development in a captive sample of immatures and related this to developmental timing using physiological and behavioural markers from the literature. The results indicated greater variation in later developmental milestones (puberty, maturation) compared to early developmental milestones (infancy/juvenescence). After behavioural onset of puberty, the timing of physiological puberty, sexual and social maturity is variable in both the captive and wild context. The timing of maturation depends on both the nutritional and the social environment; some preliminary evidence suggests that maturation is slower in the natal group and accelerated upon dispersal.

In Chapter 5 (The benefits of slow maturation), I compared the activity budgets and social behaviour of immature hylobatids across development, relative to the behaviour of adults. I also described the behaviour and social relationships of four subadult offspring that had completed growth. The frequency of social and non-social behaviour confirms behavioural onset of puberty at ~5 years. Selection of social partners by older offspring indicates a preference towards playing with younger individuals, simultaneous with continued close association with parents. Fully grown offspring show very little sexual or aggressive behaviour. Some social behaviours of older offspring therefore contrast with other behaviours typical of “adolescent” primates, such as spatial distancing, and receipt of aggression from parents. Prosocial behaviour by older offspring in the natal group could facilitate longer exploitation of the parental territory and allow delayed dispersal in the wild when breeding options are limited.

Finally, in Chapter 6 (Sibship composition and social relationships), I examined the influence of increased group size (birth of a sibling and presence of younger siblings) on parent-offspring relationships and on the timeline of development in older siblings. The results indicated that sibling births and larger family size are not disruptive to parent-offspring relationships, at least in captivity. The social behaviour of immatures indicates that this may be enabled by the availability of alternative social partners (father and/or older siblings). Flexible social behaviour might therefore facilitate reduction in conflict within the family.

Overall, the data resulting from this project suggest that hylobatid development and social behaviour depend on intra-group social factors. I found that parental behaviour is conditional on the contributions of others and that physiological and social maturity may be conditional on the current social environment. Interestingly, the behaviour of the adult pairs in this study suggests that the adult pair bond is not broadly conditional on the social or reproductive context. These flexible social roles and ‘unconditional’ spatial pair bonds indicate that cooperation may be an important driver of basic social behaviours in hylobatids. In the following discussion, I integrate previously separate aspects of hylobatid socioecology and life history and incorporate ideas developed from discussions of human and avian life history. This holistic and comparative approach emphasises the necessity of considering all aspects of a species’ life history and ecology together, and may explain the distinctive sociodemographic and behavioural characteristics of the small apes.

LIFE IN THE SLOW AND FAST LANES: SOCIAL CORRELATES OF OVERLAPPING OFFSPRING IN HYLOBATIDS, HUMANS AND BIRDS

Life history theory frames the allocation of individuals' limited time and energy to growth, maintenance and reproduction (Gadgil & Bossert 1970; Stearns 1992).

Ecological factors such as food availability and extrinsic mortality risk drive the optimal allocation of time and energy to each function. This framework provides adaptive explanations for differences in the timing of major life events among species. Life history measures scale with adult body size across species; larger mammals take longer to reach maturity, produce fewer offspring and have longer lifespans than do smaller mammals (Purvis & Harvey 1995; Ross & Jones 1999). Life history variables also co-vary independently of body size, such that species with a relatively late age at first reproduction have relatively lower birth rates and relatively longer lifespans (Hawkes 2006; Stearns 1983).

This co-variation persists in primates and produces a contrast between species with 'fast' versus 'slow' life histories (Ross 1988). However, in species with 'slow' life histories, not all life stages are extended equally. The extent to which particular aspects of a species' life history are slowed may reveal the relative importance of particular selective pressures for a slow pace of life in that species. Apes, including hylobatids, have relatively 'slow' life histories for primates of their body size, including longer lactation periods, longer juvenile/adolescent periods and longer adult lifespans (van Schaik et al. 2006). Interestingly, the length of the juvenile/adolescent period in hylobatids is absolutely as long as in the other nonhuman apes (~ 7 years, Table 7.1), despite their much smaller body size (~5.3 - 10.9kg, Leigh & Shea 1995).

Several other characteristics are associated with 'slow' life histories, including: large relative brain size (van Schaik et al. 2006), low adult mortality (Promislow & Harvey

1990), frugivory (and the associated tropical rainforest habitats) (Wiersma et al. 2007; Jones 2011), arboreality (van Schaik & Deaner 2003), and cooperative breeding (Arnold & Owens 1998; Hrdy 2009, p. 197). Hylobatids undoubtedly display the first four characteristics, including two ecological factors that are shared with orang-utans (diet specialising in ripe fruit and strict arboreality). However, despite their overall ‘slow’ life history strategy and the similarity in their ecological niche with that of orang-utans, hylobatids achieve a reproductive rate double that of orang-utans (Barrickman et al. 2008; Table 7.1). This faster reproductive rate may be possible because of their smaller body size, but it contrasts with the other ‘slow’ aspects of their life history, particularly the long juvenile/adolescent period. This contrasting, slow-but-fast life history pattern is believed to be part of the suite of traits that distinguish humans from the rest of the apes (Schwartz 2012), characterised by ‘stacking’ of dependent offspring (Robson et al. 2006; Humphrey 2010; Kramer & Ellison 2010; Schwartz 2012).

Table 7.1. Comparison of birth rate and the juvenile/adolescent period in hominoids

Species	Birth rate (offspring/year) ^{1,2}	Juvenile/Adolescent period (years) ¹
<i>Hylobates lar</i>	0.29	7.1
<i>Homo sapiens</i>	0.31	17.0
<i>Gorilla gorilla</i>	0.26	6.8
<i>Pongo pygmaeus</i>	0.14	7.2
<i>Pan troglodytes</i>	0.17	7.7

¹All data reproduced from Barrickman et al. (2008)
²Calculated as 1/IBI (years)

Despite being noted as a distinctive feature of human life history (Schwartz 2012), ‘stacking’ is difficult to compare across species without a standardised measure. Robson et al. (2006) limit their definition to overlapping *nutritionally dependent* offspring, but note that independently feeding juveniles may still be dependent on other types of parental care. Other authors (Humphrey 2010; Schwartz 2012) use the term more broadly. Herein, I focus on the degree of dependent offspring overlap including

independently feeding juveniles and adolescents as dependents, and refer to this general concept as ‘stacking’. Using this broad definition, most primates exhibit some form of stacking (van Noordwijk 2012), with humans simply being at the extreme end of the scale. Although defining stacking in this way somewhat downplays the distinctive early weaning displayed by humans (producing the characteristic life history period termed ‘childhood’), it allows a comparison with other species that would not be otherwise possible.

Greater stacking of singleton offspring involves shortening of inter-birth intervals *relative* to the length of dependence (Burley 1980). This can be achieved by:

- 1) Shortening inter-birth intervals, or weaning offspring earlier, such that the next offspring is born sooner, OR
- 2) Extending the dependence period of *older* offspring, such that birth intervals are not relatively short, but older offspring are dependent for longer

The important outcome is the increased demand faced by females providing parental care to more than one offspring at a time. Greater overlap in dependent offspring imposes energetic and time constraints on reproductive females, and is therefore linked to the evolution of cooperative breeding in humans (Gurven & Walker 2006; Kramer & Otárola-Castillo 2015). Crucially, stacking differs from multiple births as a mechanism of increasing reproductive rates, because of the mosaic of parental investment required by each offspring (Burley 1980). Older offspring (i.e. juveniles and adolescents) require different types of care (compared to infants) that can potentially be provided by individuals other than the mother. Thus stacking vs. multiple-births produces a divergent parental investment dynamic that has differential consequences for social behaviour. Under certain social conditions, stacking allows prolonged dependency without proportionally prolonged inter-birth intervals.

ESTIMATING THE DEGREE OF OFFSPRING OVERLAP

To measure the degree of offspring overlap requires a comparable definition of dependency on the mother, which varies among species. There are two potential ways to measure the degree of stacking typical of a species, depending on the focus: the first is to estimate for what proportion of the dependent period one offspring is overlapping with at least one other (stacking from the offspring's perspective). This can be estimated by subtracting the length of the lactation period from the length of the entire dependent period, and expressing the remaining time as a proportion of the entire dependency (Table 7.2). Alternatively, measuring stacking from the maternal perspective requires an estimation of how many dependent offspring she is supporting simultaneously. This can be estimated by dividing the entire dependence period by the inter-birth interval (Table 7.1). Estimating the degree of stacking typical of hominoids is currently only possible using female age at first reproduction as the end of dependency. Humans show the greatest degree of stacking using both measures of overlap, and hylobatids come in second (Table 7.2).

Table 7.2 Comparison of reproductive and life history parameters in hominoids

Species	Lactation period (years) ¹	IBI (years) ²	Female age at first reproduction (years) ¹	% Overlap between offspring ³	# Simultaneous offspring ⁴
<i>Hylobates lar</i>	2.9	3.4	10.0	71%	2.9
<i>Homo sapiens</i>	2.5	3.2	19.5	87%	6.1
<i>Gorilla gorilla</i>	3.2	3.9	10.0	68%	2.6
<i>Pongo pygmaeus</i>	6.3	7.0	13.5	53%	1.9
<i>Pan troglodytes</i>	5.4	6.0	13.1	59%	2.2

¹Reproduced from Barrickman et al. (2008)

²IBI = Mean inter-birth interval. Reproduced from Barrickman et al. (2008)

³%Overlap = (female age at first reproduction – lactation period)/female age at first reproduction

⁴# Simultaneous offspring = female age at first reproduction/IBI

Although hylobatids are not so dissimilar from gorillas and chimpanzees in their degree of overlap (Table 7.2), the most meaningful comparison is between hylobatids and

orang-utans, which occupy comparable ecological niches and thus face similar energetic constraints. But calculating the degree of overlap between dependent offspring using female age at first reproduction as the denominator is not ideal, because age at first reproduction overestimates dependency in some species. Better denominators to represent the length of dependency might be the age at dispersal from the mother's territory, the age at independent foraging, or some measure of proximity between mother and offspring, but these data are messier to obtain and thus difficult to compare across species. Furthermore, defining a 'typical' length of dependency is difficult for species in which individuals (and/or sexes) vary in age at independence.

Despite what is suggested by the 53% overlap between offspring calculated using age at first reproduction (see Table 7.2), it is often noted that female orang-utans are generally not able to provide for more than one offspring at once (van Schaik 1999; Strier 2008; van Noordwijk et al. 2012), while hylobatid females are usually accompanied by more than one offspring at a time (average group sizes for species summarised in Malone & Fuentes 2009). So why do hylobatids exhibit this greater stacking of offspring – do they have shortened inter-birth intervals or lengthened dependence periods relative to the other frugivorous nonhuman apes?

STACKING IN HYLOBATIDS

There is some evidence that the lactation period in hylobatids is relatively shorter than that of the other nonhuman apes, but it is difficult to make direct comparisons due to the disparity in body size between the small and large apes and the diversity of diet and social structure among hominoids. Relatively more brain growth is achieved during gestation in hylobatids compared to the other apes (Schultz 1973), meaning that relatively less brain growth occurs post-natally. This would predict that a relatively shorter lactation period is required to support this smaller proportion of brain growth. Accordingly, infancy represents a smaller proportion of the dependent period in

hylobatids than it does in the other frugivorous nonhuman apes (Table 7.3; Reichard & Barelli 2008) and inter-birth intervals are at the lower end of the range for hominoids (Reichard & Barelli 2008; but see Palombit 1995, Table 7.2). This is reflected in the relatively small size of hylobatid weanlings, which is proportionate to that of humans (Table 7.5). Weaning weight in both species is ~2.5 times neonatal weight, compared to the other apes, in which weaning weight is more than 4 times neonatal weight (Table 7.4; Lee et al. 1991). In mammals, weaning weight is consistently ~4 times neonatal weight (Lee et al. 1991).

Table 7.3 Percentage of dependence period spent in infancy and weaning weight/neonatal weight in hominoids

Species	% of dependence period in infancy ¹	Weaning weight/neonatal weight ²
<i>Hylobates lar</i>	29%	2.7
<i>Homo sapiens</i>	13%	2.6
<i>Gorilla gorilla</i>	32%	9.4
<i>Pongo pygmaeus</i>	47%	6.5
<i>Pan troglodytes</i>	41%	4.9

¹Calculated as lactation period/female age at first reproduction, data obtained from Barrickman et al (2008)

² All data reproduced from Lee et al (1991)

Despite this, the duration of lactation in hylobatids is still long for a primate of their body size (Reichard & Barelli 2008). A long period of maternal nutritional support is probably required in hominoids to support the relatively large brain. Hylobatids share a similar relative brain size with the other nonhuman apes (Judge & Carey 2000).

Presumably there is an energetic limit on the minimum length of the lactation period, unless there is substantial provisioning of infants with weaning foods (as in humans, Lee 1996). Hylobatids do not display direct provisioning, but may facilitate earlier semi-independence of offspring by allowing food transfers or co-feeding by weaned offspring. Food transfer attempts are mostly limited to juveniles in captivity (2 - 4 year olds, Chapter 5; Fox 1977; Bricknell 1992), suggesting that the first 2 years post-

weaning are energetically difficult for hylobatid immatures. Parents may further facilitate food transfers by using intra-group contact calls (low level vocalisations) in feeding contexts (pers. obs).

With an energetic limit on the shortest possible inter-birth intervals, offspring stacking in hylobatids must primarily arise from longer post-weaning dependence of older offspring. This long period of post weaning dependence may partially result from hylobatids growing slower and therefore spending relatively more time growing after weaning. This is difficult to assess since data on growth rates in hominoids are conflicting; some data suggest that hylobatids do grow more slowly than the other apes (Leigh & Shea 1995; Mumby & Vinicius 2008) while other data suggest that hylobatids grow faster (Vinicius & Mumby 2013). Again, it is difficult to compare growth rates among hominoids because hylobatids do not undergo growth spurts, and growth in *Pongo* is protracted (in females) or indeterminate (in males, Leigh & Shea 1995). Regardless, there is no evidence that hylobatids grow significantly faster than the other hominoids. That the small body size of hylobatids is believed to be derived (Pilbeam 1996; Ward 2007; but see Alba et al. 2015) indicates that hylobatids have retained the ancestral hominoid pattern of slow growth, disproportionate to the later reduction in body size in this taxon (Reichard & Barelli 2008).

Not all of the long juvenile/adolescent period is taken up by growth; hylobatids in the wild spend at least 8 years growing (Reichard 2003), but do not reproduce until an average of 10 years of age (Barrickman et al. 2008), with the age at first reproduction for some individuals exceeding 14 years (Brockelman et al. 1998). The majority of this time from weaning to first reproduction in hylobatids occurs in the natal territory; there are very few observations of young, solitary individuals (Brockelman et al. 1998). Other hypotheses for delayed maturation in primates invoke the need to learn complicated foraging or social skills (Joffe 1997; Ross & Jones 1999). So far, there is no evidence

that hylobatid foraging requires a long learning period in contrast to the more complicated extractive foraging learned by other hominoids (Chapter 5). Building cognitive maps of resource locations may be important (Asensio et al. 2011), but I have argued elsewhere that learning resource locations in the natal territory is unlikely to be the main selective pressure for prolonged dependency because both sexes disperse (Chapter 5).

Additionally, while hylobatid social organisation is by no means 'simple' (Chapter 1) and learning of social skills may be important (Chapter 5), the slow development of hylobatids is unlikely to be entirely explained by a need to learn social skills. In particular, social skills used within and between hylobatid groups may be cognitively demanding (Grueter 2015), but the rate and scale of monitoring large numbers of dynamic social interactions over time presumably still differs from that seen in large group living primates (Dunbar 1992). In this context, the long post-weaning period in hylobatids is puzzling, and requires further explanation.

I suggest that access to parental resources is crucial for juvenile/adolescent hylobatids and therefore parents have been selected to tolerate delayed dispersal by older offspring. While immature hylobatids can mechanically feed independently well before the end of body growth (Chapter 5), they would be unable to defend their own resources at this point, and still rely on parents to know where to forage (Brockelman & Srikosamatara 1984). This is less of a problem for orang-utans, chimpanzees and gorillas in which resources are more widely shared and less fiercely defended (Watts & Pusey 1993). Both the retention of slow hominoid patterns of growth (despite later reductions in body size) and the reliance of older offspring on parental resources result in a long post-weaning period of dependence. Ordinarily, this slow development of older offspring should limit female reproductive rates (Charnov & Berrigan 1993), but inter-birth intervals in hylobatids are not extended to the same degree as the juvenile/adolescent

period, resulting in greater stacking of offspring. Herein, I argue that in hylobatids, like humans, this greater overlap in dependent offspring is facilitated by social and life history adaptations.

A family-living social structure involving long-term pair bonds, parental tolerance of delayed dispersal by older offspring and flexible social roles of family members facilitate the pooling of individual effort within a group (Reiches et al. 2009). In particular, the extension of the post-weaning period of development minimises the daily cost of reproduction for females as well as minimising offspring mortality. This suite of characteristics might therefore allow faster and cheaper reproduction in hylobatids than would be otherwise possible for a frugivorous ape in a tropical/subtropical rainforest habitat. In the following paragraphs, I outline how all of these elements result in stacking of dependent offspring in hylobatids (outlined in Figure 7.1) and relate this to other species that show offspring stacking as a result of prolonged dependence of older immatures.

RETENTION OF SLOW GROWTH

The retention of slow growth in hylobatids may be related to their large relative brain size and general ecological niche. Temporally unpredictable resources favour a risk-averse growth strategy (Janson et al. 1993; Wiersma et al. 2007; Jones 2011). Growing slower reduces the daily energy costs associated with growth and thus can reduce the impact of food shortages on juvenile mortality rates. This may be important considering that hylobatids are primarily frugivores (Elder 2009) and unpredictable temporal variation in fruit availability is observed in wild hylobatid habitats, at least in the tropical and subtropical regions (Malone et al. 2012; Lappan 2010). In addition, compared to the larger great apes, metabolic running costs are presumably higher given their smaller body size (Kleiber 1932). The slow growth of hylobatid immatures

therefore reduces the daily energetic investment by individual offspring into their own growth.

Importantly, selection for slow growth not only influences the length of time taken to reach maturity, it also influences the daily energetic cost of reproduction for mothers. There are three general strategies through which female primates support some of the costs of reproduction: increasing energy intake, using somatic energy stores, or reducing energy expenditure during reproductive events (Dufour & Sauther 2002; Brockman & van Schaik 2005). Increased energy intake is subject to predictable periods of food abundance, and this is an unfeasible solution for primates for whom gestation and lactation periods exceed seasonal food abundance periods, or for whom food abundance fluctuates unpredictably (Brockman & van Schaik 2005).

Potential for somatic energy storage may be more limited in hylobatids than in the other apes due to the physical constraints imposed by their brachiating locomotion and suspensory feeding niche (Hollihn 1984; Swartz 1989). Storage of energy in the form of fat to sustain pregnancy and lactation may therefore not be an option for hylobatids if significant weight gain reduces foraging and travel efficiency. In addition, although reproductive females do show some energy conserving behaviour patterns (Lappan 2009; Chapter 3), the large proportion of time spent travelling by hylobatids to obtain food could limit female options for reducing energy expenditure. The efficient goal-oriented travel methods of hylobatids may reduce the impact of this problem for females (Asensio et al. 2011). Nonetheless, it is clear that the capital required for the growth of offspring cannot solely come from maternal energy stores.

Similarly, in most other primates, the total cost of offspring growth cannot be entirely supported by maternal somatic energy stores (Emery Thompson 2013). The length of the juvenile (post-weaning) growth period therefore becomes important in considering

the cost of reproduction for females (Leigh 2004). Female caloric investment in offspring growth is achieved via gestation and lactation. Thus, the length of the gestation and lactation periods *relative* to the length of the growth period determine the percentage of offspring growth that is directly energetically supported by the mother. The slightly shorter lactation period (as a proportion of the entire dependence period) in hylobatids compared to the other frugivorous nonhuman apes (see Table 7.2) reduces the total energy cost of supporting offspring growth (per offspring) for females (Figure 7.1). This allows more of the cost of growth to be subsumed by offspring themselves (as in humans, Kramer & Ellison 2010).

Consideration of this developmental pattern as a whole highlights that growth remains slow in hylobatids without proportional extension of the period of exclusive maternal care, and this minimises both total *and* daily investment into reproduction per offspring for females (Figure 7.1). Slow growth and reduced female investment can therefore explain how female hylobatids support their reproductive efforts, despite minimal opportunities to increase food intake, with constraints on energy storage, and with limited opportunities to reduce activity levels during pregnancy and lactation.

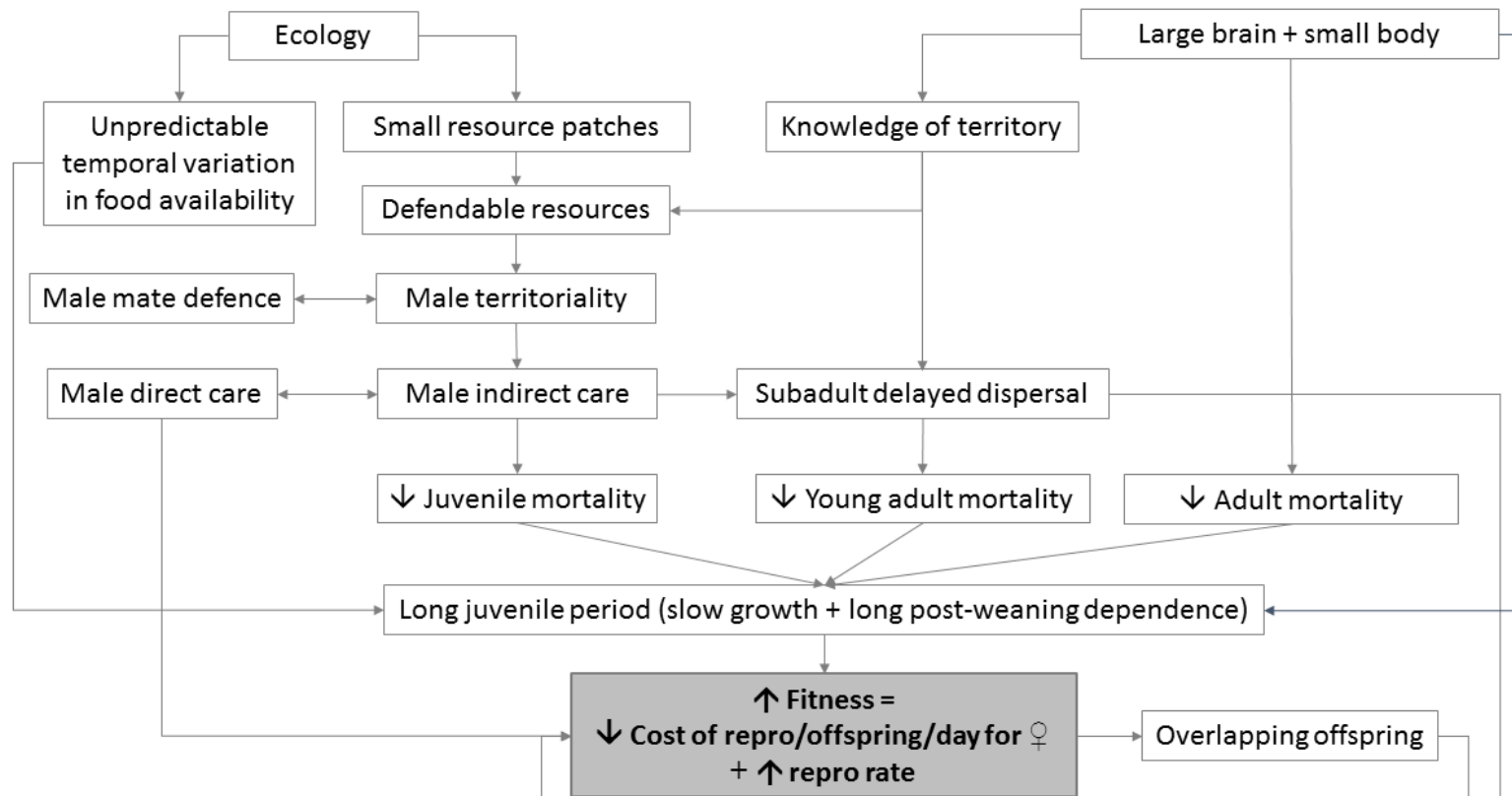


Figure 7.1 Factors facilitating low cost of reproduction without a slower reproductive rate in hylobatids. Double arrows reflect potential trade-offs for males.

SLOW GROWTH AND DELAYED DISPERSAL REQUIRE A SAFE AND CHEAP HOME

A slow rate of growth and delayed dispersal prolong the attainment of complete independence in offspring and could increase mortality risk, due to the lower competitiveness and efficiency of small juvenile primates in feeding contexts (Janson et al. 1993). This is particularly important in hylobatids because of their exploitation of defensible patches of food, and the aggressive territorial behaviour of adults. The predictable geographic location of fruiting trees, coupled with the capacity for spatial memory allows territorial defence for exclusive access to food (Brockelman 2009; Asensio et al. 2011). Maternal and paternal knowledge of the territory (Brockelman 2009) presumably reduces the cost of locating resources for semi-dependent offspring and delayed dispersers (Schuppli et al. 2012; Figure 7.1). In addition, territorial defence by adults ensures exclusive access to resources for offspring, allowing hylobatids to utilise long post-weaning dependence as an adaptation to resource uncertainty and intense between-group competition for access to resources (Figure 7.1).

Furthermore, although slow growth may be favoured in tropical rainforest habitats through reduced risk of starvation, slow growth is unlikely to be selected for unless other extrinsic mortality risks are also low (Kaplan et al. 2000; van Schaik et al. 2006). In addition to allowing exclusive access to resources, territorial resource defence by adult hylobatids may also reduce juvenile mortality by providing a safe environment in which offspring can grow (Figure 7.1). Protection from aggressive conspecifics and predation comes along with territorial resource defence to an extent. Greater vigilance by adults can further subsidise the cost of growth by allowing immatures to spend less time being vigilant, which frees up time for other activities (Heinsohn 1991; Janson et al. 1993; Griesser 2003). Other predation-avoidance behaviour of parents can directly decrease predation risk for juveniles (e.g. decoy behaviour of male Kloss' gibbons, Dooley & Judge 2014). Moreover, the large relative brain size (van Schaik et al. 2006)

and strict arboreality (van Schaik & Deaner 2003) of hylobatids limits the cost of slow growth to future reproduction by reducing adult mortality risk (Figure 7.1). Low extrinsic adult mortality can be estimated from the occurrence of age-related death (Robson et al. 2006); observations of “old adults” indicate that many hylobatids live long enough to show age-related frailty (Carpenter 1964, p. 211; Reichard 2003; Fan et al. 2015).

Although adult territorial defence reduces juvenile mortality *within* the natal group, the territorial aggression by established hylobatid groups increases mortality risk for dispersing young adults. Adolescent and subadult hylobatids have higher rates of mortality compared to younger immatures (Palombit 1999). This mortality risk presumably arises through increased risk of lethal attacks from conspecifics and reduced access to food resources controlled by those aggressive conspecifics (Emlen 1984; Strier 2008). Likewise, the low adult mortality that allows slow growth contributes to long-term habitat saturation that limits dispersal opportunities for grown offspring (Emlen 1982a; Arnold & Owens 1998). Parents and relatives should therefore be more tolerant of young adults than are unrelated individuals (Ekman et al. 2001).

Hylobatid parents are often noted to be aggressive towards maturing offspring (Crandall 1964; Aldrich-Blake & Chivers 1973; Chivers 1974; Chivers & Chivers 1975; Fox 1984; Lappan 2005; Bartlett 2009a), but many offspring delay dispersal beyond reaching adult size (Srikosamatara & Brockelman 1987; Brockelman et al. 1998; Huang et al. 2013; Dooley 2015) and co-dispersal of related individuals has been observed in at least one population (Fan et al. 2015). Delayed dispersal, and co-dispersal of related individuals may reduce early adult mortality, and thus provide additional reductions to overall mortality that allow slow life histories in hylobatids (Figure 7.1). Even in species that do not have to learn complex foraging skills during the juvenile period, remaining in the natal territory for longer and continuing to associate with parents is

advantageous for offspring because the alternative is both dangerous and less efficient (Kokko & Ekman 2002).

THE IMPACT OF RESOURCE DEFENCE ON REPRODUCTIVE ENERGY/ACTIVITY BUDGETS

Given that a low mortality environment allows slow growth and a long period of post-weaning dependence in the natal territory (Figure 7.1), parental investment requires not only direct care of offspring but also territorial defence. Although reproductive roles are limited in mammals by exclusively female gestation and lactation, other aspects of parental care can be taken on by individuals other than the mother. Both direct care of offspring and territorial defence must then factor into the energy and activity budget of a reproductive unit. A reproductive unit could consist of a single female, a male and female pair, or a larger social group, depending on the costs and benefits of social tolerance (Gaston 1978). Investment into both aspects of parental care could be achieved in several ways in hylobatids, each differing in the implications for social group structure, individual activity budgets, and participation in direct parental care:

- 1) females balance time and energy between resource defence and direct offspring care (enabling males to adopt a roving strategy)
- 2) breeding pairs (and additional group members) share resource defence and direct offspring care evenly
- 3) breeding pairs (and additional group members) share resource defence and direct offspring care via a division of labour

Option one does not seem to occur in hylobatids, as evidenced by the lack of lone females defending territories (Raemaekers & Chivers 1980, p. 291; Palombit 1994a; Brockelman 2009). There may be two reasons for this: firstly, the investment into both territorial/ indirect offspring defence and direct parental care required for successful reproduction might exceed that possible within a single individual's activity budget.

Investment into direct parental care and territorial resource defence impose differential constraints on individual activity budgets. Direct parental care may involve substantial energetic investment in offspring (via feeding, carrying or play), while territorial resource defence is more likely to involve time costs and increases in mortality risk (vigilance and participation in defensive behaviours). Some evidence suggests that the investment required for defending large, low quality territories (as well as direct parental care) may even exceed two activity budgets and promote polyandry in some hylobatid populations (Savini et al. 2009). The cost/benefit ratio for cooperative resource defence depends on both the cost of social tolerance (increased feeding competition within the group) and the benefit to defence effectiveness obtained through cooperation.

Secondly, a single adult individual engaging simultaneously in resource defence and direct parental care may reduce the effectiveness of both activities and significantly increase offspring mortality risk. In most vertebrates, territorial defence is incompatible with direct care of offspring due to the interaction between circulating testosterone levels and their influence on territorial compared to parental behaviour (Wingfield et al. 1990). In birds, more frequent aggressive male-male interactions are associated with higher testosterone levels, while paternal care is associated with low testosterone levels (Wingfield et al. 1990). *Symphalangus syndactylus* males who carry infants have lower androgen levels than males who do not carry infants (Rafacz et al. 2012; Morino 2014). However, males in groups containing infants have higher testosterone levels than males in groups without infants (Morino 2014). Similarly, androgen levels in hylobatid fathers are higher than those in non-fathers (Barelli & Heistermann 2012). This evidence indicates that higher testosterone levels may be important for territorial defence (particularly when offspring are present), but incompatible with direct care of offspring in the form of infant carrying. With greater overlap in births compared to other

nonhuman apes, female hylobatids spend more time caring for small, vulnerable offspring throughout their reproductive lifespan. Females may therefore be unable to effectively engage in territorial defence *and* maintain their reproductive rates (Mitani 1987; Bartlett 1999).

Two options involving allocation of territorial defence and direct offspring care duties over two or more individuals remain. Hylobatid social structure (minimum two-adult groups) allows pooling of individual efforts, such that participation in territorial resource defence by males or other group members can reduce female investment into territorial resource defence. Option two predicts that males and females (and other group members) are equally likely to engage in resource defence or direct care of offspring, but this also does not seem to occur in hylobatids. Despite the potential for participation in direct care provided by the two-adult grouping pattern, male participation in direct care of offspring is low in hylobatids (see Chapter 3). This is the case even when food and territories are assured, as in captive groups (Chapter 3). This suggests that option three most closely resembles the hylobatid strategy.

THE ROLE OF HYLOBATID FATHERS

Selection for allocare of infants is presumably low in hylobatids where the ratio of infant's/mother's weight is low (Wright 1990), especially if the daily cost of reproduction for females is lowered via the slow growth and long post-weaning dependence period outlined above (Mitani & Watts 1997). Similarly, in humans, females do not necessarily require help for infant care, but rather in caring for older dependent offspring (Kramer 2005). This partially explains the overall lack of direct care of infants seen in hylobatid males, compared to males of other socially monogamous species. The exceptions that prove the rule are the siamangs (*S. syndactylus*), which grow faster than the smaller gibbons (Mumby & Vinicius 2008), particularly during infancy (Leigh & Shea 1995), and in which males sometimes

contribute to infant transport (Lappan 2008; Morino 2014). Male hylobatids overall participate more in territorial defence and are more vigilant than females (Chivers 1974; Gittins 1980; Brockelman & Srikosamatara 1984; Palombit 1993; Orgeldinger 1997; Reichard & Sommer 1997; Heine & Geissmann 2000; Bartlett 2003; Brockelman 2009). Although gibbons do not actively “patrol” territorial boundaries (independent of foraging activity), responding to territorial intrusions requires a) vigilance and b) the time and energy involved to engage in neutral or aggressive inter-group encounters (Morino 2009). This investment by males into territorial defence competes with and renders males unsuitable for direct care of offspring (Figure 7.1).

It is argued that male territorial defence solely functions for mate guarding or infanticide prevention and not for resource defence, because territorial aggression by males is mostly intra-sexual (Reichard 2003; van Schaik & Kappeler 2003). However, males do sometimes chase neighbouring females, and aggression towards neighbouring females may not be necessary to defend resources if females otherwise avoid each other or if females avoid neighbouring males (Brockelman 2005). Furthermore, defence of resources and mate defence or infanticide prevention by males may be incompatible (Brockelman 2009); mate guarding and infanticide prevention require monitoring of and proximity to the mate and infant respectively, whilst resource defence requires attention to extra-group individuals and decreases proximity between mates (Reichard & Sommer 1997; Bartlett 2009a, p. 104). The trade-off between resource defence and mate defence has implications for the paternity confidence of male hylobatids in the form of extra-pair copulations (Palombit 1994b; Reichard 1995; Reichard 2009; Huang et al. 2013). Longitudinal research on hylobatids reveals that some hylobatid families are blended families, rather than the previously assumed nuclear families (Palombit 1994a).

A high rate of turnover in group membership (Sommer & Reichard 2000), combined with decreased paternity confidence may select against direct paternal care in

hylobatids. Together, these factors produce a division of labour in which the default male behaviour is to engage in territorial (resource and mate) defence, and avoid direct care of offspring (Figure 7.1). Male participation in territorial defence further reduces the cost of reproduction for females because it reduces the need for direct protection of all offspring against predators and conspecifics. Importantly, male participation in resource defence may come at the cost of mate defence (Figure 7.1), suggesting that the reduction in the cost of reproduction provided by male-female cooperation outweighs the potential cost to male paternity certainty.

PARALLELS WITH OTHER SPECIES THAT STACK OFFSPRING BY EXTENDING THE JUVENILE/ADOLESCENT PERIOD

Many of the life history and social adaptations discussed herein for hylobatids parallel those of other species that stack offspring, notably: humans (Mace & Sear 2005; Robson et al. 2006; Hrdy 2005; Hrdy 2007; Hrdy 2009; Reiches et al. 2009; Kramer & Ellison 2010; Kramer & Otárola-Castillo 2015), other *Homo* (Kaplan et al. 2000; Robson & Wood 2008) and many tropical and southern hemisphere birds (Martin 1996; Langen 2000). Life history features common to these species include a long juvenile period of dependence incorporating a reliance on parental resources, slow growth and short inter-birth intervals relative to the length of dependence (Robson et al. 2006; Kramer & Ellison 2010; Figure 7.2). Together, these life history characteristics produce greater overlap in dependent offspring *without* increasing the daily cost of reproduction per offspring for females (Aiello & Key 2002) and *without* increasing offspring mortality (Hrdy 2005). I argue here that this is made possible by the cooperative and flexible nature of social behaviour in hylobatids as it is in humans and many birds (Figure 7.2).

The life history features outlined above occur in combination with social characteristics, including: cooperative group living, division of labour within the group and variable,

complementary social roles (Figure 7.2). Delayed dispersal in birds is almost always associated with cooperative breeding, but cooperative breeding in the strict sense is not an inevitable outcome of this life history strategy (Ekman et al. 2001). Recognition of cooperative breeding as a social and reproductive system originated in birds, and was later developed for mammals (Solomon & French 1997; Hatchwell 2009). Cooperative breeders usually exhibit reproductive skew, such that reproduction is usually limited to a single adult pair, and other group members (termed allocarers) provide ‘help’ that contributes to the development of the resulting offspring (Solomon & French 1997). Definitions of *allocare* and cooperative breeding vary; some authors limit the definition to species in which helpers forego personal reproduction and provide substantial direct provisioning and transport of young offspring (Lukas & Clutton-Brock 2012), while others define the terms more broadly (Hrdy 2007; Kramer 2010).

Across species, cooperative breeding is associated with increases in reproductive rates when compared to independent breeding (Cockburn 1998; Isler & van Schaik 2012). It is hypothesised that cooperation allows the evolution of faster reproduction by lightening the load on the female (Isler & van Schaik 2012). Faster reproductive rates, or greater production of offspring can be achieved through increasing litter size, decreasing the time between births, decreasing the age at maturity or increasing the lifespan (Ross 1988). The ‘helping’ behaviours and/or life history adaptations that allow each of these strategies are likely to differ depending on the ecological and energetic context. The expression and regularity of infant care behaviour presumably depends on both the opportunities available to allocarers and the relative benefit of each behaviour to reproductive females.

Provisioning and carrying behaviours may be more common in the “fully-fledged” cooperatively breeding species (*sensu* Hrdy 2009) because of greater opportunities for food provisioning (e.g. in birds and canids) or faster postnatal growth rates (e.g. in

Callitrichids, Ross 1991; Mitani & Watts 1997; Mumby & Vinicius 2008). Faster growth may be more advantageous for small new world primates because of higher predation risk (Mitani & Watts 1997). Humans do show some direct provisioning of infants by allocarers because offspring are weaned relatively early, but humans – like hylobatids – have also prolonged the juvenile/adolescent period of dependence. Importantly, growth rates are relatively slow in both species. In the absence of selection for fast growth, extensive participation in infant caregiving behaviour by helpers is less beneficial, because the daily cost of infant caregiving for females is lower. However, this does not mean that in the absence of allocare of infants that alloparents cannot influence the reproductive rates of primary breeders.

Importantly, greater stacking of offspring as a result of the extension of the juvenile/adolescent period relies on different forms of allocare, beyond infant caregiving. This particular form of stacking is facilitated by other cooperative behaviours and a division of labour that can result in facultative paternal and allocarer involvement in direct care of infants and older offspring (Hrdy 2005; see also chapters 5 & 6 of Hrdy 2009). For example, in pied babblers, helpers provide care for fledged young while breeders invest in a new brood (Ridley & Raihani 2008). Similarly in humans, fathers and other allocarers provide food for older offspring (Kramer 2010; Kaplan et al. 2000), babysitting (Wells 2012), socialisation (Morelli & Tronick 1992; Geary 2000; Lamb 2010) and alliances that benefit offspring later in life (e.g. improving access to mates or resources, Hames 1992). In humans, recognition of these social characteristics contributed to their inclusion with other cooperatively breeding species (Lovejoy 1981; Hrdy 2005; Hrdy 2007; Hrdy 2009; Isler & van Schaik 2012). However, ideas about humans as cooperative breeders took some time to emerge (Hrdy 2009, p. 179), perhaps due to the historical focus on mother-child attachment (Hrdy 2005) and differences in the extent and type of care provided by allocarers.

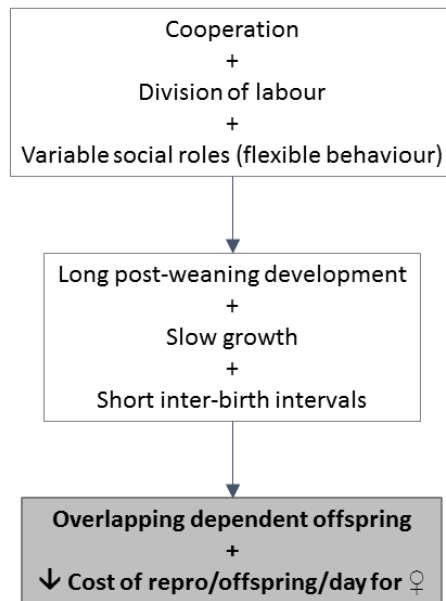


Figure 7.2 Life history and social characteristics in hylobatids and humans that produce greater overlap in dependent offspring and decreased cost of reproduction for females per offspring per day.

In other cooperatively breeding species, allocarers contribute to offspring development and the cost of reproduction for females in other ways, beyond infant care (see Table 7.3 for cooperative behaviours noted in cooperatively breeding primates, and in hylobatids). For example, although human females do receive some help with infant care, they also receive help with balancing the demands of older and younger offspring simultaneously, as well as with the demands of foraging and other activities (Kramer 2005). Some human mothers adjust time spent caring for older children and reduce foraging work when pregnant or lactating, rather than adjusting time spent caring for younger children (Kaplan et al. 2000; Kramer 2005). Human females are therefore able to reduce their investment in other activities without compromising on energy balance and reproductive rates (Kramer 2010). This is made possible by cooperative social groups and behavioural flexibility (Hrdy 2005; Hrdy 2009).

Table 7.4 Cooperative behaviours (and their associated life history characteristics) observed in 'cooperatively breeding' Callitrichidae, Homo, and in hylobatids

	Callitrichidae	Homo	Hylobatidae
<i>Behaviour</i>			
Substantial infant transport	✓	✗	✗
Active infant provisioning	✓	✓	✗
Babysitting	✓	✓	✓
Cooperative resource defence	✓	?	✓
Cooperative vigilance	✓	?	✓
Cooperative resource collection	-	✓	-
<i>Life history characteristics</i>			
Larger litter size	✓	✗	✗
Fast offspring growth	✓	✗	✗
Shorter IBI (and/or stacking of singleton offspring)	✓	✓	✓

The cooperatively breeding Callitrichidae also show this general cooperative behaviour and flexibility in social roles on top of their infant caregiving behaviour (Koenig & Rothe 1991; Burkart et al. 2009; Table 7.3). Likewise, allocarer contributions in other cooperatively breeding species go beyond provisioning, but are discussed less often, perhaps because they are more difficult to measure (Emlen 1984; Arnold et al. 2005). In hylobatids, the presence of a male in the social group at all times allows the shifting of thermoregulatory care of older offspring to males (Chivers 1974, p. 183; Fan & Jiang 2008; Lappan 2008; but see Reichard 1998), and there is a capacity for other individuals to provide this service also (e.g. subadult offspring, Chapter 6). Thus social monogamy and a division of labour facilitates stacking in hylobatids in the same way that cooperative breeding and a division of labour facilitate stacking in humans and birds.

The presence of additional older offspring, or additional adults in the group in hylobatids allows further sharing of direct care of juveniles or sharing of territorial resource defence (Figure 7.1; Chapter 5; Chapter 6). The contributions of these other individuals could constitute cooperative breeding despite a lack of provisioning if it can be shown that participation is costly to the performer and has an impact on the fitness of

the breeding pair. It could be argued that greater overlap in dependent offspring is associated with group living in a broader sense, since weaned offspring benefit from the protection afforded by group vigilance and territoriality in any social species (Schuppli et al. 2012). For brevity, I limit the scope of this discussion to a family-living social context, adding that participation in allocare is predicted to increase with relatedness (Emlen & Wrege 1988). This reproductive strategy may be understood further by using the pooled energy model proposed by Reiche et al. (2009) for human reproduction. The pooled energy model does not focus solely on the female's energy budget over time, but incorporates the behaviour of other group members, as well as selection on other life history stages (e.g. the length of the post-weaning period of dependence) to explain life history and reproductive patterns in humans (Gurven & Walker 2006; Kramer & Ellison 2010; Kramer & Otárola-Castillo 2015).

Humans are more easily classified as cooperative breeders because juvenile/adolescent offspring are almost entirely dependent on food collected cooperatively by adults. However, the reliance on parental resources by juvenile/adolescent hylobatids produces a similar parental investment dynamic and opportunities for allocare by others. The important conclusion is not that human or hylobatid females would be unable to reproduce without the aid of others, but that the presence and help of others allows females to reproduce faster than would be otherwise possible, regardless of the nature of that help. The pooling of energy budgets involving a division of labour and flexible behaviour is a particularly important concept for two reasons:

- 1) It provides a framework for exploring variation in behaviour and life history within (and among) species, and
- 2) The associated outcome of cooperation and coordination informs discussion about social behaviour within hylobatid groups.

IMPLICATIONS FOR THE PAIR BOND

The impact of male resource defence (and some direct care of juveniles) on female activity budgets is important to establish for any discussion of the evolution of social monogamy in hylobatids. If the activity of monogamous males allows greater offspring stacking by their mate, then the cost of being monogamous (rather than defending multiple female territories) is offset by the increase in reproductive rates. However, this hypothesis is difficult to test in the wild because males already do the majority of the territorial defence. As with hypotheses surrounding infanticide avoidance, if an efficient social system evolved in the past to prevent a particular behaviour (in this case resource defence and care of older offspring by females), then the behaviour is unlikely to be seen in extant groups (van Schaik & Kappeler 2003). There are some predictions that could be tested depending on the variation observed:

- 1) Groups in which females are seen to be contributing to territorial resource defence will be those in which males are contributing less,
- 2) Territorial resource defence by females may occur more frequently when females are not reproductively active, compared to when they are,
- 3) Groups in which females participate more in territorial resource defence over their reproductive lifetime will have lower reproductive rates than groups in which females participate less.

The pooled energy model also has implications for the appearance of the social pair bond. By definition, pair bonds are strong social bonds between a single male and female. However, the degree of social investment by both individuals may depend on the ultimate explanation for this social relationship. While a two-adult grouping pattern (with a male and female occupying the same territory) *allows* the formation of long-term social bonds between the breeding pair, it does not necessarily *predict* that pairs travel together or engage in overt social interactions, or that the degree of affiliative

behaviour has an impact on reproductive success. In fact, ecological constraints in the wild may favour low levels of social interaction due to the impact on time budgets (i.e. this may represent a trade-off with male territorial defence) and predation risks associated with activities that narrow focus (like grooming and play). If hylobatid pair bonds are cooperative in nature, and are important for maintaining the production of overlapping offspring, then the method by which proximity between the adult pair is maintained may be unimportant, as long as it results in coordinated behaviour.

If coordination is the most important outcome of the hylobatid pair bond, searching for pair maintenance behaviours universal to hylobatid pairs may be fruitless. For example, the formation of territorial two-adult groups accurately predicts some pair bonding behaviours in hylobatids, such as duetting and mutual display against neighbouring groups (Cowlshaw 1992). However, duetting is absent in two hylobatid species (*H. moloch*, Geissmann & Nijman 2006; *H. klossii*, Dooley et al. 2013), despite the overall homogeneity in ecology and social organisation. Interestingly, loud songs in both species still involve joint participation by mother/daughter pairs (in *H. klossii*, Dooley et al. 2013) or the entire group (in *H. moloch*), so they still function as mechanisms that maintain group cohesion. In addition, in *H. klossii*, the male and female songs are temporally separated, but the male remains with the female while she sings, without forming a duet (Dooley et al. 2013). This indicates that cohesion within pairs is not solely reliant on duetting behaviour (Dooley 2015) and therefore that there is more than one way to achieve joint territory defence.

Selection for “coordination” between mates *per se* as a driver of pair bonding predicts two things:

- 1) the frequency of social interactions between pair mates should be high during introduction and decrease with time together and

2) pair coordination should increase over time.

Notably, coordination does not necessarily imply spatial or social proximity. More frequent duetting in new pairs compared to more established pairs provides some evidence for the first prediction (Chapter 2; Geissmann 1986; Dooley & Judge 2007). Similarly, while I did not specifically measure coordination or synchrony of behaviour, more established pairs showed more equal responsibility for maintaining proximity to their mates than did newer pairs (Chapter 2). Likewise, Kaplan et al (2000) suggested that “complementarity” may form the basis of human pair bonding, and that this difference results in a partnership between men and women that is discontinuous with the other apes. Clearly more research is needed to determine whether hylobatid pair bonds are an exception to this rule, and whether hylobatid pair bonds, like those of humans, are inherently flexible relative to local factors.

IMPLICATIONS FOR PARENT-OFFSPRING RELATIONSHIPS

Cooperative pooling of energy/activity budgets may also decrease the cost/benefit ratio of delayed dispersal by grown offspring, further promoting the cycle of long post-weaning dependence that allows slow growth (Figure 7.1). Although subadults benefit from contributing to their natal family through inclusive fitness benefits (Chapter 5), these fitness benefits may not always outweigh the cost of parents sustaining an extra adult sized individual in the group (Ekman et al. 2004). This could explain some of the variation in parent-offspring aggression observed in wild groups (Chivers 1976; Bartlett 2003; Lappan 2005). The benefits of philopatry to both subadults *and* parents increase if subadults are able to reduce the investment of parents into any of parental care, territory defence or predation avoidance. For example, participation in group activities (such as singing and territorial defence) or allocare (e.g. playing with younger siblings) may constitute a form of ‘rent’ that reduces the cost to parents of delayed dispersal by

offspring (i.e. greater feeding competition), and facilitates access to natal territory resources for subadults (Gaston 1978; Cockburn 1998).

‘Rent’ could take many forms in hylobatids including contribution to territorial defence, vigilance for predators, grooming, and direct care of younger siblings (Chapter 5). I could not distinguish between the effect of younger and older siblings on juvenile behaviour, but juveniles with siblings showed more mature behaviour and interacted less with parents (Chapter 6). Future research on juvenile hylobatids with and without older siblings could assess the direct impact of older offspring on younger sibling development. Although the active participation of subadults could simply result from kin selection via *additional* increases in the fitness of parents and siblings, the ‘rent’ hypothesis specifically predicts a complementary impact of subadult behaviour on parental activity budgets, that is:

- Participation by subadults in alloparental or group defence should result in decreased participation by parents in the same activities.

Any analysis of the contributions of older offspring must therefore incorporate the effect on parents as well as the effect on the development of younger siblings. That both parents participate less in social play with young offspring when older siblings are present supports this complementary prediction (Chapter 3). In addition, older offspring direct their social activities towards younger siblings when they are present, and reduce their own social interaction with parents (Chapter 6). Parents participate in social play with offspring within the group, but not during peaceful intergroup encounters in which offspring play with neighbouring immatures (Reichard & Sommer 1997). In one wild *H. lar* group, parents played more with their infant after their subadult offspring dispersed (Brockelman et al. 1998). In this way, the behaviour of subadults functions not as *additional* fitness benefits (which would predict unchanging parental effort), but

functions as coordination of activity budgets between parents and offspring. This hypothesis is similar to reproductive skew theory in which dominants concede some reproduction by subordinates to incentivise their help (Emlen 1982b; Reeve et al. 1998), but provides a contrast in which offspring concede participation in care or defence for continued access to the natal territory (Gaston 1978).

If allocare by subadults additionally increases parental tolerance of their presence, subadult behaviour may also allow longer exploitation of the natal territory when other breeding options are limited (Balshine-Earn et al. 1998; Bergmüller & Taborsky 2005).

This is supported by observations that parental aggression towards subadult offspring was not higher when younger siblings were present, and in fact showed a trend towards decreased rates of aggression, compared to when siblings were absent (Chapter 6).

Similarly, MacKinnon and MacKinnon (1977) note a subadult male *H. lar* who was temporarily tolerated by his father (following his initial peripheralisation) during an extreme territorial contest with a neighbouring group. Parental tolerance may also be garnered by subadults adjusting their behaviour to avoid conflict, for example acting less adult-like and engaging in overt signals of subordination. There is some preliminary evidence suggesting that social maturation is delayed for individuals in the natal group, compared to same-aged individuals that have dispersed (or been removed from the natal group in a captive setting, Chapter 4).

Behavioural maturation begins between the ages of 4 and 6 in captivity, while offspring are still growing (Chapters 4 & 5). However, the continued social activity of the adult-sized offspring in the current study suggests that they remain socially “immature” after reaching adult size, at least when they remain in the natal group. Subadults are similar to breeding adults in the time that they devote to maintenance activities (including resting, feeding and solo play, Chapter 5). In contrast, the proportion of time that subadults spend in social activities is more similar to younger offspring, including

greater participation in social play, lower participation in grooming activities, and lower frequencies of aggression, relative to adult activity levels (Chapter 5). This pattern of behaviour within the natal group may explain how some subadults are able to stay at home for extended periods of time after growth is complete, despite the frequency with which parent-offspring aggression is recorded by researchers. Anecdotal reports of submissive or reconciliatory signals in the current study and other captive and wild groups of hylobatids suggests that this is a promising area for future research (Ellefson 1974; Baldwin & Teleki 1976; Gittins & Raemaekers 1980; Lappan 2005, p. 121).

IMPLICATIONS FOR FAMILY DYNAMICS

Successful cooperation may be unique to each pairing experience or each group composition and presumably has to be learned and/or refined (Burkart & van Schaik 2010). Similarly, social roles for a particular individual presumably depend on the group composition and the behaviour of others (Koenig & Rothe 1991). In humans, social roles within groups vary in time depending on current food availability and mortality risks (Kaplan et al. 2000). Interestingly, this might mean that social relationships not only differ between species and populations, but among groups as well. If individuals are very different when pairs form, the pair bond may at first appear to be one-sided, and become more equal with longer time together. The initial mismatch in activity and in each individual's response to their mate's social advances could create tension that increases the frequency of aggression during pair formation (Chapter 2). Similarly, antagonism between parents and mature offspring may reflect that offspring are required to learn how to coordinate their behaviour with other individuals. If each individual adjusts its behaviour to either more closely approximate the other individual, or to reduce conflict, then coordination between the individuals should improve and conflict will be transient.

The flexible behaviour that allows this cooperative social organisation to exist therefore creates intra-group and extra-group variation in the appearance of social relationships. The conclusions presented here suggest that social monogamy may be important for both sexes in hylobatids but that it reflects a partnership involving division of labour and facultative participation in otherwise sex-specific behaviours. Likewise the prolonged development of hylobatid offspring reflects a fundamentally ‘slow’ life history, but variation in maturation and reproductive rates indicate significant individual plasticity in the pace of life. I suggest that this plasticity results in substantial variation in social behaviour among individuals and groups. Future research should focus on mapping the changes in social relationships within hylobatid families over time and in different contexts with a focus on coordination. Some of this can be assessed in captivity as I have shown, but longitudinal field studies are increasingly important for understanding the relationship between ecology, life history and social organisation. In particular, the impact of resource defence and predation avoidance and their contribution to pooled energy budgets are difficult to assess in captivity and must be explored in the field.

CONCLUSION

The slow life history and social organisation of hylobatids involving differentiation of roles within the family may increase female reproductive rates by allowing females to produce more offspring at reduced individual cost to the female. For example, the slow growth and long post-weaning dependence of hylobatid offspring reduces the total and daily energetic cost of reproduction for females. In addition, the greater role played by male hylobatids in resource defence reduces female investment in resource defence, thereby releasing energy for reduction of inter-birth intervals. The tendency to form small breeding units (vs solitary females or large groups) may allow these characteristics, and facilitate pooling of parental care and resource defence duties across

the entire group's activity budget. The required parental investment by each parent at a particular point in time may depend on the current energetic load of the breeding female and the presence and investment of other group members (e.g. older siblings or additional adults). Therefore, flexible behaviour may enable pooled energy- and time-budgets and contribute to variation in social behaviour among hylobatid groups. The application of this framework leads to the counter-intuitive conclusion that paternal avoidance of direct offspring care, asocial pair bonds, and delayed dispersal might be adaptive rather than aberrant for these enigmatic primates.

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APPENDIX A

RESEARCH AND ETHICS APPROVALS

IN CONFIDENCE

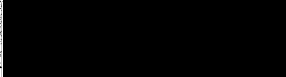
THE UNIVERSITY OF WESTERN AUSTRALIA

OW

ANIMAL ETHICS COMMITTEE OBSERVATIONAL / WILDLIFE FIELD STUDIES

Studies involving the observation of free living animals have the potential to interfere with normal behaviour (section 5.1 of the code). This form should not be used when the handling of animals will occur or there is potential to interfere with normal behaviour, in such cases a full application would be required. For further information, please refer to the Animal Ethics website at:

www.research.uwa.edu.au/welcome/research_services/Ethics/animal_ethics/forms_information

OFFICE USE ONLY	FILE REF: F18979
<input checked="" type="checkbox"/> Approved	
<input type="checkbox"/> Further information required	
<input checked="" type="checkbox"/> Email confirmation sent	
SIGNATURE AEO: 	@ REC DATE 16 October 2009

1. PROTOCOL DETAILS	
Protocol Title: Family life: A comparative study of behavioural development and family social dynamics in captive gibbons (<i>Hylobates moloch</i>, <i>Nomascus leucogenys</i> and <i>Symphalangus syndactylus</i>) (full title)	
Proposed starting date: 01/10/2009 (dd/mm/yy)	Expected completion date: 1/09/2012 (dd/mm/yy)

2. CHIEF INVESTIGATOR	
Title, First name, last name, qualifications: Dr Debra S Judge (Ph.D Ecology, University of California, Davis)	Staff number (UWA staff only): 00048050
Work mailing address (include UWA MBDP): School of Anatomy and Human Biology M309, University of Western Australia	
I	

3. SPECIFY THE ANIMAL SPECIES AND NUMBERS TO BE OBSERVED (species name and common name)
2 families of Silvery gibbons (<i>Hylobates moloch</i>)
1 family and 4 adult pairs of White-cheeked gibbons (<i>Nomascus leucogenys</i>)
4 families and 3 adult pairs of Siamang (<i>Symphalangus syndactylus</i>)

4. DESCRIPTION OF THE PROPOSED STUDY (use lay language and include details of any potential animal welfare concerns)
This study will be undertaken by PhD student Belinda Burns (see attached).

5. DETAILS OF THE LOCATION OF THE STUDY
Ethics and research approval has been obtained from Perth Zoo , 20 Labouchere Road, South Perth, W.A. 6151 (See attached)
Research applications for the following locations are in process (a copy of each approval will be forwarded to the UWA animal ethics committee when received):
Mogo Zoo 222 Tomakin Road, Mogo, N.S.W. 2536



Our Ref: ZA/4991 #32878
Your Ref:
Enquiries: Pamela Smith, 9474 0355

26 August 2009

Belinda Burns

Dear Belinda

Project Title: Family life: A comparative study of behavioural development and family social dynamics in captive gibbons (*Hylobates moloch*, *Nomascus leucogenys* and *Symphalangus syndactylus*)

This letter is to confirm that the Perth Zoo Research Sub-Committee and the Animal Ethics Committee have approved the above named project.

Investigators are reminded that approval is granted for the duration of the project for up to a maximum of three years. An annual report must be lodged with the Zoo at the end of each calendar year and a new application submitted after 3 years. The Animal Ethics Committee must be informed prior to any changes being made to the procedures stated in the original application.

Additional applications should be made to the Committees for specific experimentation beyond the scope of this application. On completion of the project please forward the attached Annual Report Form to the Research Office at Perth Zoo.

With best wishes for success in your work.

Yours sincerely



Dr Wen-Haur Cheng
Acting Chair, Perth Zoo Animal Ethics Committee



ORIGINAL

Form A



Perth Zoological Parks Authority Animal Research and Ethics Committees

COVER SHEET

(To be completed by applicant, copy to be returned to applicant when approved)

- PROJECT TITLE: Family life: A comparative study of behavioural development and family social dynamics in captive gibbons (*Hylobates moloch*, *Nomascus leucogenys* and *Symphalangus syndactylus*)
- CHIEF INVESTIGATOR: Belinda Burns
Current appointment: PhD Student
- EXPECTED DATE OF COMMENCEMENT AND DURATION OF PROJECT: Commencing in August 2009, duration 3 years.

COMMITTEE USE ONLY:

APPROVAL

The Perth Zoological Parks Authority Research and/or Animal Ethics Committees have considered this proposal and have approved it for the period 26/8/09 to 26/8/10 subject to the following conditions:

- Annual Report required (date):
- Perth Zoo seminar presentation (date):
- Comments: _____
- Chief Investigator to inform the Animal Welfare Officer of any changes to research staff.

AEC APPROVAL NUMBER: 31.12.10
File Number: 2A/4991

Chair - Research Committee: _____ Date: 19/8/09

Chair - Ethics Committee: _____ Date: 27/8/09



222 Tomakin Road
Mogo NSW 2536, Australia
ABN: 79 685 575 006

Telephone 02 4474 5130
Facsimile 02 4474 4855

info@mogozoo.com.au
www.mogozoo.com.au

16th November, 2009

To Whom it May Concern,

Re: Approval of Research Project at Mogo Zoo

I confirm approval for you to conduct a comparative study of the behavioural development and family social dynamics in captive gibbons at Mogo Zoo.

Could you please provide me with your insurance particulars for the period of the project.

I look forward to hearing from you in this regard.

Yours faithfully,



CORINNE RUSSO
Office Manager
Mogo Zoo
222 Tomakin Rd
Mogo NSW 2536
Ph: (02) 4474 5130
Fax: (02) 44744855
Email to: corinnew@mogozoo.com.au
Website: www.mogozoo.com.au

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Australia

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Fax: 08 8267 0637

www.zoossa.com.au

6th July 2010

To whom it may concern,

Re: Approval of Gibbon Research Project at Adelaide Zoo

I confirm approval for Belinda Burns of the University of Western Australia to conduct a comparative study of the behavioural development and family social dynamics in captive gibbons at Adelaide Zoo.

Yours sincerely,



Dr Wendy Foster
Manager of Conservation Programs





26 October 2010

To whom it may concern,

Re: Approval of research project at Auckland Zoo

I confirm approval for Belinda Burns of the University of Western Australia to conduct a comparative study of the behavioural development and family social dynamics in captive gibbons at Auckland Zoo.

Signed,



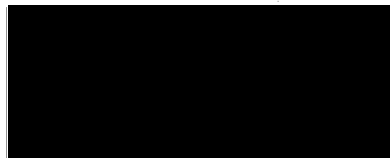
John Potter BVSc MACVSc
Convenor
Auckland Zoo Animal Ethics Committee

27 September 2010

To whom it may concern,

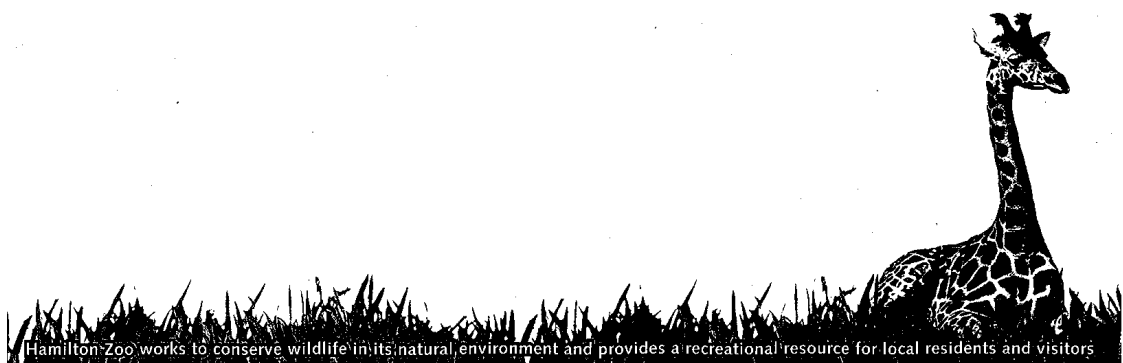
Re: Approval of research project at Hamilton Zoo

I confirm approval for Belinda Burns of the University of Western Australia to conduct a comparative study of the behavioural development and family social dynamics in captive gibbons at Hamilton Zoo.



Samantha Kudeweh

Team leader Mammals
Hamilton Zoo
New Zealand
+64 21 775 648





14 September 2010

To whom it may concern,

Re: Approval of research project at Wellington Zoo

I confirm approval for Belinda Burns of the University of Western Australia to conduct a comparative study of the behavioural development and family social dynamics in captive gibbons at Wellington Zoo.

Yours truly,



Mauritz Basson
General Manager Operations
Wellington Zoo Trust.

APPENDIX B

ENCLOSURE DETAILS

The gibbon enclosures were variable in size and complexity (Table B1), consisting of either a rectangular wire cage or an island with a surrounding moat. One group was temporarily housed in an enclosure previously used for cats (Silv-F2) and one group only had access to their holding yard during observation times due to temporary rotation on and off exhibit with a group of orang-utans (Siam-F3). All enclosures contained a combination of trees, shrubs, ropes and platforms, as well as adjoining night quarters.

Enclosure	Dimensions (L,W,H, in metres)	2D Area (m ²)	3D Area (m ³)	Groups housed
Perth white-cheeked gibbon enclosure	30x8x8	240	1920	WC-F1
Perth “Rainforest” enclosure	30x8x8	240	1920	Silv-F1 (T1 – T4), WC-StepF (T2)
Perth gibbon island	20x3x20	150	1200	WC-P1, WC-P2, Silv-F1 (T4 – T6)
Perth quarantine enclosure	8x8x3	64	192	WC-StepF (T1)
Mogo silvery gibbon enclosure	8x4x4	32	128	Silv-F2
Mogo island	32x16x10	512	5120	Siam-F1
Adelaide white-cheeked gibbon island	22x6x8	132	1056	WC-P3
Adelaide siamang island	17x10x13	170	2210	Siam-F2
Adelaide siamang holding enclosure	12x4x4	48	192	Siam-F3
Auckland siamang enclosure	22x6x6	132	792	Siam-P2
Hamilton siamang enclosure	11x5x5	55	275	Siam-P1
Wellington gibbon island	20x10x10	200	2000	WC-P4

APPENDIX C

BEHAVIOUR DEFINITIONS

Data set	Behaviour	Definition
DATA SET 1 (activity budget data)	% Out of sight	Focal animal not in view of observer
	% Resting	Not engaged in any other behaviour, incl. alert (e.g. vigilance) and non-alert behaviour (e.g. sleeping)
	% Movement	Any movement from A to B incl. brachiation, climbing, running. From 2008 onwards this behaviour was recorded separately as brachiating and non-brachiating movement, and the two categories were merged for analysis
	% Feeding	Recorded separately as foraging (picking up of food items) + eating (mastication), then combined for analysis as feeding. Does not include nursing for infants
	% Solo play	Any unnecessary or non-directional movement. Includes object play and sustained solicitation for social play that goes unanswered
	% Self groom	Scratching, or ritualised grooming of self
	% Social play	Total proportion of time spent playing with any group members. From 2008 onwards this behaviour was recorded separately as chasing and wrestling, and the two categories were merged for analysis
	% Grooms others	Mean proportion of time spent grooming others (recorded separately for each group member)
	% Groomed by others	Mean proportion of time groomed by others
	% Sing	Engaged in singing a duet or solo song, recorded for both adults and immatures
	% Embrace	Includes full embrace (ventral/ventral) between the focal animal and another group member, or side-by-side embrace in which one individual embraced the other with one arm
	% Carried by mother	Only recorded for semi-dependent infants
	% Carried by other group member	Only recorded for semi-dependent infants
DATA SET 2 (social activity data)	% Proximity to other group member	The proportion of time that each focal animal spent within arm's reach (~1m) of each group member. From Sep 2010 onwards, this was recorded as two separate categories: % time in contact proximity and % time in non-contact proximity, and both were combined for analysis

	% Play with other group member	Proportion of time each focal animal spent playing with each group member (recorded separately with each group member)
	% Time alone	Focal animal not within arm's reach of or playing with any other group member
DATA SET 3 (event data, frequency per hour of focal sampling)	Food transfer (F/Hr)	Frequency of food transfer per hour (tolerated or non-tolerated theft of a food item from the victim's hand or mouth) during focal samples, divided by the total time the group was observed
	Aggression to others (F/Hr)	Frequency of aggressive behaviour per hour by the focal animal directed at any other group member during focal samples. Distinguished from play by short duration and temporary ceasing of interaction following the act. Definition used here includes all threats and attempts to make aggressive physical contact (open mouth threat, vocalisation, bite at, hit at, lunge at, tap at, grab at and chase) and also instances of physical contact (bite, hit, tap, grab, grapple)
	Grooming solicitation (F/Hr)	Frequency per hour of solicitation for grooming by focal animal
	Approach other group member (F/Hr)	Frequency per hour that focal animal approaches to within arm's reach of another group member
	Retreat from other group member (F/Hr)	Frequency per hour that focal animal moves out of arm's reach of another group member
	Frequency of grooming others (F/Hr)	Total frequency per hour of grooming others by focal animal (recorded separately for each group member)
	Frequency of play initiation (F/Hr)	Total frequency of play solicitation/initiation directed towards others by focal animal (recorded separately for each group member)
	Duet frequency (F/10 days)	Frequency per hour of song bouts produced by <i>S. syndactylus</i> and <i>N. leucogenys</i> pairs in a 10-day period
Distance	Distance (m)	<p>Mean distance (in m²) between each group member dyad, estimated using 3D maps of each enclosure. Enclosure dimensions were estimated using either institutional blueprints or google maps, and divided into ~1m cubits. Distances between 2 individuals calculated using the following equation:</p> $\text{Distance between A and B} = \sqrt{[(x_B - x_A)^2 + (y_B - y_A)^2 + (z_B - z_A)^2]},$ <p>where x,y,z are length, width and height in the enclosure for each individual.</p>
Hinde's index	Hinde's index	Calculated from approaches and retreats for each group member dyad, see Chapter 2 methods