

Problems with primate sex ratios

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SOCIETY
 Problems with primate sex ratios

Craig Packer1* **, D. Anthony Collins**² **and Lynn E. Eberly**³

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ion of Biostatistics, School of Public Health, University of Minnesota, 2221 University Avenue, Minneapolis, MN 55414, U
Birth sex ratios of baboons in Gombe National Park, Tanzania, show an overall male bias of *ca*. 20%, Birth sex ratios of baboons in Gombe National Park, Tanzania, show an overall male bias of *ca*. 20%, but
there is no obvious explanation for this trend. Individual females did not alter their sex ratios according
to persi Birth sex ratios of baboons in Gombe National Park, Tanzania, show an overall male bias of *ca*. 20%, but
there is no obvious explanation for this trend. Individual females did not alter their sex ratios according
to persi there is no obvious explanation for this trend. Individual females did not alter their sex ratios according
to persistent levels of local resource competition. Sex ratios showed an unexpected relationship between
age and r to persistent levels of local resource competition. Sex ratios showed an unexpected relationship between age and rank: subordinate females had more sons when they were young; dominant females had more sons when they were o sons when they were old. The sex ratio of low-ranking females also varied with the severity of the product of more complex processes than is generally recognized or that sex-determining mechanisms environmental conditions during pregnancy. Our findings suggest that m
the product of more complex processes than is generally recognized or tha
impose sufficient constraints to prevent adaptive variation in all contexts. mplex processes than is generally recognized or that sex-determints to prevent adaptive variation in all contexts.
Keywords: sex ratio; local resource competition; primates

1. INTRODUCTION

1. INTRODUCTION
Sex allocation is one of the most productive and provoca-
tive tonics in behavioural ecology. Although no one the intervention of the most productive and provocative topics in behavioural ecology. Although no one
doubts the nower of evolutionary theory to predict the Sex allocation is one of the most productive and provocative topics in behavioural ecology. Although no one doubts the power of evolutionary theory to predict the optimal sex ratios of bankodinloids virtually every review tive topics in behavioural ecology. Although no one suggested that these conflicting trends were appropriate
doubts the power of evolutionary theory to predict the for their respective environments. Where matrilines
optima doubts the power of evolutionary theory to predict the
optimal sex ratios of haplodiploids, virtually every review
of sex ratio variation in birds and mammals has
concluded that chromosomal sex determination presents a optimal sex ratios of haplodiploids, virtually every review
of sex ratio variation in birds and mammals has
concluded that chromosomal sex determination presents a
fundamental constraint against significant deviations of sex ratio variation in birds and mammals has
concluded that chromosomal sex determination presents a
fundamental constraint against significant deviations
from 50:50 (Maynard Smith 1978: Williams 1979: concluded that chromosomal sex determination presents a
fundamental constraint against significant deviations
from 50:50 (Maynard Smith 1978; Williams 1979;
Charnov 1982; Clutton-Brock & Jason 1986; Hiraiwa fundamental constraint against significant deviations
from 50:50 (Maynard Smith 1978; Williams 1979;
Charnov 1982; Clutton-Brock & Iason 1986; Hiraiwa-Hasegawa 1993). However, a growing list of extrafrom 50:50 (Maynard Smith 1978; Williams 1979;
Charnov 1982; Clutton-Brock & Iason 1986; Hiraiwa-Hasegawa 1993). However, a growing list of extra-
ordinary sex ratios has been published in recent years Charnov 1982; Clutton-Brock & Iason 1986; Hiraiwa-Hasegawa 1993). However, a growing list of extra-
ordinary sex ratios has been published in recent years
(see for example Komdeur *et al.* 1997: Kilner 1998; Hasegawa 1993). However, a growing list of extra-
ordinary sex ratios has been published in recent years
(see, for example, Komdeur *et al.* 1997; Kilner 1998;
Sheldon *et al.* 1999) and indirect evidence is also accumuordinary sex ratios has been published in recent years
(see, for example, Komdeur *et al.* 1997; Kilner 1998;
Sheldon *et al.* 1999) and indirect evidence is also accumu-
lating of selective abortion or resorption of embry (see, for example, Komdeur *et al.* 1997; Kilner 1998;
Sheldon *et al.* 1999) and indirect evidence is also accumulating of selective abortion or resorption of embryos of
one sex or the other (see, for example, Knutk *et* Sheldon *et al.* 1999) and indirect evidence is also accumulating of selective abortion or resorption of embryos of one sex or the other (see, for example, Kruuk *et al.* 1999). lating of selective abortion or resorption of embryos of
one sex or the other (see, for example, Kruuk *et al.* 1999).
In addition, studies of transgenic mice have shown that a
transmission ratio distorter (TRD) can succes one sex or the other (see, for example, Kruuk *et al.* 1999).
In addition, studies of transgenic mice have shown that a transmission ratio distorter (TRD) can successfully alter the sex ratio: the presence of a TRD on the In addition, studies of transgenic mice have shown that a
transmission ratio distorter (TRD) can successfully alter
the sex ratio: the presence of a TRD on the Y chromo-
some produces twice as many sons as daughters owing transmission ratio distorter (TRD) can successfully alter
the sex ratio: the presence of a TRD on the Y chromo-
some produces twice as many sons as daughters owing to effects on sperm motility (Herrmann *et al.* 1999). me produces twice as many sons as daughters owing to

fects on sperm motility (Herrmann *et al.* 1999).

Even assuming that individuals can adaptively alter

sir sex ratios, published reports often show striking

effects on sperm motility (Herrmann *et al.* 1999).
Even assuming that individuals can adaptively alter
their sex ratios, published reports often show striking
inconsistencies (see for example Clutton-Brock & Isson Even assuming that individuals can adaptively alter
their sex ratios, published reports often show striking
inconsistencies (see, for example, Clutton-Brock & Iason
1986: Hiraiwa-Hasegawa 1993), However, two important their sex ratios, published reports often show striking
inconsistencies (see, for example, Clutton-Brock & Iason
1986; Hiraiwa-Hasegawa 1993). However, two important
papers have recently provided plausible explanations for inconsistencies (see, for example, Clutton-Brock & Iason
1986; Hiraiwa-Hasegawa 1993). However, two important
papers have recently provided plausible explanations for
these apparent contradictions focusing on predictions 1986; Hiraiwa-Hasegawa 1993). However, two important papers have recently provided plausible explanations for these apparent contradictions, focusing on predictions papers have recently provided plausible explanations for
these apparent contradictions, focusing on predictions
generated by Trivers & Willard's (1973) hypothesis on the
effect of maternal phenotyne on offenring sex ratio these apparent contradictions, focusing on predic
generated by Trivers & Willard's (1973) hypothesis of
effect of maternal phenotype on offspring sex ratio.
First Van Schaik & Hrdy (1991) re-examined nerated by Trivers & Willard's (1973) hypothesis on the
'ect of maternal phenotype on offspring sex ratio.
First, Van Schaik & Hrdy (1991) re-examined the
nflicting relationship between dominance rank and sex

effect of maternal phenotype on offspring sex ratio.
First, Van Schaik & Hrdy (1991) re-examined the
conflicting relationship between dominance rank and sex
ratio in non-human primates. Altmann (1980) had found First, Van Schaik & Hrdy (1991) re-examined the
conflicting relationship between dominance rank and sex
ratio in non-human primates. Altmann (1980) had found
that high-ranking female baboons gave birth to a preconflicting relationship between dominance rank and sex
ratio in non-human primates. Altmann (1980) had found
that high-ranking female baboons gave birth to a pre-
ponderance of daughters, whereas subordinate females ratio in non-human primates. Altmann (1980) had found
that high-ranking female baboons gave birth to a pre-
ponderance of daughters, whereas subordinate females
had more sons (see also Altmann *et al.* 1988; Simpson *et a* that high-ranking female baboons gave birth to a pre-
ponderance of daughters, whereas subordinate females
had more sons (see also Altmann *et al.* 1988; Simpson *et al.*

1982). However, Meikle *et al.* (1984) found that dominant 1982). However, Meikle *et al.* (1984) found that dominant female rhesus monkeys gave birth to a higher proportion of sons than did subordinates Van Schaik & Hrdy (1991) 1982). However, Meikle *et al.* (1984) found that dominant female rhesus monkeys gave birth to a higher proportion of sons than did subordinates. Van Schaik & Hrdy (1991) suggested that these confliction trends were appro female rhesus monkeys gave birth to a higher proportion
of sons than did subordinates. Van Schaik & Hrdy (1991)
suggested that these conflicting trends were appropriate
for their respective environments. Where matrilines of sons than did subordinates. Van Schaik & Hrdy (1991)
suggested that these conflicting trends were appropriate
for their respective environments. Where matrilines
compete intensely against each other dominant females suggested that these conflicting trends were appropriate compete intensely against each other, dominant females compete intensely against each other, dominant females
benefit from recruiting more daughters, whereas the juve-
nile daughters of subordinate females are vulnerable to
harassment (Silk 1983) However where feeding competibenefit from recruiting more daughters, whereas the juve-
nile daughters of subordinate females are vulnerable to
harassment (Silk 1983). However, where feeding competi-
tion is mild, bigh-ranking mothers should produce mo nile daughters of subordinate females are vulnerable to
harassment (Silk 1983). However, where feeding competi-
tion is mild, high-ranking mothers should produce more
males because they could endow sons with ranid growth harassment (Silk 1983). However, where feeding competition is mild, high-ranking mothers should produce more males because they could endow sons with rapid growth tion is mild, high-ranking mothers should produce more
males because they could endow sons with rapid growth
and thereby greater competitive ability (as originally
envisioned by Trivers $\&$ Willard). Consistent with this males because they could endow sons with rapid growth
and thereby greater competitive ability (as originally
envisioned by Trivers & Willard). Consistent with this
argument was the demonstration by Van Schaik & Hrdy and thereby greater competitive ability (as originally
envisioned by Trivers & Willard). Consistent with this
argument was the demonstration by Van Schaik & Hrdy
that the sex ratio of dominant females changed from envisioned by Trivers & Willard). Consistent with this
argument was the demonstration by Van Schaik & Hrdy
that the sex ratio of dominant females changed from
female-biased in areas of low population growth to maleargument was the demonstration by Van Schaik & Hrdy
that the sex ratio of dominant females changed from
female-biased in areas of low population growth to male-
hiased in ranidly growing populations that the sex ratio of dominant females changed from
female-biased in areas of low population growth to male-
biased in rapidly growing populations. male-biased in areas of low population growth to male-
seed in rapidly growing populations.
Second, Kruuk *et al.* (1999) followed a similar argu-
ent in their long-term study of red deer. On the island

biased in rapidly growing populations.
Second, Kruuk *et al.* (1999) followed a similar argument in their long-term study of red deer. On the island
of Rum, bigh-raping females gain a greater return from Second, Kruuk *et al.* (1999) followed a similar argument in their long-term study of red deer. On the island of Rum, high-ranking females gain a greater return from sons than daughters (and bias their sex ratio according ment in their long-term study of red deer. On the island
of Rum, high-ranking females gain a greater return from
sons than daughters (and bias their sex ratio accordingly),
but only at low population densities. At high den of Rum, high-ranking females gain a greater return from sons than daughters (and bias their sex ratio accordingly), but only at low population densities. At high densities, females of all ranks show a sex ratio close to 50:50. Kruuk *et al.* point out that high-ranking ungulat females of all ranks show a sex ratio close to 50:50. females of all ranks show a sex ratio close to 50:50.
Kruuk *et al.* point out that high-ranking ungulates show
male-biased sex ratios only in studies in which the popu-
lation density is below the carrying canacity. Thus Kruuk *et al.* point out that high-ranking ungulates show
male-biased sex ratios only in studies in which the popu-
lation density is below the carrying capacity. Thus their
conclusions are virtually the same as Van Schaik male-biased sex ratios only in studies in which the population density is below the carrying capacity. Thus their conclusions are virtually the same as Van Schaik & Hrdy (1991) except that bigh-rapking female primates swin lation density is below the carrying capacity. Thus their
conclusions are virtually the same as Van Schaik & Hrdy
(1991), except that high-ranking female primates swing
from a female bias to a male bias in richer environme conclusions are virtually the same as Van Schaik & Hrdy
(1991), except that high-ranking female primates swing
from a female bias to a male bias in richer environments,
whereas high-ranking ungulates swing from an unbiased (1991), except that high-ranking female primates swing
from a female bias to a male bias in richer environments,
whereas high-ranking ungulates swing from an unbiased
sex ratio to a male bias from a female bias to a male bias in richer environments,
whereas high-ranking ungulates swing from an unbiased
sex ratio to a male bias.
Given the repeated ability of behavioural ecologists to whereas high-ranking ungulates swing from an unbiased

discover individual variations in sex ratio and the consis-Given the repeated ability of behavioural ecologists to
discover individual variations in sex ratio and the consis-
tent pattern in these analyses of primates and ungulates,
adaptive sex ratios might well prove to be more discover individual variations in sex ratio and the consistent pattern in these analyses of primates and ungulates, adaptive sex ratios might well prove to be more wide-
spread than the early scentics had considered possib tent pattern in these analyses of primates and ungulates,
adaptive sex ratios might well prove to be more wide-
spread than the early sceptics had considered possible.
Perhaps environmental variations are more important adaptive sex ratios might well prove to be more wide-
spread than the early sceptics had considered possible.
Perhaps environmental variations are more important
than anyone had recognized and the contradictory data spread than the early sceptics had considered possible.
Perhaps environmental variations are more important
than anyone had recognized, and the contradictory data

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Figure 1. Sex-specific survival and impact on maternal Figure 1. Sex-specific survival and impact on maternal
reproductive rate or success. Bars indicate standard errors of
the mean: numbers are sample sizes (a) Survival rates do. Figure 1. Sex-specific survival and impact on maternal
reproductive rate or success. Bars indicate standard errors of
the mean; numbers are sample sizes. (*a*) Survival rates do
not differ between males and females during reproductive rate or success. Bars indicate standard errors of
the mean; numbers are sample sizes. (*a*) Survival rates do
not differ between males and females during the first and
second vears of life ($h > 0.20$) (*b*) S the mean; numbers are sample sizes. (*a*) Survival rates do not differ between males and females during the first and second years of life ($p > 0.20$). (*b*) Survival of the next offspring was not significantly influenced by the sex of a surviving older sibling ($p > 0.20$). (*c*) Interbirth interval (IBI) was not influenced by the sex of a surviving offspring $(p > 0.20)$.

 $(p > 0.20)$.
sets resulted from analyses that were either too coarsely
grained or ignored relevant variables. However, sexsets resulted from analyses that were either too coarsely
grained or ignored relevant variables. However, sex-
determining mechanisms might, nevertheless impose sets resulted from analyses that were either too coarsely
grained or ignored relevant variables. However, sex-
determining mechanisms might nevertheless impose
serious constraints on individual sex ratios—constraints grained or ignored relevant variables. However, sex-
determining mechanisms might nevertheless impose
serious constraints on individual sex ratios—constraints
that can only be overcome under a strong force of determining mechanisms might nevertheless impose
serious constraints on individual sex ratios—constraints
that can only be overcome under a strong force of
selection - that can only be overcome under a strong force of selection.
- Here we present results from a long-term study of olive

selection.
Here we present results from a long-term study of olive
baboons at Gombe National Park, Tanzania, comparable
in scone with the analyses by Van Schaik & Hrdy (1991) Here we present results from a long-term study of olive
baboons at Gombe National Park, Tanzania, comparable
in scope with the analyses by Van Schaik & Hrdy (1991)
and Kruuk et al. (1999) We examine a variety of ecobaboons at Gombe National Park, Tanzania, comparable
in scope with the analyses by Van Schaik & Hrdy (1991)
and Kruuk *et al.* (1999). We examine a variety of eco-
logical and demographic factors that have been predicted in scope with the analyses by Van Schaik & Hrdy (1991) The duration of post-partum amenorrhoea depends on infant
and Kruuk *et al.* (1999). We examine a variety of eco-
logical and demographic factors that have been predi and Kruuk *et al.* (1999). We examine a variety of ecological and demographic factors that have been predicted to influence individual sex ratios in these animals, taking care to determine the interaction between rank and logical and demographic factors that have been predicted
to influence individual sex ratios in these animals, taking
care to determine the interaction between rank and local
resource levels. The Gombe population provides a to influence individual sex ratios in these animals, taking
care to determine the interaction between rank and local
resource levels. The Gombe population provides an
important comparison with earlier analyses because care to determine the interaction between rank and local
resource levels. The Gombe population provides an
important comparison with earlier analyses because
adiacent troops show differences in reproductive rates as resource levels. The Gombe population provides an
important comparison with earlier analyses because
adjacent troops show differences in reproductive rates as
high as those included in Van Schaik & Hrdy's review $\frac{1}{2}$ important comparison with earlier analyses because
adjacent troops show differences in reproductive rates as
high as those included in Van Schaik & Hrdy's review.
We also test the models of Fisher (1930) and Cla adjacent troops show differences in reproductive rates as

high as those included in Van Schaik & Hrdy's review.
We also test the models of Fisher (1930) and Clark
(1978) for population sex ratio. Fisher predicted that
parents should invest equally in offspring of either sex so We also test the models of Fisher (1930) and Clark
(1978) for population sex ratio. Fisher predicted that
parents should invest equally in offspring of either sex, so
population sex ratios should be inversely related to th (1978) for population sex ratio. Fisher predicted that parents should invest equally in offspring of either sex, so population sex ratios should be inversely related to the *Phil. Trans. R. Soc. Lond.* B (2000)

Figure 2. The relationship between troop size and interbirth
interval (IBI) after the birth of a surviving offspring. IBI
increases significantly with increasing troop size (R FMI Figure 2. The relationship between troop size and interbirth
interval (IBI) after the birth of a surviving offspring. IBI
increases significantly with increasing troop size (REML
estimation $F = 10.02 \; k = 0.0018$) estimation, $F = 10.02$, $p = 0.0018$.

average costs of raising each sex. Clark pointed out that members of the philopatric sex are more costly because average costs of raising each sex. Clark pointed out that
members of the philopatric sex are more costly because
they eventually compete against their parents for limited
resources. Species such as olive baboons with femal members of the philopatric sex are more costly because
they eventually compete against their parents for limited
resources. Species such as olive baboons with female-
hiased philopatry, should, therefore, show, male-hiased they eventually compete against their parents for limited
resources. Species such as olive baboons with female-
biased philopatry should therefore show male-biased
population sex ratios due to 'local resource competition' resources. Species such as olive baboons with female-biased philopatry should therefore show male-biased population sex ratios due to 'local resource competition' biased philopatry should therefore show male-biased
population sex ratios due to 'local resource competition'
(LRC). Population sex ratios are often skewed in the
direction predicted by sex-biased natal philopatry population sex ratios due to 'local resource competition'
(LRC). Population sex ratios are often skewed in the
direction predicted by sex-biased natal philopatry
(Clutton-Brock & Jason 1986; Johnson 1988; Gowaty (LRC). Population sex ratios are often skewed in the
direction-predicted by sex-biased natal philopatry
(Clutton-Brock & Iason 1986; Johnson 1988; Gowaty
1993: Hiraiwa-Hasegawa 1993) and LRC is fundamental direction predicted by sex-biased natal philopatry
(Clutton-Brock & Iason 1986; Johnson 1988; Gowaty
1993; Hiraiwa-Hasegawa 1993), and LRC is fundamental
to the interpretations of individual sex-ratios by Silk (1983) (Clutton-Brock & Iason 1986; Johnson 1988; Gowaty 1993; Hiraiwa-Hasegawa 1993), and LRC is fundamental to the interpretations of individual sex ratios by Silk (1983) and Van Schaik & Hrdy (1991). 1993; Hiraiwa-Hasegawa 1993), and LRC is fundamental

2. METHODS

Gombe National Park covers 40 km^2 of steep valleys running $\frac{1}{2}$ Gombe National Park covers 40 km^2 of steep valleys running
down from the rift escarpment to the shore of Lake Tanganyika.
The valley are filled with somi symmetry forest, and the slopes Gombe National Park covers 40 km^2 of steep valleys running
down from the rift escarpment to the shore of Lake Tanganyika.
The valleys are filled with semi-evergreen forest, and the slopes The valleys are filled with semi-evergreen forest, and the slopes
and ridge-tops are covered by grassland, savanna woodland and The valleys are filled with semi-evergreen forest, and the slopes
and ridge-tops are covered by grassland, savanna woodland and
semi-deciduous forest (Goodall 1986). Members of nine different
treats, are, recognized indivi and ridge-tops are covered by grassland, savanna woodland and
semi-deciduous forest (Goodall 1986). Members of nine different
troops are recognized individually from facial features and
natural morbings. All maior domograp troops are recognized individually from facial features and
natural markings. All major demographic events have been
recorded since 1967; most deaths are inferred from disappearnatural markings. All major demographic events have been ances. Menarche typically occurs during the fourth year of life; recorded since 1967; most deaths are inferred from disappear-
ances. Menarche typically occurs during the fourth year of life;
age estimates for females therefore extend to 1963. Dominance
reals are based on the outcome of ances. Menarche typically occurs during the fourth year of life;
age estimates for females therefore extend to 1963. Dominance
ranks are based on the outcome of aggressive and/or competi-
tive interactions. To fosilitate c ranks are based on the outcome of aggressive and/or competitive interactions. To facilitate comparisons across troops of ranks are based on the outcome of aggressive and/or competi-
tive interactions. To facilitate comparisons across troops of
different sizes, the 'relative rank' was determined for each
female. Belative rank is the prepartie five interactions. To facilitate comparisons across troops of
different sizes, the 'relative rank' was determined for each
female. Relative rank is the proportion of females dominated by
a positively found a three than the female. Relative rank is the proportion of females dominated by
a particular female, thus the top-ranking female in a given female. Relative rank is the proportion of females dominated by
a particular female, thus the top-ranking female in a given
troop has a relative rank of 1.0, and that of the bottom-ranking
female is 0. a particular
troop has a r
female is 0.
The duret op has a relative rank of 1.0, and that of the bottom-ranking
nale is 0.
The duration of post-partum amenorrhoea depends on infant
wivel (Altmann et al. 1979), and the trainel birth magina in

female is 0.
The duration of post-partum amenorrhoea depends on infant
survival (Altmann *et al.* 1978), and the typical birth spacing in
this a multium is two weap (Dashan ti d. 1995–1999). Thus we this population is two years (Packer *et al.* 1995, 1998). Thus we survival (Altmann *et al.* 1978), and the typical birth spacing in
this population is two years (Packer *et al.* 1995, 1998). Thus we
examine interbirth intervals only after offspring that survived to
their second birthdo this population is two years (Packer *et al.* 1995, 1998). Thus we examine interbirth intervals only after offspring that survived to their second birthday. Offspring older than two years of age are considered to be indep their second birthday. Offspring older than two years of age are considered to be independent of their mother (see Packer *et al.*) their second birthday. Offspring older than two years of age are
considered to be independent of their mother (see Packer *et al.*
1998). The Gombe baboons show male-biased dispersal: 70% of
malse leave their notel traces considered to be independent of their mother (see Packer *et al.* 1998). The Gombe baboons show male-biased dispersal: 70% of males leave their natal troops by their ninth birthday and 100%
has their 19th birthday (Das 1998). The Gombe baboons show male-biased dispersal: 70% of
males leave their natal troops by their ninth birthday and 100%
by their 12th birthday (Packer *et al.* 1995), whereas females never
move between new quisting tro males leave their natal troops by their ninth birth
by their 12th birthday (Packer *et al.* 1995), whereas
move between pre-existing troops (Packer 1979).
Possible from nine different troop their 12th birthday (Packer *et al.* 1995), whereas females never
we between pre-existing troops (Packer 1979).
Results are available from nine different troops, but four of
see mlit from nre-existing troops in the lest fo

move between pre-existing troops (Packer 1979).
Results are available from nine different troops, but four of
these split from pre-existing troops in the last few months of the
table Them mosifie grouth notes for these fou these split from pre-existing troops in the last few months of the study. Troop-specific growth rates for these four troops are based

great-grandmother's rank
Figure 3. Matrilineal inheritance of female dominance rank.
Relative rank is highly correlated between mothers and Figure 3. Matrilineal inheritance of female dominance rank
Relative rank is highly correlated between mothers and
their (a) daughters ($x^2 = 0.555$, $n = 97$, $k < 0.01$, linear Figure 3. Matrilineal inheritance of female dominance rand
Relative rank is highly correlated between mothers and
their (*a*) daughters ($r^2 = 0.555$, $n = 97$, $p < 0.01$, linear
regression) (*b*) granddaughters ($r^2 = 0.3$ Relative rank is highly correlated be
their (*a*) daughters ($r^2 = 0.555$, $n = 9$
regression), (*b*) granddaughters ($r^2 = 3$
and (*c*) great-granddaughters ($r^2 = 0$ $x^2 = 0.304, n = 50, p < 0.01$ their (*a*) daughters ($r^2 = 0.555$, *n* =
regression), (*b*) granddaughters (r^2
and (*c*) great-granddaughters (r^2 = and (c) great-granddaughters $(r^2 = 0.807, n = 12, p < 0.01)$.

on their respective troops of origin. Analysis is based on 686 live
hinths to 167 formales: only one noin of twins has been bern in on their respective troops of origin. Analysis is based on 686 live
births to 167 females; only one pair of twins has been born in births to 167 females; only one pair of twins has been born in this population.

All analyses on binary outcomes (e.g. male or female offspring, this population.
All analyses on binary outcomes (e.g. male or female offspring,
or survival or no survival to first birthday) were performed with
morginal ganconlined linear mived models (CLMMs) with a All analyses on binary outcomes (e.g. male or female offspring,
or survival or no survival to first birthday) were performed with
marginal generalized linear mixed models (GLMMs) with a
locit link. Such models can account marginal generalized linear mixed models (GLMMs) with a logit link. Such models can account for correlation between the multiple observations taken on each mother. Model parameters logit link. Such models can account for correlation between the
multiple observations taken on each mother. Model parameters
were estimated with the Generalized Estimating Equations
(CEE) engages (Lings & Zegen 1996) in th multiple observations taken on each mother. Model parameters
were estimated with the Generalized Estimating Equations
(GEE) approach (Liang & Zeger 1986) in the SAS analysis
package A three dramadent (banded Temlitz) worki were estimated with the Generalized Estimating Equations
(GEE) approach (Liang & Zeger 1986) in the SAS analysis
package. A three-dependent (banded Toeplitz) working correla-
tion structure was used which allows for groups (GEE) approach (Liang & Zeger 1986) in the SAS analysis
package. A three-dependent (banded Toeplitz) working correla-
tion structure was used, which allows, for example, for the sex of
care of mains to be completed with th tion structure was used, which allows, for example, for the sex of any offspring to be correlated with the sex of any of the three subsequent offspring of the same mother. Significance of effects any offspring to be correlated with the sex of any of the three
subsequent offspring of the same mother. Significance of effects
was determined by an approximate ζ -test based on GEE's
semisical (solust) estimates of s subsequent offspring of the same mother. Significance of effects
was determined by an approximate ζ -test based on GEE's
empirical (robust) estimates of standard error of the mean.
Results were rebut to other choices o empirical (robust) estimates of standard error of the mean.
Results were robust to other choices of correlation structures.
All analyses on the continuous-outcome interbirth intervals Results were robust to other choices of correlation structures.

used general linear models (GLMs; Searle *et al*. 1992) and a

three-dependent correlation structure to account for correlation
hetween interhirth intervals of the same mather. Interhirth three-dependent correlation structure to account for correlation
between interbirth intervals of the same mother. Interbirth
intervals astisfied assumptions of normality. Model nonprotent between interbirth intervals of the same mother. Interbirth intervals satisfied assumptions of normality. Model parameters between interbirth intervals of the same mother. Interbirth
intervals satisfied assumptions of normality. Model parameters
were estimated from residual maximum likelihood (REML),
and the simifeance of effects was determine intervals satisfied assumptions of normality. Model parameters
were estimated from residual maximum likelihood (REML),
and the significance of effects was determined by an approxi-
mate t test. Besults were relust to other and the significance of effects was determined by an approximate *t*-test. Results were robust to other choices of correlation structures.

3. RESULTS

Individuals are expected to gain differing costs and **below** is a sexted to gain differing costs and
benefits from a son or a daughter according to their
specific circumstances. We first consider the environ-Individuals are expected to gain differing costs and
benefits from a son or a daughter according to their
specific circumstances. We first consider the environ-
mental and social factors that are likely to influence sex benefits from a son or a daughter according to their
specific circumstances. We first consider the environ-
mental and social factors that are likely to influence sex
allocation in the Gombe baboons before presenting the specific circumstances. We first consider the environ-
mental and social factors that are likely to influence sex
allocation in the Gombe baboons before presenting the
results of the sex ratio analysis mental and social factors that a
allocation in the Gombe baboo
results of the sex ratio analysis.

results of the sex ratio analysis.
(**a**) *Effects of environmental and phenotypic factors*
(*i*) *Library ethicles of environmental deal to* (a) *Effects of environmental and phe*
(i) *Inherent attributes of sons versus daughters*
Baboons, are sexually dimorphic so

(i) Inherent attributes of sons versus daughters
Baboons are sexually dimorphic, so males might be (i) Inherent attributes of sons versus daughters
Baboons are sexually dimorphic, so males might be
expected to suffer higher mortality than females
(Clutton-Brock *et al.* 1985) or to inflict greater costs on Baboons are sexually dimorphic, so males might be
expected to suffer higher mortality than females
(Clutton-Brock *et al.* 1985) or to inflict greater costs on
maternal reproduction (Clutton-Brock *et al.* 1989) expected to suffer higher mortality than females
(Clutton-Brock *et al.* 1985) or to inflict greater costs on
maternal reproduction (Clutton-Brock *et al.* 1982).
However, the Gombe males do not suffer greater (Clutton-Brock *et al.* 1985) or to inflict greater costs on maternal reproduction (Clutton-Brock *et al.* 1982).
However, the Gombe males do not suffer greater mortality than females in their first two years of life maternal reproduction (Clutton-Brock *et al.* 1982).
However, the Gombe males do not suffer greater mortality than females in their first two years of life (figure 1*a*), nor do they inflict higher mortality on their However, the Gombe males do not suffer greater mortality than females in their first two years of life (figure 1*a*), nor do they inflict higher mortality on their mother's next offspring (figure 1*b*) or take any longer to θ (figure 1*a*), nor do they inflict h
mother's next offspring (figure 1
'fledge' than females (figure 1*c*). *'fledge' than females (figure lc).*
(ii) *Rainfall patterns*

Harsher conditions during pregnancy lowers the sex (ii) *Rainfall patterns*
Harsher conditions during pregnancy lowers the sex
ratio in red deer (Kruuk *et al.* 1999), possibly because
male foetuses are more vulnerable to stress. The dry Harsher conditions during pregnancy lowers the sex
ratio in red deer (Kruuk *et al.* 1999), possibly because
male foetuses are more vulnerable to stress. The dry
season at Gombe runs from lune to October, and interratio in red deer (Kruuk *et al.* 1999), possibly because
male foetuses are more vulnerable to stress. The dry
season at Gombe runs from June to October, and inter-
hirth intervals are longer when lactating females experimale foetuses are more vulnerable to stress. The dry season at Gombe runs from June to October, and inter-
birth intervals are longer when lactating females experiseason at Gombe runs from June to October, and inter-
birth intervals are longer when lactating females experi-
ence below-average rainfall in the dry season (Packer *et*
 al , 1995). In the following analysis we focus on t birth intervals are longer when lactating females experience below-average rainfall in the dry season (Packer *et al.* 1995). In the following analysis we focus on the effects of a harsh dry season during pregnancy. A stre ence below-average rainfall in the dry season (Packer *et al.* 1995). In the following analysis we focus on the effects of a harsh dry season during pregnancy. A stressful preg-
nancy not only might have a direct influenc al. 1995). In the following analysis we focus on the effects of a harsh dry season during pregnancy. A stressful pregnancy not only might have a direct influence on the sex ratio but also might affect rates of development of a harsh dry season during pregnancy. A stressful pregnancy not only might have a direct influence on the sex ratio but also might affect rates of development in full-
term infants nancy not only might have a direct influence on the sex
ratio but also might affect rates of development in full-
term infants.

(iii) *Local resource competition*

(i) Local resource competition
LRC has been estimated from reproductive per-(iii) *Local resource competition*

LRC has been estimated from reproductive per-

formance (Johnson 1988) and from population growth

(Van Schaik & Hrdy 1991) on the assumption that slow LRC has been estimated from reproductive per-
formance (Johnson 1988) and from population growth
(Van Schaik & Hrdy 1991) on the assumption that slow
growth reflects scarce resources We examined the possible formance (Johnson 1988) and from population growth
(Van Schaik & Hrdy 1991) on the assumption that slow
growth reflects scarce resources. We examined the possible
effects of LRC in three ways. First, the Gombe troops (Van Schaik & Hrdy 1991) on the assumption that slow
growth reflects scarce resources. We examined the possible
effects of LRC in three ways. First, the Gombe troops
show persittent differences in growth rate, and females growth reflects scarce resources. We examined the possible
effects of LRC in three ways. First, the Gombe troops
show persistent differences in growth rate, and females in
the slowest troop also showed the slowest rate of effects of LRC in three ways. First, the Gombe troops
show persistent differences in growth rate, and females in
the slowest troop also showed the slowest rate of sexual
maturation and the longest interbirth intervals (Pac show persistent differences in growth rate, and females in
the slowest troop also showed the slowest rate of sexual
maturation and the longest interbirth intervals (Packer *et*
 al , 1995) These inter-troop differences have the slowest troop also showed the slowest rate of sexual
maturation and the longest interbirth intervals (Packer *et*
al. 1995). These inter-troop differences have persisted over
decades: the annual growth rate in troop maturation and the longest interbirth intervals (Packer *et al.* 1995). These inter-troop differences have persisted over decades: the annual growth rate in troop C averaged *al.* 1995). These inter-troop differences have persisted over decades: the annual growth rate in troop C averaged 1.71% between 1970 and 1996, whereas troop D averaged 9.04% between 1978 and 1996. Second adding more decades: the annual growth rate in troop C averaged
1.71% between 1970 and 1996, whereas troop D averaged
9.04% between 1978 and 1996. Second, adding more
females to a troop might increase overall levels of feeding 1.71% between 1970 and 1996, whereas troop D averaged 9.04% between 1978 and 1996. Second, adding more females to a troop might increase overall levels of feeding competition as suggested by the fact that interbirth 9.04% between 1978 and 1996. Second, adding more females to a troop might increase overall levels of feeding competition, as suggested by the fact that interbirth intervals become longer in larger troops (figure 2). Tr females to a troop might increase overall levels of feeding. competition, as suggested by the fact that interbirth intervals become longer in larger troops (figure 2). Troops can
grow only through the recruitment of daughters, so troop
size might provide a good estimate of the exten vals become longer in larger troops (figure 2). Troops can
grow only through the recruitment of daughters, so troop
size might provide a good estimate of the extent of LRC.
Third, the risk of LRC should be greatest for you grow only through the recruitment of daughters, so troop
size might provide a good estimate of the extent of LRC.
Third, the risk of LRC should be greatest for young
mothers because they are more likely to survive until th size might provide a good estimate of the extent of LRC.
Third, the risk of LRC should be greatest for young
mothers because they are more likely to survive until their
daughters reach maturity (and suffer from the greates Third, the risk of LRC should be greatest for young
mothers because they are more likely to survive until their
daughters reach maturity (and suffer from the greatest

Figure 4. Effect of mother's rank on the dominance rank of sons. (*a*) Males in their natal troop, (*b*) males in their new troop. To control for the effect of male age (see figure 5*d*), each panel presents the relations **CIENCES** Figure 4. Effect of mother's rank on the dominance rank of sons. (a) Males in their natal troop, (b) males in their new troop. To control for the effect of male age (see figure 5d), each panel presents the relationship be control for the effect of male age (see figure 5*d*), each panel presents the relationship between maternal rank and male rank for
sons of a particular age. Because male rank is lower for males still resident in their nat sons of a particular age. Because male rank is lower for males still resident in their natal troop, data are also separated according to the male's dispersal status. None of these 15 data sets show a significant correlati

sons ($p > 0.10$).
cumulative number of daughters) (see Clutton-Brock & do
Iason 1986). Although the pattern of maternal investment cumulative number of daughters) (see Clutton-Brock & Iason 1986). Although the pattern of maternal investment
in sons and daughters varies with age (see $83(b)$), we cumulative number of daughters) (see Clutton-Brock & Iason 1986). Although the pattern of maternal investment
in sons and daughters varies with age (see $\S 3(b)$), we
could find no strong evidence that adult daughters Iason 1986). Although the pattern of maternal investment
in sons and daughters varies with age (see $\S 3(b)$), we
could find no strong evidence that adult daughters in sons and daughters varies with age (see $\S 3(b)$), we retarded their mother's reproduction.
(iv) *Maternal rank*

OYA

 \mathbf{R} \mathbf{E} FELL

PHILOSOPHICAL
TRANSACTIONS

Influence of maternal rank on the fitness of adult offspring

 \bullet influence the fitness of daughters (owing to matrilineal inheritance of rank) than sons (owing to a high degree influence the fitness of daughters (owing to matrilineal
inheritance of rank) than sons (owing to a high degree
of sexual dimorphism and male natal dispersal) (Silk
1983) Female rank at Gombe is bigbly correlated with inheritance of rank) than sons (owing to a high degree
of sexual dimorphism and male natal dispersal) (Silk
1983). Female rank at Gombe is highly correlated with
maternal grandmaternal and great-grandmaternal rank of sexual dimorphism and male natal dispersal) (Silk
1983). Female rank at Gombe is highly correlated with
maternal, grandmaternal and great-grandmaternal rank
(figure 3). In contrast, male rank is independent of 1983). Female rank at Gombe is highly correlated with
maternal, grandmaternal and great-grandmaternal rank
 \pm (figure 3). In contrast, male rank is independent of maternal, grandmaternal and great-grandmaternal rank
(figure 3). In contrast, male rank is independent of
maternal rank, regardless of age or residence in the
natal troop (figure 4). Because maternal rank might (figure 3). In contrast, male rank is independent of maternal rank, regardless of age or residence in the natal troop (figure 4). Because maternal rank might influence the behavior of only those males that grew up maternal rank, regardless of age or residence in the
natal troop (figure 4). Because maternal rank might
influence the behavior of only those males that grew up
together we examined pairs of same-aged males from natal troop (figure 4). Because maternal rank might 'or
influence the behavior of only those males that grew up his
together, we examined pairs of same-aged males from al.
the same natal troop that resided in the same noninfluence the behavior of only those males that grew up
together, we examined pairs of same-aged males from
the same natal troop that resided in the same non-natal
troop as adults. However, sons of bigh-rapking mothers together, we examined pairs of same-aged males from
the same natal troop that resided in the same non-natal
troop as adults. However, sons of high-ranking mothers troop as adults. However, sons of high-ranking mothers *Phil. Trans. R. Soc. Lond.* B (2000)

dominated the sons of low-ranking mothers in only six dominated the solution
out of 18 pairs. minated the sons of low-ranking mothers in only six
t of 18 pairs.
Gombe females attain adult rank by the age of four
ars and maintain a similar rank for the rest of their

High-ranking females might be better able to higher-miscarriage-rates-and-more-frequent-reproductive-
Huence the fitness of daughters (owing to matrilineal pathologies (Packer *et al.* 1995). Instead, female reproout of 18 pairs.
Gombe females attain adult rank by the age of four
years and maintain a similar rank for the rest of their
lives (foure 5*a*). However, overall reproductive perfor-Gombe females attain adult rank by the age of four
years and maintain a similar rank for the rest of their
lives (figure 5*a*). However, overall reproductive perfor-
mance is not strongly correlated with rank in this popul years and maintain a similar rank for the rest of their
lives (figure 5*a*). However, overall reproductive perfor-
mance is not strongly correlated with rank in this popula-
tion: high-ranking females, enjoy shorter, inter lives (figure 5*a*). However, overall reproductive performance is not strongly correlated with rank in this population: high-ranking females enjoy shorter interbirth intervals and bigher infant survival but they suffer fro mance is not strongly correlated with rank in this popula-
tion: high-ranking females enjoy shorter interbirth
intervals and higher infant survival, but they suffer from
higher miscarriage rates and more frequent reproduct tion: high-ranking females enjoy shorter interbirth
intervals and higher infant survival, but they suffer from
higher miscarriage rates and more frequent reproductive
pathologies (Packer et al. 1995) Instead female reprointervals and higher infant survival, but they suffer from
higher miscarriage rates and more frequent reproductive
pathologies (Packer *et al.* 1995). Instead, female repro-
duction depends on age: females reproduce at a c higher miscarriage rates and more frequent reproductive pathologies (Packer *et al.* 1995). Instead, female reproduction depends on age: females reproduce at a constant pathologies (Packer *et al.* 1995). Instead, female reproduction depends on age: females reproduce at a constant
rate until senescence (figure 5*c*) (see also Packer *et al.* 1998). In contrast, male rank depends on compet rate until senescence (figure 5c) (see also Packer et al.
1998). In contrast, male rank depends on competitive
ability (Saunders & Hausfater 1978; Packer 1979),
reaching a peak after full physical development 1998). In contrast, male rank depends on competitive ability (Saunders & Hausfater 1978; Packer 1979), reaching a peak after full physical development (figure $5b$). Males compete intensively for temporary reaching a peak after full physical development reaching a peak after full physical development
(figure 5b). Males compete intensively for temporary
'ownership' of oestrous females, and 'consortships' are
highly correlated with reproductive success (Altmann et (figure 5*b*). Males compete intensively for temporary 'ownership' of oestrous females, and 'consortships' are highly correlated with reproductive success (Altmann *et* a^{l} 1996). Consorting activity is closely correla ² 'ownership' of oestrous females, and 'consortships' are highly correlated with reproductive success (Altmann *et* al. 1996). Consorting activity is closely correlated with dominance (Hausfater 1975; Packer 1979) and sh highly correlated with reproductive success (Altmann *et al.* 1996). Consorting activity is closely correlated with dominance (Hausfater 1975; Packer 1979) and shows a similar change with age (figure 5*d*) al. 1996). Consorting activity is close
dominance (Hausfater 1975; Packer
similar change with age (figure 5*d*).

Consorting shows a similar overall pattern to male rank, although it peaks at the age of 11 years.
Thus, whereas female rank is largely inherited (figure 3), suffer less harassment and h Figure 5. The effect of age on dominance and reproductive rates in females and males. (a,b) 'Relative rank' is the proportion of the top-ranking female is assigned 1.0 the bottom-ranking female is assigned 1.0 the bottomlike-sexed individuals dominated by each animal, where the top-ranking female is assigned 1.0 the bottom-ranking female is assigned 0. Female rank (a) shows no significant change with age; male rank (b) reaches a peak a like-sexed individuals dominated by each animal, where the top-ranking female is assigned 1.0 the bottom-ranking female is
assigned 0. Female rank (*a*) shows no significant change with age; male rank (*b*) reaches a peak assigned 0. Female rank (*a*) shows no significant change with age; male rank (*b*) reaches a peak at the age of ten years, then declines monotonically ($p = 0.0000$, analysis of variance). (*c*) Gross maternity is the num declines monotonically ($p = 0.0000$, analysis of variance). (*c*) Gross maternity is the number of live offspring produced at eage (modified from Packer *et al.* 1998). Female reproductive rates remain constant from the a age (modified from Packer *et al.* 1998). Female reproductive rates remain constant from the age of six to 20 years before declining in old age. (*d*) Consorting activity is the proportion of days per month that each male

female fitness is influenced only slightly by social rank Thus, whereas female rank is largely inherited (figure 3),
female fitness is influenced only slightly by social rank
(Packer *et al.* 1995). Although male fitness is strongly
influenced by rank (figure 5*h d*) sons do not female fitness is influenced only slightly by social rank (Packer *et al.* 1995). Although male fitness is strongly influenced by rank (figure 5*b*,*d*), sons do not inherit their mothers' rank (figure 4) (Packer *et al.* 1995). Althinfluenced by rank (figure 4).
mothers' rank (figure 4). mothers' rank (figure 4).
Maternal rank and sex-dependent productivity of offspring

High-ranking females might be better able to rear Maternal rank and sex-dependent productivity of offspring

High-ranking females might be better able to rear

daughters (Altmann *et al.* 1988), perhaps owing to selective

harassment, stemming, from I RC (Silk 1983), Vari High-ranking females might be better able to rear
daughters (Altmann *et al.* 1988), perhaps owing to selective
harassment stemming from LRC (Silk 1983). Various
studies have shown that daughters of subordinate females daughters (Altmann *et al.* 1988), perhaps owing to selective
harassment stemming from LRC (Silk 1983). Various
studies have shown that daughters of subordinate females
suffer the bighest mortality of any inveniles (see fo harassment stemming from LRC (Silk 1983). Various
studies have shown that daughters of subordinate females
suffer the highest mortality of any juveniles (see, for studies have shown that daughters of subordinate females
suffer the highest mortality of any juveniles (see, for
example, Dittus 1979; Silk *et al.* 1981), and subordinate
mothers might also suffer greater costs from raisi suffer the highest mortality of any juveniles (see, for example, Dittus 1979; Silk *et al.* 1981), and subordinate mothers might also suffer greater costs from raising daugh-
ters than sons (Gommendio *et al.* 1990) For d example, Dittus 1979; Silk *et al.* 1981), and subordinate mothers might also suffer greater costs from raising daugh-
ters than sons (Gommendio *et al.* 1990). For dominant females in contrast infant mortality might be gr mothers might also suffer greater costs from raising daughters than sons (Gommendio *et al.* 1990). For dominant females, in contrast, infant mortality might be greater for sons than for daughters (Altmann *et al.* 1988). ters than sons (Gommendio et al. 1990). For dominant females, in contrast, infant mortality might be greater for
sons than for daughters (Altmann *et al.* 1988). Thus, sub-
ordinate females would often gain a higher productivity offspring sex (table 2). First, as mothers gro sons than for daughters (Altmann *et al.* 1988). Thus, sub-
ordinate females would often gain a higher productivity
through sons, whereas dominants would gain more
through daughters However Van Schaik & Hrdy (1991) ordinate females would often gain a higher productivity
through sons, whereas dominants would gain more
through daughters. However, Van Schaik & Hrdy (1991)
pointed out that these effects are likely to be restricted to through sons, whereas dominants would gain more
through daughters. However, Van Schaik & Hrdy (1991)
pointed out that these effects are likely to be restricted to
nonulations with extensive female-female connetition through daughters. However, Van Schaik & Hrdy (1991)
pointed out that these effects are likely to be restricted to
populations with extensive female-female competition.
Where LRC is minimal low-ranking daughters should pointed out that these effects are likely to be restricted to
populations with extensive female–female competition.
Where LRC is minimal, low-ranking daughters should *Phil. Trans. R. Soc. Lond.* B (2000)
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suffer less harassment and high-ranking mothers might be better able to enhance the physical development of their sons (Trivers & Willard 1973).

(b) *Multivariate analysis of infant survival and interbirth intervals*

and interbirth intervals
Tables 1 and 2 present the minimal models of a and **interbirth intervals**
Tables 1 and 2 present the minimal models of a
GLMM analysis of infant survival and a GLM analysis
on interbirth interval. In both analyses we tested for Tables 1 and 2 present the minimal models of a
GLMM analysis of infant survival and a GLM analysis
on interbirth interval. In both analyses we tested for
effects of offensing sex, rainfall during the mother's preg-GLMM analysis of infant survival and a GLM analysis
on interbirth interval. In both analyses we tested for
effects of offspring sex, rainfall during the mother's preg-
nancy whether the infant was conceived during the dry on interbirth interval. In both analyses we tested for effects of offspring sex, rainfall during the mother's pregnancy, whether the infant was conceived during the dry season, troop growth rate, troop size, maternal age a effects of offspring sex, rainfall during the mother's pregmaternal rank. Maternal rank and maternal age were the season, troop growth rate, troop size, maternal age and
maternal rank. Maternal rank and maternal age were the
only two factors that significantly influenced offspring
survival (table 1): there were no significant interact maternal rank. Maternal rank and maternal age were the
only two factors that significantly influenced offspring
survival (table 1); there were no significant interactions
involving the sex of the offspring. The analysis of only two factors that significantly influenced offspring
survival (table 1); there were no significant interactions
involving the sex of the offspring. The analysis of inter-
hirth intervals revealed two significant intera survival (table 1); there were no significant interactions birth intervals revealed two significant interactions with birth intervals revealed two significant interactions with
offspring sex (table 2). First, as mothers grow older, they
take longer to 'fledge' sons, whereas they fledge daughters
more quickly (figure 6*a*). These findings offspring sex (table 2). First, as mothers grow older, they
take longer to 'fledge' sons, whereas they fledge daughters
more quickly (figure 6*a*). These findings suggest that,
whereas mothers become increasingly adent at take longer to 'fledge' sons, whereas they fledge daughters
more quickly (figure 6a). These findings suggest that,
whereas mothers become increasingly adept at raising
daughters they find it increasingly difficult to raise more quickly (figure $6a$). These findings suggest that, whereas mothers become increasingly adept at raising daughters, they find it increasingly difficult to raise sons. Second, although dominance rank does not influenc whereas mothers become increasingly adept at raising

Table 2. *Minimal GLM model for effects on interbirth intervals*

long it takes a mother to rear her son, high-ranking long it takes a mother to rear her son, high-ranking
females are able to rear daughters more quickly than are
low-ranking females (figure 6b), a trend consistent with long it takes a mother to rear her son, high-ranking
females are able to rear daughters more quickly than are
low-ranking females (figure 6*b*), a trend consistent with
that found by Gommendio *et al.* (1990) Note that in females are able to rear daughters more quickly than are low-ranking females (figure 6*b*), a trend consistent with that found by Gommendio *et al.* (1990). Note that interlow-ranking females (figure $6b$), a trend consistent with
that found by Gommendio *et al.* (1990). Note that inter-
birth intervals showed no significant interaction between
offering sex and any of our measures of LBC. T that found by Gommendio *et al.* (1990). Note that inter-
birth intervals showed no significant interaction between
offspring sex and any of our measures of LRC. This
means that low-ranking mothers in large troops (for birth intervals showed no significant interaction between
offspring sex and any of our measures of LRC. This
means that low-ranking mothers in large troops (for
example) found it no more difficult to raise daughters offspring sex and any of our measures of LRC. This
means that low-ranking mothers in large troops (for
example) found it no more difficult to raise daughters means that low-ranking mothers in large troops (for than sons, compared with mothers in small troops.
(c) *Sex ratio analysis*

 Y_0
(c) **Sex ratio analysis**
The population sex ratio deviated significantly from (finite). (c) **Sex ratio analysis**
The population sex ratio deviated significantly from
50:50; 55% of 662 live-born infants were male
 $(x^2 - 6.187, h < 0.02)$ Five of six stillborn or miscarried $(\chi^2 = 6.187, \ p < 0.02)$. Five of six stillborn or miscarried The population sex ratio deviated significantly from

2.50; 55% of 662 live-born infants were male
 $e^2 = 6.187$, $p < 0.02$). Five of six stillborn or miscarried

Forther were male suggesting that the primary sex ratio 50:50; 55% of 662 live-born infants were male $(\chi^2 = 6.187, p < 0.02)$. Five of six stillborn or miscarried offspring were male, suggesting that the primary sex ratio might be even more male biased than at birth. Although $(\chi^2 = 6.187, p < 0.02)$. Five of six stillborn or miscarried
offspring were male, suggesting that the primary sex ratio
might be even more male biased than at birth. Although
no factor significantly influenced sex ratio in offspring were male, suggesting that the primary sex ratio
might be even more male biased than at birth. Although
no factor significantly influenced sex ratio in a univariate
analysis, the GIMM model revealed that maternal might be even more male biased than at birth. Although
no factor significantly influenced sex ratio in a univariate
analysis, the GLMM model revealed that maternal rank
interacted significantly with age and with dry-season interaction in a univariate they aged (figure $7a$). It is therefore unclear analysis, the GLMM model revealed that maternal rank these sex ratio variations are in any way adaptive.
interacted significantly with age and w analysis, the GLMM model revealed that maternal rank
interacted significantly with age and with dry-season
rainfall (table 3). The sex ratio of high-ranking mothers
became male biased as they grew older whereas the sex interacted significantly with age and with dry-season
rainfall (table 3). The sex ratio of high-ranking mothers
became male biased as they grew older, whereas the sex
ratio of subordinate mothers was male biased when they rainfall (table 3). The sex ratio of high-ranking mothers
became male biased as they grew older, whereas the sex
ratio of subordinate mothers was male biased when they
were young (figure $7a$). The sex ratio of high-ranki became male biased as they grew older, whereas the sex
ratio of subordinate mothers was male biased when they
were young (figure 7*a*). The sex ratio of high-ranking
mothers was unaffected by dry-season rainfall, but lowratio of subordinate mothers was male biased when they
were young (figure 7*a*). The sex ratio of high-ranking
mothers was unaffected by dry-season rainfall, but low-
ranking mothers shifted their sex ratio from female were young (figure 7*a*). The sex ratio of high-ranking
mothers was unaffected by dry-season rainfall, but low-
ranking mothers shifted their sex ratio from female
biased during barsh years to male biased during mild Omothers was unaffected by dry-season rainfall, but low-

biased female-biased sex ratios after harsh winters,

biased during mothers shifted their sex ratio from female

biased during mild

biased during mild

biased in biased during harsh years to male biased during mild

4. DISCUSSION

None of these data are easy to interpret. The popula-None of these data are easy to interpret. The popula-
tion sex ratio is significantly male biased, but sons and fall patterns are highly erratic at Gombe, with a lag (i.e. daughters do not differ in infant mortality nor in their tion sex ratio is significantly male biased, but sons and
daughters do not differ in infant mortality nor in their
impact on the survival of younger siblings or on their
mother's subsequent reproductive rate. If we assume daughters do not differ in infant mortality nor in their
impact on the survival of younger siblings or on their
mother's subsequent reproductive rate. If we assume a
population-wide effect of LBC from additional females in impact on the survival of younger siblings or on their
mother's subsequent reproductive rate. If we assume a
population-wide effect of LRC from additional females in *Population-wide effect of LRC from additional females in Phil. Trans. R. Soc. Lond.* B (2000)

each troop (figure 2), each female adds only 10.4 days to
an average interbirth interval of 670 days; this is far too each troop (figure 2), each female adds only 10.4 days to
an average interbirth interval of 670 days; this is far too
small to account for the 22% excess of males each troop (figure 2), each female adds only 1
an average interbirth interval of 670 days; this
small to account for the 22% excess of males.
Contrary to the assumptions of Van Schaik an average interbirth interval of 670 days; this is far too small to account for the 22% excess of males.
Contrary to the assumptions of Van Schaik & Hrdy's

small to account for the 22% excess of males.
Contrary to the assumptions of Van Schaik & Hrdy's
(1991) meta-analysis, the relative costs of raising sons and
daughters did not vary with changes in I RC as measured Contrary to the assumptions of Van Schaik & Hrdy's
(1991) meta-analysis, the relative costs of raising sons and
daughters did not vary with changes in LRC as measured
by troop growth rates or by troop size. The relative co (1991) meta-analysis, the relative costs of raising sons and
daughters did not vary with changes in LRC as measured
by troop growth rates or by troop size. The relative costs
of daughters and sons did change with maternal daughters did not vary with changes in LRC as measured by troop growth rates or by troop size. The relative costs of daughters and sons did change with maternal age, but the relationship between age and sex ratio was complex. Young mothers take longer to rear daughters than to of daughters and sons did change with maternal age, but
the relationship between age and sex ratio was complex.
Young mothers take longer to rear daughters than to rear
sons, whereas older mothers take longer to rear sons the relationship between age and sex ratio was complex. Young mothers take longer to rear daughters than to rear
sons, whereas older mothers take longer to rear sons
(figure 6*a*), predicting that mothers should have sons when
they are young and daughters when they are old. Alt sons, whereas older mothers take longer to rear sons
(figure 6*a*), predicting that mothers should have sons when
they are young and daughters when they are old. Although
young subordinate females did have more sons, their (figure 6*a*), predicting that mothers should have sons when
they are young and daughters when they are old. Although
young subordinate females did have more sons, their sex
ratios became unbiased as they grew older wherea they are young and daughters when they are old. Although
young subordinate females did have more sons, their sex
ratios became unbiased as they grew older, whereas domiyoung subordinate females did have more sons, their sex
ratios became unbiased as they grew older, whereas domi-
nant mothers had increasingly male-biased sex ratios as
they aged (figure $7a$). It is therefore unclear whe ratios became unbiased as they grew older, whereas dominant mothers had increasingly male-biased sex ratios as
they aged (figure 7*a*). It is therefore unclear whether
these sex ratio variations are in any way adaptive nant mothers had increasingly male-biased sex rat
they aged (figure 7*a*). It is therefore unclear with
these sex ratio variations are in any way adaptive.
Daughters are costlier to low-ranking females (figure they aged (figure 7*a*). It is therefore unclear whether
these sex ratio variations are in any way adaptive.
Daughters are costlier to low-ranking females (figure 6*b*),

these sex ratio variations are in any way adaptive.
Daughters are costlier to low-ranking females (figure 6*b*),
but subordinate females produce excess daughters after
the harshest dry seasons (figure 7*b*). The interacti Daughters are costlier to low-ranking females (figure $6b$),
but subordinate females produce excess daughters after
the harshest dry seasons (figure 7*b*). The interaction
between rainfall and rank is analogous to the res the harshest dry seasons (figure $7b$). The interaction between rainfall and rank is analogous to the results of the harshest dry seasons (figure 7*b*). The interaction
between rainfall and rank is analogous to the results of
Kruuk *et al.* (1999), in which red deer (of all ranks)
showed female-biased sex ratios after harsh winters between rainfall and rank is analogous to the results of Kruuk *et al.* (1999), in which red deer (of all ranks) showed female-biased sex ratios after harsh winters, possibly owing to bigher foetal mortality in males Kruuk et al. (1999), in which red deer (of all ranks) showed female-biased sex ratios after harsh winters, possibly owing to higher foetal mortality in males.
However miscarriages are more common in highshowed female-biased sex ratios after harsh winters, possibly owing to higher foetal mortality in males.
However, miscarriages are more common in high-
ranking Gombe females than in subordinates (Packer *et*
 a^{l} 1995) and low-ranking females show male-biased sex *However, miscarriages are more common in high-
ranking Gombe females than in subordinates (Packer <i>et*
al. 1995), and low-ranking females show male-biased sex
ratios after mild dry seasons (which would require the ranking Gombe females than in subordinates (Packer *et al.* 1995), and low-ranking females show male-biased sex ratios after mild dry seasons (which would require the selective abortion of daughters when conditions were al. 1995), and low-ranking females show male-biased sex ratios after mild dry seasons (which would require the selective abortion of daughters when conditions were exceptionally good). Regardless of the mechanism, rain-
fall patterns are highly erratic at Gombe, with a lag₁ (i.e.
one year lag) correlation of only 0.097 (*n* = 27 years). A
harsh dry season should therefore be viewed fall patterns are highly erratic at Gombe, with a lag_l (i.e.
one year lag) correlation of only 0.097 ($n = 27$ years). A
harsh dry season should therefore be viewed as a stressor
rather than a predictor of future condi one year lag) correlation of only 0.097 ($n = 27$ years). A harsh dry season should therefore be viewed as a stressor rather than a predictor of future conditions, and the variation in figure 7*h* is unlikely to be adaptiv harsh dry season should therefore be viewed as a stressor rather than a predictor of future conditions, and the variation in figure 7*b* is unlikely to be adaptive.

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Figure 6. Significant interactions on interbirth intervals that include offspring sex. (*a*) With increasing maternal age, interlintervals become shorter after the birth of a daughter but longer after the birth of a son. (Figure 6. Significant interactions on interbirth intervals that include offspring sex. (a) With increasing maternal age, interbirth intervals become shorter after the birth of a daughter but longer after the birth of a so

It is hard to reconcile our data with the clear advantages of sex ratio variation reported for birds (Komdeur It is hard to reconcile our data with the clear advantages of sex ratio variation reported for birds (Komdeur *et al.* 1997; Sheldon *et al.* 1999) and red deer (Kruuk *et al.* 1999). One possibility is that the Gombe babo tages of sex ratio variation reported for birds (Komdeur *et al.* 1997; Sheldon *et al.* 1999) and red deer (Kruuk *et al.* 1999). One possibility is that the Gombe baboons gain important advantages from factors that we ha *et al.* 1997; Sheldon *et al.* 1999) and red deer (Kruuk *et al.* 1999). One possibility is that the Gombe baboons gain important advantages from factors that we have over-looked in our analysis. Perhans young subordinate 1999). One possibility is that the Gombe baboons gain
important advantages from factors that we have over-
looked in our analysis. Perhaps young subordinates and older dominants gain unsuspected bene¢ts from sons; or looked in our analysis. Perhaps young subordinates and
older dominants gain unsuspected benefits from sons; or
perhaps the results in figure 7 are misleading and the
Gombe baboons are unable to alter their sex ratios older dominants gain unsuspected benefits from sons; or
perhaps the results in figure 7 are misleading and the
Gombe baboons are unable to alter their sex ratios
adaptively. It is possible that these females gain fewer perhaps the results in figure 7 are misleading and the Gombe baboons are unable to alter their sex ratios adaptively. It is possible that these females gain fewer advantages from altering their sex ratios than other popula Gombe baboons are unable to alter their sex ratios
adaptively. It is possible that these females gain fewer
advantages from altering their sex ratios than other popu-
lations. Although the interbirth intervals in figure 6 adaptively. It is possible that these females gain fewer
advantages from altering their sex ratios than other popu-
lations. Although the interbirth intervals in figure 6 *Phil. Trans. R. Soc. Lond.* B (2000)

would translate into an advantage of $10-25%$ to any
female who could control ber sex ratio, there is no strong would translate into an advantage of 10–25% to any
female who could control her sex ratio, there is no strong
effect of maternal rank on offspring fitness in this populawould translate into an advantage of $10-25%$ to any
female who could control her sex ratio, there is no strong
effect of maternal rank on offspring fitness in this popula-
tion (see for example figure 4). In contrast, bi female who could control her sex ratio, there is no strong
effect of maternal rank on offspring fitness in this popula-
tion (see, for example, figure 4). In contrast, high rank
confers strong fitness effects on adult sons effect of maternal rank on offspring fitness in this population (see, for example, figure 4). In contrast, high rank confers strong fitness effects on adult sons in red deer (Clutton-Brock *et al.* 1986); and high-ranking tion (see, for example, figure 4). In contrast, high rank
confers strong fitness effects on adult sons in red deer
(Clutton-Brock *et al.* 1986); and high-ranking Amboseli
baboons might impart high fitness to their adult d confers strong fitness effects on adult sons in red deer (Clutton-Brock *et al.* 1986); and high-ranking Amboseli baboons might impart high fitness to their adult daugh-
ters as well as gain a higher productivity from a f (Clutton-Brock *et al.* 1986); and high-ranking Amboseli
baboons might impart high fitness to their adult daugh-
ters as well as gain a higher productivity from a female-
biased sex ratio (Altmann *et al.* 1988) baboons might impart high fitness to ters as well as gain a higher productive biased sex ratio (Altmann *et al.* 1988).
In contrast, Gombe, might, have

biased sex ratio (Altmann *et al.* 1988).
In contrast, Gombe might have undergone such biased sex ratio (Altmann *et al.* 1988).
In contrast, Gombe might have undergone such
profound ecological perturbations that the baboons are
not yet adapted to current circumstances. Gombe became In contrast, Gombe might have undergone such
profound ecological perturbations that the baboons are
not yet adapted to current circumstances. Gombe became

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Figure 7. Interactions between maternal rank, maternal age and dry-season rainfall on offspring sex. (a) Daughters have more Figure 7. Interactions between maternal rank, maternal age and dry-season rainfall on offspring sex. (*a*) Daughters have more
daughters when they are younger, whereas dominant females have more sons as they grow older. (Figure 7. Interactions between maternal rank, maternal age and dry-season rainfall on offspring sex. (a) Daught
daughters when they are younger, whereas dominant females have more sons as they grow older. (b) Subordinate

a reserve in 1943 when the human inhabitants were rea reserve in 1943 when the human inhabitants were re-
located (Kjekshus 1977), and the amount of vegetation
has increased continuously in the absence of cultivation a reserve in 1943 when the human inhabitants were re-
located (Kjekshus 1977), and the amount of vegetation
has increased continuously in the absence of cultivation
and fire Consequently the 90 individuals in the original located (Kjekshus 1977), and the amount of vegetation
has increased continuously in the absence of cultivation
and fire. Consequently the 90 individuals in the original and fire. Consequently the 90 individuals in the original *Phil. Trans. R. Soc. Lond.* B (2000)

to have daughters after a harsh dry season.
study increased to 260 animals between 1967 and 1996.
The male-biased population sex, ratio might, reflect an study increased to 260 animals between 1967 and 1996.
The male-biased population sex ratio might reflect an study increased to 260 animals between 1967 and 1996.
The male-biased population sex ratio might reflect an
ancestral adaptation to a harsher environment (with a
concomitantly higher mortality of male foetuses) which The male-biased population sex ratio might reflect an ancestral adaptation to a harsher environment (with a concomitantly higher mortality of male foetuses), which

would have resulted in a 50:50 sex ratio at birth. Under current conditions, the relative costs to high- and lowwould have resulted in a 50:50 sex ratio at birth. Under
current conditions, the relative costs to high- and low-
ranking females of producing sons and daughters might
have been abnormal. However, most of the data in Van current conditions, the relative costs to high- and low-
ranking females of producing sons and daughters might
have been abnormal. However, most of the data in Van
Schaik & Hrdv's review came from cantivity in which ranking females of producing sons and daughters might
have been abnormal. However, most of the data in Van
Schaik & Hrdy's review came from captivity, in which
'ecological conditions' were totally outside the experience have been abnormal. However, most of the data in Van Schaik & Hrdy's review came from captivity, in which 'ecological conditions' were totally outside the experience Schaik & Hrdy's review came from captivity, in which 'ecological conditions' were totally outside the experience of any species, and the study by Kruuk *et al.* (1999) was conducted in a novel environment 'ecological conditions' were totally of
of any species, and the study by Kr
conducted in a novel environment.
We can conclude only that prime any species, and the study by Kruuk *et al.* (1999) was
nducted in a novel environment.
We can conclude only that primate sex ratios remain
oblematic even after a fine-grained and ecologically

conducted in a novel environment.
We can conclude only that primate sex ratios remain
problematic, even after a fine-grained and ecologically
sensitive analysis. It remains mysterious why some nonu-We can conclude only that primate sex ratios remain
problematic, even after a fine-grained and ecologically
sensitive analysis. It remains mysterious why some popu-
lations modify their sex ratios according to precise evol problematic, even after a fine-grained and ecologically
sensitive analysis. It remains mysterious why some popu-
lations modify their sex ratios according to precise evolu-
tionary predictions whereas others do not. A more sensitive analysis. It remains mysterious why some populations modify their sex ratios according to precise evolutionary predictions whereas others do not. A more serious lations modify their sex ratios according to precise evolutionary predictions whereas others do not. A more serious consideration of the significance of `non-significant' results is overdue tionary predictions
consideration of t
results is overdue.

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