

BIOLOGICAL
SCIENCES

THE ROYAL

PHILOSOPHICAL
TRANSACTIONS ৳

collective action Genomic imprinting, sibling solidarity and the logic of

David Haig and Jon F. Wilkins

doi: 10.1098/rstb.2000.0720 Phil. Trans. R. Soc. Lond. B 2000 **355**, 1593-1597

References <http://rstb.royalsocietypublishing.org/content/355/1403/1593#related-urls> Article cited in:

Email alerting service Receive free email alerts when new articles cite
top right-hand corner of the article or click **[here](http://rstb.royalsocietypublishing.org/cgi/alerts/ctalert?alertType=citedby&addAlert=cited_by&saveAlert=no&cited_by_criteria_resid=royptb;355/1403/1593&return_type=article&return_url=http://rstb.royalsocietypublishing.org/content/355/1403/1593.full.pdf)** Receive free email alerts when new articles cite this article - sign up in the box at the

To subscribe to Phil. Trans. R. Soc. Lond. B go to: **<http://rstb.royalsocietypublishing.org/subscriptions>**

BIOLOGICAL
SCIENCES

THE ROYAL *SOCIETY*

PHILOSOPHICAL
TRANSACTIONS

GENAL
 Genomic imprinting, sibling solidarity

and the logie of collective estion **and the logic of collective action**
and the logic of collective action

David Haig* **and Jon F. Wilkins**

Department of Organismic and Evolutionary Biology, Harvard University, Cambridge, MA 02138, USA

Department of Organismic and Evolutionary Biology, Harvard University, Cambridge, MA 02138, USA
Genomic imprinting has been proposed to evolve when a gene's expression has fitness consequences for
individuals with differen Genomic imprinting has been proposed to evolve when a gene's expression has fitness consequences for individuals with different coefficients of matrilineal and patrilineal relatedness, especially in the context of competit Genomic imprinting has been proposed to evolve when a gene's expression has fitness consequences for individuals with different coefficients of matrilineal and patrilineal relatedness, especially in the context of competit individuals with different coefficients of matrilineal and patrilineal relatedness, especially in the context
of competition between offspring for maternal resources. Previous models have focused on pre-emptive
hierarchies of competition between offspring for maternal resources. Previous models have focused on pre-emptive
hierarchies, where conflict arises with respect to resource allocation between present and future offspring.
Here we pres hierarchies, where conflict arises with respect to resource allocation between present and future offspring.
Here we present a model in which imprinting arises from scramble competition within litters. The model
predicts p but reduces the size of the resource pool, and maternal-specific expression of a gene with opposite effects. predicts paternal-specific expression of a gene that increases an offspring's fractional share of resources
but reduces the size of the resource pool, and maternal-specific expression of a gene with opposite effects.
These but reduces the size of the resource pool, and maternal-specific expression of a gene with opposite effects.
These predictions parallel the observation in economic models that individuals tend to underprovide
public goods, These predictions parallel the observation in economic models that individuals tend to underprovide
public goods, and that the magnitude of this shortfall increases with the number of individuals in the
group. Maternally d public goods, and that the magnitude of this shortfall increases with the number of individuals in the group. Maternally derived alleles are more willing than their paternally derived counterparts to contribute to public g Maternary derived ancies are more winnig than their paternary derived counterpart
bute to public goods because they have a smaller effective group size.
Keywords: genomic imprinting; public goods; evolutionarily stable s

we a smaner enective grou
ublic goods; evolutionaril
scramble competition

1. INTRODUCTION

Models of sibling competition address how a set of sibs-**COLLET ISLAMED ANDELLA COLLET SUBS**

or rather the genes expressed in a set of sibs—divide

something of value (such as resources or parental invest-Models of sibling competition address how a set of sibs—
or rather the genes expressed in a set of sibs—divide
something of value (such as resources or parental invest-
ment) between themselves. These models can be grouned or rather the genes expressed in a set of sibs—divide
something of value (such as resources or parental invest-
ment) between themselves. These models can be grouped
into two broad classes: (i) models of pre-emptive biersomething of value (such as resources or parental invest-
ment) between themselves. These models can be grouped
into two broad classes: (i) models of pre-emptive hier-
archies, and (ii) models of scramble competition (Mock into two broad classes: (i) models of pre-emptive hierinto two broad classes: (i) models of pre-emptive hierarchies, and (ii) models of scramble competition (Mock & Parker 1997). The distinction can be illustrated by an analogy in which the resource to be divided is represent archies, and (ii) models of scramble competition (Mock & Parker 1997). The distinction can be illustrated by an analogy in which the resource to be divided is represented by a milkshake (Hair 1992). In hierarchy models a q & Parker 1997). The distinction can be illustrated by an analogy in which the resource to be divided is represented by a milkshake (Haig 1992). In hierarchy models, a queue of offenring wait in line to suck on a single str analogy in which the resource to be divided is represented
by a milkshake (Haig 1992). In hierarchy models, a queue
of offspring wait in line to suck on a single straw. The
more milk that is taken by the individual at the by a milk shake (Haig 1992). In hierarchy models, a queue of offspring wait in line to suck on a single straw. The
more milk that is taken by the individual at the head of
the queue, the less that is available for other offspring
who are yet to take their turn. Such models apply more milk that is taken by the individual at the head of
the queue, the less that is available for other offspring
who are yet to take their turn. Such models apply to
situations in which offspring are produced sequentiall the queue, the less that is available for other offspring to subset of the conceived sequentially—
situations in which offspring are produced sequentially—
an offensing yet to be conceived can do little to limit the who are yet to take their turn. Such models apply to situations in which offspring are produced sequentially—an offspring yet to be conceived can do little to limit the situations in which offspring are produced sequentially—
an offspring yet to be conceived can do little to limit the
resources consumed by an older sib—but also to competi-
tion within litters if the most dominant sib is f an offspring yet to be conceived can do little to limit the resources consumed by an older sib—but also to competition within litters, if the most dominant sib is free to choose how much she takes, the next most dominant i resources consumed by an older sib—but also to competition within litters, if the most dominant sib is free to choose how much she takes, the next most dominant is free to choose how much of the remainder he takes and tion within litters, if the most dominant sib is free to choose how much she takes, the next most dominant is free to choose how much of the remainder he takes, and so on By contrast in models of scramble competition choose how much she takes, the next most dominant is
free to choose how much of the remainder he takes, and
so on. By contrast, in models of scramble competition,
each offenring has its own straw and all suck at once free to choose how much of the remainder he takes, and
so on. By contrast, in models of scramble competition,
each offspring has its own straw and all suck at once.
Such models apply to competition within litters when so on. By contrast, in models of scramble competition,
each offspring has its own straw and all suck at once.
Such models apply to competition within litters when
stronger offspring are unable to exclude weaker offspring each offspring has its own straw and all suck at once.
Such models apply to competition within litters when
stronger offspring are unable to exclude weaker offspring
from access to a resource Such models apply to constronger offspring are unab
from access to a resource.
The crucial difference be stronger offspring are unable to exclude weaker offspring
from access to a resource.
The crucial difference between the two types of model

from access to a resource.
The crucial difference between the two types of model
is who bears the cost of increased consumption. If the
queue of offensing in a single-straw model contains a The crucial difference between the two types of model
is who bears the cost of increased consumption. If the
queue of offspring in a single-straw model contains a
random mixture of greedy and abstemious genotypes is who bears the cost of increased consumption. If the
queue of offspring in a single-straw model contains a
random mixture of greedy and abstemious genotypes,
members of both classes will suffer when the milkshake queue of offspring in a single-straw model contains a
random mixture of greedy and abstemious genotypes,
members of both classes will suffer when the milkshake
runs dry whereas if some offspring suck harder than

others in a multi-straw model, the offspring with higher sucking rates increase their intake at the expense of the others in a multi-straw model, the offspring with higher
sucking rates increase their intake at the expense of the
poor suckers (Haig 1992). Roughly speaking, sibling greed
is limited by relatedness in single-straw models, sucking rates increase their intake at the expense of the
poor suckers (Haig 1992). Roughly speaking, sibling greed
is limited by relatedness in single-straw models, but not
in multi-straw models (Metcalf *et al*, 1979) poor suckers (Haig 1992). Roughly speaking,
is limited by relatedness in single-straw mo
in multi-straw models (Metcalf *et al.* 1979).
Single-straw models predict, the evolution is limited by relatedness in single-straw models, but not
in multi-straw models (Metcalf *et al.* 1979).
Single-straw models predict the evolution of genomic

imprinting (gene expression specific to parent of origin) Single-straw models predict the evolution of genomic
imprinting (gene expression specific to parent of origin)
at loci that influence an offspring's consumption of
maternal recources if an allele's effects when maternally imprinting (gene expression specific to parent of origin)
at loci that influence an offspring's consumption of
maternal resources if an allele's effects when maternally
derived are evolutionarily senarable from its effects at loci that influence an offspring's consumption of
maternal resources if an allele's effects when maternally
derived are evolutionarily separable from its effects when
naternally derived (Haig 1992: Mochizuki *et al* 199 maternal resources if an allele's effects when maternally
derived are evolutionarily separable from its effects when
paternally derived (Haig 1992; Mochizuki *et al.* 1996).
That is whenever mothers have offerring by more derived are evolutionarily separable from its effects when
paternally derived (Haig 1992; Mochizuki *et al.* 1996).
That is, whenever mothers have offspring by more than
one father, two randomly chosen sibs will be more li paternally derived (Haig 1992; Mochizuki *et al.* 1996).
That is, whenever mothers have offspring by more than
one father, two randomly chosen sibs will be more likely
to share alleles inherited from their mother than all That is, whenever mothers have offspring by more than
one father, two randomly chosen sibs will be more likely
to share alleles inherited from their mother than alleles
inherited from their father(s). Therefore, the inclus one father, two randomly chosen sibs will be more likely
to share alleles inherited from their mother than alleles
inherited from their father(s). Therefore, the inclusive-
fitness cost of reduced maternal investment in fu to share alleles inherited from their mother than alleles
inherited from their father(s). Therefore, the inclusive-
fitness cost of reduced maternal investment in future
offension will be greater for an offension's materna inherited from their father(s). Therefore, the inclusive-
fitness cost of reduced maternal investment in future
offspring will be greater for an offspring's maternally
derived alleles than for its paternally derived allele fitness cost of reduced maternal investment in future offspring will be greater for an offspring's maternally derived alleles than for its paternally derived alleles, and alleles of paternal origin will be selected to take offspring will be greater for an offspring's maternally derived alleles than for its paternally derived alleles, and origin. Share of maternal investment than will alleles of maternal
origin.
At first sight, multi-straw models seem inimical to the

members of both classes will suffer when the milkshake restraint by offspring with the allele merely frees
runs dry, whereas, if some offspring suck harder than resources for sibs without the allele. For this reason,
multi evolution of genomic imprinting. Any newly arisen allele that increases an offspring's demand is seemingly evolution of genomic imprinting. Any newly arisen allele
that increases an offspring's demand is seemingly
favoured by natural selection, regardless of the allele's
parental origin, because litter-mates with the allele tak that increases an offspring's demand is seemingly
favoured by natural selection, regardless of the allele's
parental origin, because litter-mates with the allele take
resources from those without the allele Conversely any favoured by natural selection, regardless of the allele's
parental origin, because litter-mates with the allele take
resources from those without the allele. Conversely, any
allele, that reduces an offensing's demand, eith parental origin, because litter-mates with the allele take
resources from those without the allele. Conversely, any
allele that reduces an offspring's demand, either by
producing less of a demand enhancer or more of a resources from those without the allele. Conversely, any allele that reduces an offspring's demand, either by
producing less of a demand enhancer or more of a
demand inhibitor, is disadvantaged when rare because
restraint by offspring with the allele merely frees producing less of a demand enhancer or more of a
demand inhibitor, is disadvantaged when rare because
restraint by offspring with the allele merely frees
resources for sibs without the allele For this reason demand inhibitor, is disadvantaged when rare because
restraint by offspring with the allele merely frees
resources for sibs without the allele. For this reason,
multi-straw, models predict an infinite escalation of restraint by offspring with the allele merely frees demand if increased solicitation is without cost. However,

unbounded escalation of demand is prevented if costs of
solicitation are included in the models $(M_2cN_3)r$, k unbounded escalation of demand is prevented if costs of (the solicitation are included in the models (MacNair & the Parker 1979) Such costs create an opportunity for natural unbounded escalation of demand is prevented if costs of
solicitation are included in the models (MacNair &
Parker 1979). Such costs create an opportunity for natural
selection to act differently on alleles of maternal and solicitation are included in the models (MacNair &
Parker 1979). Such costs create an opportunity for natural
selection to act differently on alleles of maternal and
paternal origin Parker 1979). Such
selection to act
paternal origin.
The model pres selection to act differently on alleles of maternal and paternal origin.
The model presented below $(\S 2)$ shows that paternally

derived alleles will be selected to produce more of a The model presented below $(\S 2)$ shows that paternally
derived alleles will be selected to produce more of a
demand factor than maternally derived alleles, if increased
demand reduces the amount of resources to be divide derived alleles will be selected to produce more of a
demand factor than maternally derived alleles, if increased
demand reduces the amount of resources to be divided
between a set of sibs but increases the share of the di demand factor than maternally derived alleles, if increased
demand reduces the amount of resources to be divided
between a set of sibs but increases the share of the dimin-
ished pool received by offspring that are more de demand reduces the amount of resources to be divided
between a set of sibs but increases the share of the dimin-
ished pool received by offspring that are more demanding.
Conversely, a maternally derived allele that reduce between a set of sibs but increases the share of the dimin-
ished pool received by offspring that are more demanding.
Conversely, a maternally derived allele that reduces an
offspring's level of demand, relative to litter-Conversely, a maternally derived allele that reduces an offspring's level of demand, relative to litter-mates without the allele, can be favoured by natural selection if the offspring's level of demand, relative to litter-mates without
the allele, can be favoured by natural selection if the
reduction in demand causes all offspring (including those
with reduced demand) to be better off the allele, can be favoured by natura
reduction in demand causes all offsprin
with reduced demand) to be better off.

2. A MULTI-STRAW MODEL OF SIBLING COMPETITION

A MULTI-STRAW MODEL OF SIBLING COMPETITION
An evolutionarily stable strategy (ESS) occurs at a
rus when the strategy employed by most alleles in the 2. A MULTI-STRAW MUDEL OF SIBLING COMPETITION

An evolutionarily stable strategy (ESS) occurs at a

locus when the strategy employed by most alleles in the

nonulation cannot be displaced by any alternative An evolutionarily stable strategy (ESS) occurs at a
locus when the strategy employed by most alleles in the
population cannot be displaced by any alternative
strategy that is initially rare (Maynard Smith & Price locus when the strategy employed by most alleles in the
population cannot be displaced by any alternative
strategy that is initially rare (Maynard Smith & Price
1973) Our model will consider two loci: A encoding a population cannot be displaced by any alternative strategy that is initially rare (Maynard Smith & Price strategy that is initially rare (Maynard Smith & Price 1973). Our model will consider two loci: A , encoding a demand-factor antagonist Two alleles will be considered at each locus: 1973). Our model will consider two loci: A , encoding a demand-factor antagonist. Two alleles will be considered at each locus:
an established allele nossessed in homozygous form by demand factor, and B , encoding a demand-factor antagonist. Two alleles will be considered at each locus:
an established allele possessed in homozygous form by most individuals in the population, and a rare allele an established allele possessed in homozygous form by
most individuals in the population, and a rare allele
possessed by a few heterozygous individuals. The estab-
lished allele's strategy will constitute an ESS if all rar most individuals in the population, and a rare allele
possessed by a few heterozygous individuals. The estab-
lished allele's strategy will constitute an ESS if all rare
alternative strategies are associated with lower fit possessed by a few heterozygous individuals. The established allele's strategy will constitute an ESS if all rare alternative strategies are associated with lower fitness. For the nurnoses of investigating genomic imprinti lished allele's strategy will constitute an ESS if all rare
alternative strategies are associated with lower fitness. For
the purposes of investigating genomic imprinting, each
allele's strategy will be represented by a tw alternative strategies are associated with lower fitness. For
the purposes of investigating genomic imprinting, each
allele's strategy will be represented by a two-element
vector, the first element of which represents the the purposes of investigating genomic imprinting, each
allele's strategy will be represented by a two-element
vector, the first element of which represents the allele's
level of expression when maternally derived and the allele's strategy will be represented by a two-element vector, the first element of which represents the allele's level of expression when maternally derived and the second element its level of expression when paternally level of expression when maternally derived and the
second element its level of expression when paternally
derived. We shall assume that the value of the first
element is evolutionarily unconstrained by the value of second element its level of expression when paternally
derived. We shall assume that the value of the first
element is evolutionarily unconstrained by the value of
the second element (and vice versa) derived. We shall assume that the
element is evolutionarily unconstrain
the second element (and vice versa).
At the demand-factor locus, the

element is evolutionarily unconstrained by the value of
the second element (and vice versa).
At the demand-factor locus, the established allele A_1
has strategy $\{x_1^m, x_1^p\}$ and the rare allele A_2 has strategy
 $_{1}^{\mathrm{m}},x_{1}^{\mathrm{p}}$ a (and vice versa).
factor locus, the established allele A_1
 A_1
 B_2 and the rare allele A_2 has strategy
is rare A_2 . genotines are very rare $\{x_{\,2}^{\rm m}, x_{\,2}^{\rm p}\}.$ the demand-factor locus, the established allele A_1
rategy $\{x_1^m, x_1^p\}$ and the rare allele A_2 has strategy
 $\{x_2^p\}$. When A_2 is rare, A_2A_2 genotypes are very rare,
*i*ll be ignored $A_1A_2A_3A_4A_5$ o has strategy $\{x_1^m, x_1^p\}$ and the rare allele A_2 has strategy $\{x_2^m, x_2^p\}$. When A_2 is rare, A_2A_2 genotypes are very rare, and will be ignored. A_1A_1 , A_2A_1 , A_1A_2 offspring (mater-
nally deri $\{x_2^m, x_2^p\}$. When A_2 is rare, A_2A_2 genotypes are very ra
and will be ignored. A_1A_1 , A_2A_1 , A_1A_2 offspring (mat
nally derived alleles listed first) produce amounts X_1 , X
 X where nally derived alleles listed first) produce amounts X_1 , X_m , X_p , where d will be
lly derived
, where

$$
\begin{cases}\nX_1 = x_1^m + x_1^p, \\
X_m = x_2^m + x_1^p, \\
X_p = x_1^m + x_2^p, \\
x_1^m, x_1^p, x_2^m, x_2^p \ge 0.\n\end{cases}
$$
\n(1*a*)

At the antagonist locus, the established allele B_1 has strategy $\{y_1^m, y_1^p\}$ nist locus, the established allele B_1 has $\begin{bmatrix} p_1 \\ p_2 \end{bmatrix}$, the rare allele B_2 has strategy $\{y^m_2, y^p_2\}$
and *B.B.* offensing produce *Y*. *Y*, and *Y*. strategy $\{y_1^m, y_1^p\}$ the rare allele B_2 has strategy $\{y_2^m, y_2^p\}$
and B_1B_1 , B_2B_1 and B_1B_2 offspring produce \mathcal{Y}_1 , \mathcal{Y}_m and \mathcal{Y}_p : antagonist locus, the established alle
 $\{y_1^m, y_1^p\}$ the rare allele B_2 has strategy
, B_2B_1 and B_1B_2 offspring produce $\mathcal{Y}_1, \mathcal{Y}_1$

$$
\begin{cases}\nT_1 = y_1^m + y_1^p, \\
T_m = y_2^m + y_1^p, \\
T_p = y_1^m + y_2^p, \\
y_1^m, y_1^p, y_2^m, y_2^p \ge 0.\n\end{cases}
$$
\n(1*b*)

 $y_1^m, y_1^p, y_2^m, y_2^p \ge 0.$
An offspring's level of demand \mathcal{Z}_{\bullet} is assumed to be an
increasing function of Y but a decreasing function of Y An offspring's level of demand \mathcal{Z}_{\bullet} is assumed to be an increasing function of X_{\bullet} but a decreasing function of Y_{\bullet} increasing function of X_{\bullet} but a decreasing function of Y_{\bullet}
Phil. Trans. R. Soc. Lond. B (2000)

(the subscripted dot is used here, and below, as a dummy (the subscripted dot is used here, and below, as a dummy
that can be replaced in any given equation by either p or (the subscripted d
that can be replac
m). Specifically,

$$
\begin{aligned}\n\mathcal{Z}_{\bullet} &= X_{\bullet} f(T_{\bullet}), \\
0 &< f(T_{\bullet}) \le 1, \quad f(0) = 1, \\
\partial f(T_{\bullet})/\partial T_{\bullet} < 0.\n\end{aligned}
$$
\n(2)

For simplicity, the model will consider `average' litters containing a rare allele (rather than summing across all For simplicity, the model will consider 'average' litters
containing a rare allele (rather than summing across all
possible litter compositions). An average heterozygous
carrier of a rare allele belongs to a litter in whic containing a rare allele (rather than summing across all
possible litter compositions). An average heterozygous
carrier of a rare allele belongs to a litter in which he is
one of r heterozygous sibs producing X Y . The possible litter compositions). An average heterozygous carrier of a rare allele belongs to a litter in which he is one of r_{\bullet} heterozygous sibs producing X_{\bullet} , \hat{T}_{\bullet} . The other members of the litter are $(n-r)$ h *r*, heterozygous sibs producing X_{\bullet} , Υ_{\bullet} . The other rs of the litter are $(n-r_{\bullet})$ homozygous sibs produ-
, Y_1 (the model assumes $n > 1$ because scramble ition is absent from 'litters' of a single offensing' carrier of a rare allele belongs to a litter in which he is cing X_1 , Y_1 (the model assumes $n > 1$ because scramble
competition is absent from 'litters' of a single offspring).
All members of the litter are assumed to extract resources
from a common pool of size S, that is a members of the litter are $(n-r_{\bullet})$ homozygous sibs producing X_1 , Y_1 (the model assumes $n > 1$ because scramble competition is absent from 'litters' of a single offspring).
All members of the litter are assumed to ex competition is absent from 'litters' of a single offspring).
All members of the litter are assumed to extract resources
from a common pool of size S_{\bullet} that is a decreasing func-
tion of Z the level of demand of each All members of the litter are assumed to extract resources
from a common pool of size S_{\bullet} that is a decreasing func-
tion of \mathcal{Z}_{\bullet} , the level of demand of each of the heterozygous
offspring: offspring:

$$
S_{\bullet}(\mathcal{Z}_{\bullet}) \ge 0, \quad \frac{\partial S_{\bullet}}{\partial \mathcal{Z}_{\bullet}} < 0. \tag{3}
$$

 $S_{\bullet}(\angle_{\bullet}) \ge 0$, $\frac{\partial \zeta_{\bullet}}{\partial \zeta_{\bullet}} < 0$. (3)
Thus, increased production of the demand factor
increases an offension's fractional share of maternal Thus, increased production of the demand factor increases an offspring's fractional share of maternal resources but decreases the total amount of resources Thus, increased production of the demand factor
increases an offspring's fractional share of maternal
resources but decreases the total amount of resources
available to its litter whereas increased production of the increases an offspring's fractional share of maternal
resources but decreases the total amount of resources
available to its litter, whereas increased production of the
antagonist has opposite effects. Production of the de resources but decreases the total amount of resources
available to its litter, whereas increased production of the
antagonist has opposite effects. Production of the demand
factor confers an individual benefit but a shared available to its litter, whereas increased production of the antagonist has opposite effects. Production of the demand factor confers an individual benefit but a shared cost, whereas production of the antagonist confers a antagonist has opposite effects. Production of the demand
factor confers an individual benefit but a shared cost,
whereas production of the antagonist confers a shared
henefit but an individual cost factor confers an individual b
whereas production of the anti-
benefit but an individual cost.
In the language of trait-group

benefit but an individual cost.
In the language of trait-group selection (Wilson 1977), benefit but an individual cost.

In the language of trait-group selection (Wilson 1977),
 r_m/n is the 'average subjective frequency' of heterozygotes

who inherit the rare allele from their mother whereas In the language of trait-group selection (Wilson 1977),
 r_m/n is the 'average subjective frequency' of heterozygotes

who inherit the rare allele from their mother, whereas
 r/n is the corresponding frequency for hetero r_m/n is the 'average subjective frequency' of heterozygotes who inherit the rare allele from their mother, whereas r_p/n is the corresponding frequency for heterozygotes who inherit the rare allele from their father. If who inherit the rare allele from their mother, whereas r_p/n is the corresponding frequency for heterozygotes who inherit the rare allele from their father. If all litters are sired by a single male $r = r - \frac{1}{r} + 1$ other r_p/n is the corresponding frequency for heterozygotes who inherit the rare allele from their father. If all litters are sired by a single male, $r_p = r_m = \frac{1}{2}(n+1)$, otherwise $r < r - \frac{1}{n+1}$ $r_{\rm p} < r_{\rm m} = \frac{1}{2}(n+1).$ ed by a single male, $r_p = r_m = \frac{1}{2}(n+1)$, otherwise
 $\langle r_m = \frac{1}{2}(n+1)$.

An offspring's fractional share of *S*_• is assumed to be

 $r_p < r_m = \frac{1}{2}(n+1)$.
An offspring's fractional share of S_{\bullet} is assumed to be
the ratio of its own level of demand to the aggregate
demand of the litter. Thus, the amount of resources An offspring's fractional share of S_{\bullet} is assumed to be the ratio of its own level of demand to the aggregate demand of the litter. Thus, the amount of resources acquired by heterogygous offspring considered as a grou the ratio of its own level of demand to the aggregate
demand of the litter. Thus, the amount of resources
acquired by heterozygous offspring considered as a group
 (R_{\bullet}) is given by demand of the litter. Thus, the amount of resources

$$
R_{\bullet} = \frac{r_{\bullet} \mathcal{Z}_{\bullet}}{(n - r_{\bullet}) \mathcal{Z}_{1} + r_{\bullet} \mathcal{Z}_{\bullet}} S_{\bullet}(\mathcal{Z}_{\bullet}).
$$
\n(4)

Finally, we shall assume that a heterozygous offspring's fitness is a monotonically increasing function of R_{\bullet} . Finally, we shall assume that a heterozygous offspring's
fitness is a monotonically increasing function of R_{\bullet} .
Maxima of fitness will therefore occur when R_{\bullet} is maxi-
mized mized. axima of fitness will therefore occur when R_{\bullet} is maxi-
ized.
Before presenting a formal analysis of ESS conditions,
is worth discussing two qualitative ameets of the model

Before presenting a formal analysis of ESS conditions, it is worth discussing two qualitative aspects of the model. Before presenting a formal analysis of ESS conditions,
it is worth discussing two qualitative aspects of the model.
First, the size of the pool of resources, *S*, is maximal
when the demand function \overline{Z} is zero for al it is worth discussing two qualitative aspects of the model.
First, the size of the pool of resources, *S*, is maximal
when the demand function, ζ , is zero for all offspring. ζ
is therefore a measure of the ineffi First, the size of the pool of resources, *S*, is maximal
when the demand function, ζ , is zero for all offspring. ζ
is therefore a measure of the inefficiencies that arise from
sibling rival expression in a model when the demand function, ζ , is zero for all offspring. ζ is therefore a measure of the inefficiencies that arise from sibling rivalry. Second, in a model of pure scramble competition, such as this, a rare allele is therefore a measure of the inefficiencies that arise from sibling rivalry. Second, in a model of pure scramble competition, such as this, a rare allele can increase in frequency only if it increases the amount of resou sibling rivalry. Second, in a model of pure scramble competition, such as this, a rare allele can increase in frequency only if it increases the amount of resources, *R*, obtained by heterozygous offspring. This condition frequency only if it increases the amount of resources, R , obtained by heterozygous offspring. This condition applies to both the demand factor and its antagonist. An allele R , that increases production of the antagon allele B_2 that increases production of the antagonist will by heterozygous offspring. This condition
both the demand factor and its antagonist. An
that increases production of the antagonist will
the fractional share of resources received by applies to both the demand factor and its antagonist. An allele B_2 that increases production of the antagonist will decrease the fractional share of resources received by

BIOLOGICAL
SCIENCES CIENCES

THE ROYA

PHILOSOPHICAL
TRANSACTIONS

BIOLOGICAL

heterozygotes. If such an allele is to increase in frequency, heterozygotes. If such an allele is to increase in frequency,
this decrease in fractional share must be more than
compensated for by an increase in the size of the pool. A heterozygotes. If such an allele is to increase in frequency,
this decrease in fractional share must be more than
compensated for by an increase in the size of the pool. A
similar restriction need not apply in models that this decrease in fractional share must be more than
compensated for by an increase in the size of the pool. A
similar restriction need not apply in models that include
effects on subsequent litters because an increase in i compensated for by an increase in the size of the pool. A similar restriction need not apply in models that include effects on subsequent litters because an increase in inclusive fitness is nossible—despite the decrease in similar restriction need not apply in models that include
effects on subsequent litters because an increase in inclusive
fitness is possible—despite the decrease in individual
fitness—if the benefit to future siblings is s effects on subsequent litters because an increase in inclusive
fitness is possible—despite the decrease in individual **(a)** *Demand-factor ESS*

BIOLOGICAL
SCIENCES

THE ROYAL

PHILOSOPHICAL
TRANSACTIONS

BIOLOGICAL
SCIENCES

PHILOSOPHICAL THE ROYAL

(a) **Demand-factor ESS**
For purposes of describing the ESS at the demand-
tor locus, all alleles at the antagonist locus will be (a) **Demand-factor ESS**
For purposes of describing the ESS at the demand-
factor locus, all alleles at the antagonist locus will be
assumed to be B , As a result all offerring produce the For purposes of α
factor locus, all alle
assumed to be B_1 . of describing the ESS at the demand-
alleles at the antagonist locus will be
. As a result, all offspring produce the
antagonist, and an offspring's share of factor locus, all alleles at the antagonist locus will be assumed to be B_1 . As a result, all offspring produce the same amount of antagonist, and an offspring's share of resources is proportional to its own level of pr assumed to be B_1 . As a result, all offspring produce the same amount of antagonist, and an offspring's share of resources is proportional to its own level of production of demand factor relative to the aggregate produc same amount of antagonist, and an offspring's share of
resources is proportional to its own level of production of
demand factor relative to the aggregate production by its
litter For simplicity $S(X)$ is defined to be the resources is proportional to its own level of production of
demand factor relative to the aggregate production by its
litter. For simplicity, $S_{\bullet}(X_{\bullet})$ is defined to be the size of the
pool of resources for a litter co demand factor relative to the aggregate production by its litter. For simplicity, $S_{\bullet}(X_{\bullet})$ is defined to be the size of the producing X_1 , and r_{\bullet} members producing X_{\bullet} . Therefore, plicity, $S_{\bullet}(X_{\bullet})$ is defined to be the size of the rces for a litter containing $(n-r_{\bullet})$ members , and r_{\bullet} members producing X_{\bullet} . Therefore, of forring considered as a group will receive \bullet heterozygous offspring considered as a group will receive

$$
R_{\bullet} = \frac{r_{\bullet}X_{\bullet}}{(n-r_{\bullet})X_1 + r_{\bullet}X_{\bullet}}S_{\bullet}(X_{\bullet}).
$$
\n⁽⁵⁾

 $K_{\bullet} = \frac{1}{(n-r_{\bullet})X_1 + r_{\bullet}X_{\bullet}} S_{\bullet}(X_{\bullet}).$ (3)
The best strategic response of A_2 to A_1 will occur at
maxima of equation (5) The relevant partial derivatives The best strategic response of A_2 to A_1 will occur at maxima of equation (5). The relevant partial derivatives are $\overline{0}$

$$
\frac{\partial R_{\bullet}}{\partial x_{2}^{\bullet}} = \frac{r_{\bullet} X_{\bullet}}{(n - r_{\bullet}) X_{1} + r_{\bullet} X_{\bullet}} S'_{\bullet}(X_{\bullet}) + \frac{r_{\bullet}(n - r_{\bullet}) X_{1}}{[(n - r_{\bullet}) X_{1} + r_{\bullet} X_{\bullet}]^{2}} S_{\bullet}(X_{\bullet}).
$$
\n(6)

 $+\frac{1}{\left[(n-r_{\bullet})X_1 + r_{\bullet}X_{\bullet}\right]^2}S_{\bullet}(A_{\bullet}).$
An infinite population fixed for *A*₁ cannot be invaded by
any allele with a different pattern of expression if $\{x^m, x^p\}$ An infinite population fixed for A_1 cannot be invaded by
any allele with a different pattern of expression if $\{x_1^m, x_1^p\}$
is the best remonse to itself. Therefore, a candidate ESS any allele with a different pattern of expression if $\{x_1^m, x_1^p\}$
is the best response to itself. Therefore, a candidate ESS
can be found by evaluating equation (6) when
 $\{x_1^m, x_2^p\} = \{x_1^m, x_2^p\}$. An infinite population fixed for A_1 cannot be invaded by
any allele with a different pattern of expression if $\{x_1^m, x_1^p\}$
is the best response to itself. Therefore, a candidate ESS
can be found by evaluating equa ${x_2^m, x_2^p} = {x_1^m, x_1^p}$:

$$
\begin{aligned} \n\{\mathbf{x}_2^{\mathrm{m}}, \mathbf{x}_2^{\mathrm{r}}\} &= \{\mathbf{x}_1^{\mathrm{m}}, \mathbf{x}_1^{\mathrm{r}}\}.\\ \n\frac{\partial R_{\mathrm{m}}}{\partial \mathbf{x}_2^{\mathrm{m}}} \bigg|_{X_{\mathrm{m}} = X_1} &= \frac{r_{\mathrm{m}}}{n} \bigg[S'(X) + (n - r_{\mathrm{m}}) \frac{S(X)}{nX} \bigg], \n\end{aligned} \tag{7a}
$$

$$
\left.\frac{\partial R_{\rm p}}{\partial x_{\rm 2}^{\rm p}}\right|_{X_{\rm p}=X_{\rm 1}}\ =\ \frac{r_{\rm p}}{n}\left[S'(X)\,+\,\left(n-r_{\rm p}\right)\frac{S(X)}{nX}\right].\eqno(7b)
$$

Subscripts are dropped from $S_{\bullet}(X_{\bullet})$ and X_{\bullet} because Subscripts are dropped from $S_{\bullet}(X_{\bullet})$ and X_{\bullet} because $S_{\rm m}(X_{\rm m}) = S_{\rm p}(X_{\rm p})$ when $X_{\rm p} = X_{\rm m} = X_{\rm l}$. The term within the square brackets is larger for equation (7b) than for equation Subscripts are dropped from $S_{\bullet}(X_{\bullet})$ and X_{\bullet} because $S_{\rm m}(X_{\rm m}) = S_{\rm p}(X_{\rm p})$ when $X_{\rm p} = X_{\rm m} = X_{\rm l}$. The term within the square brackets is larger for equation (7*b*) than for equation (7*a*) except when $S_m(X_m) = S_p(X_p)$ when $X_p = X_m = X_1$. The term within the square brackets is larger for equation (7*b*) than for equation (7*a*), except when $r_m = r_p$ (single paternity). With this one exception (7*a*) < 0, when (7*b*) = 0, and square brackets is larger for equation (7*b*) than for equation

(7*a*), except when $r_m = r_p$ (single paternity). With this one

subscripts are dropped from $S_{\bullet}(T_{\bullet})$ and T_{\bullet} because
 \bullet exception, (7*a*) < 0 when \bigcup (7*a*) = 0. Therefore, the maternally derived allele will be exception, $(7a) < 0$ when $(7b) = 0$ and $(7b) > 0$ when $(7a) = 0$. Therefore, the maternally derived allele will be silent at an imprinted ESS of the form $\{0, X^*\}$. This is an expression of the 'loudest-voice-prevails' p (7*a*) = 0. Therefore, the maternally derived allele will be silent at an imprinted ESS of the form $\{0, X^*\}$. This is an expression of the 'loudest-voice-prevails' principle (Haig 1996 1997 σ) 1996,1997*a*).

1996, 1997*a*).

Put into words rather than equations, both alleles at a locus contribute their products to a common pool. When-

ever the combined level of demand factor is greater than Put into words rather than equations, both alleles at a
locus contribute their products to a common pool. When-
ever the combined level of demand factor is greater than
the (lower) maternal optimum, maternally derived alle locus contribute their products to a common pool. When-
ever the combined level of demand factor is greater than
the (lower) maternal optimum, maternally derived alleles
would benefit from producing less. Conversely, whene ever the combined level of demand factor is greater than
the (lower) maternal optimum, maternally derived alleles
would benefit from producing less. Conversely, whenever the (lower) maternal optimum, maternally derived alleles
would benefit from producing less. Conversely, whenever
the combined level is less than the (higher) paternal
optimum, paternally derived alleles would benefit from would benefit from producing less. Conversely, whenever
the combined level is less than the (higher) paternal fa-
optimum, paternally derived alleles would benefit from (10-
producing more Each increase in paternal product the combined level is less than the (higher) paternal
optimum, paternally derived alleles would benefit from
producing more. Each increase in paternal production
can be matched by a decrease in maternal production optimum, paternally derived alleles would benefit from
producing more. Each increase in paternal production
can be matched by a decrease in maternal production,
until maternal production reaches zero, at which point no producing more. Each increase in paternal production
can be matched by a decrease in maternal production,
until maternal production reaches zero, at which point no *Phil. Trans. R. Soc. Lond.* B (2000)

then free to produce their favoured amount. Fraction is possible. Paternally derived alleles are
en free to produce their favoured amount.
In the case of single paternity, $r_m = r_p = \frac{1}{2}(n + 1)$. There-
re $(7a) - (7b) - 0$ at an ESS This implies

then free to produce their favoured amount.
In the case of single paternity, $r_m = r_p = \frac{1}{2}$
fore, $(7a) = (7b) = 0$ at an ESS. This implies

$$
S'(X) + \frac{1}{2}(n-1)S(X)/nX = 0.
$$
 (8)

Condition (8) specifies a continuum of ESSs of the form Condition (8) specifies a continuum of ESSs of the form $\{x_m^*, x_p^*\}$, where $x_m^* + x_p^* = X^*$. The unimprinted strategy $\{x^{*+1}, x^{*}\}$ lies at the midpoint of this continuum Condition (8) specifies a continuum of ESSs of t
 $\{x_m^*, x_p^*\}$, where $x_m^* + x_p^* = X^*$. The unimprinted s
 $\{\frac{1}{2}X^*, \frac{1}{2}X^*\}$ lies at the midpoint of this continuum.

The assumption that an offering's fractional s $\{x_n^*, x_p^*\}$, where $x_m^* + x_p^* = X^*$. The unimprinted strategy $X^*, \frac{1}{2}X^*\}$ lies at the midpoint of this continuum.
The assumption that an offspring's fractional share of courses is proportional to its value of Z re

 $\{\frac{1}{2}X^*, \frac{1}{2}X^*\}$ lies at the midpoint of this continuum.
The assumption that an offspring's fractional share of
resources is proportional to its value of ζ relative to the
aggregate ζ in its litter ensures The assumption that an offspring's fractional share of
resources is proportional to its value of ζ relative to the
aggregate ζ in its litter ensures that $X > 0$ at an ESS. The
evolutionary instability of a populat resources is proportional to its value of Z relative to the aggregate Z in its litter ensures that $X > 0$ at an ESS. The evolutionary instability of a population in which the established allele has strategy $\{0, 0\}$ aggregate ζ in its litter ensures that $X > 0$ at an ESS. The evolutionary instability of a population in which the established allele has strategy $\{0, 0\}$ can be seen by considevolutionary instability of a population in which the established allele has strategy $\{0, 0\}$ can be seen by considering the effect of an initially rare allele that produced an infinitesimally small amount δX . Such an allele would have little effect on the total amount ering the effect of an initially rare allele that produced an infinitesimally small amount δX . Such an allele would have little effect on the total amount of resources to be divided by in mixed litters all resources wo infinitesimally small amount δX . Such an allele would have little effect on the total amount of resources to be divided, but, in mixed litters, all resources would be have little effect on the total amount of resources to
be divided, but, in mixed litters, all resources would be
obtained by offspring that produced δX and none by
offspring that produced zero. This implication is clea be divided, but, in mixed litters, all resources would be obtained by offspring that produced δX and none by offspring that produced zero. This implication is clearly unrealistic. Nevertheless, our model retains the as obtained by offspring that produced δX and none by offspring that produced zero. This implication is clearly unrealistic. Nevertheless, our model retains the assumption of pro rata shares for reasons of mathematical tr offspring that produced zero. This implication is clearly unrealistic. Nevertheless, our model retains the assumption of pro rata shares for reasons of mathematical tractunrealistic. Nevertheless, our model retains the assumption of pro rata shares for reasons of mathematical tractability, and because similar assumptions have been employed in most previous models of scramble competition of pro rata shares for reasons of mathematical tract-
ability, and because similar assumptions have been
employed in most previous models of scramble competi-
tion within litters (Mock & Parker 1997) ability, and because similar assumption
employed in most previous models of scra
tion within litters (Mock & Parker 1997). **(b)** *Antagonist ESS*

(b) *Antagonist ESS*
For purposes of describing the ESS at the antagonist locus, all alleles at the demand-factor locus will be For purposes of describing the ESS at the antagonist
locus, all alleles at the demand-factor locus will be
assumed to be A_1 . In this section, $S_{\bullet}(Y_{\bullet})$ will be defined to
be the size of the pool of resources availab locus, all alleles at the demand-factor locus will be assumed to be A_1 . In this section, $S_{\bullet}(T_{\bullet})$ will be defined to be the size of the pool of resources available to a litter containing $(n-r)$ members producing $T_{$ assumed to be A_1 . In this section, $S_{\bullet}(T_{\bullet})$ will be defined to be the size of the pool of resources available to a litter containing $(n-r_{\bullet})$ members producing T_1 and r_{\bullet} members producing T_{\bullet} . Therefore producing Y_{\bullet} . Therefore, heterozygous offspring as a group will receive f the pool of resources available to a litter $-r_{\bullet}$) members producing \mathcal{Y}_1 and r_{\bullet} members . Therefore, heterozygous offspring as a size containing $(n-r_{\bullet})$ me
producing T_{\bullet} . Ther
group will receive

$$
R_{\bullet} = \frac{r_{\bullet} f(\Upsilon_{\bullet})}{(n - r_{\bullet}) f(\Upsilon_{1}) + r_{\bullet} f(\Upsilon_{\bullet})} S_{\bullet}(\Upsilon_{\bullet}).
$$
\n(9)

The ESS is obtained by evaluating partial derivatives of The ESS is obtained by evaluating paraduating paraduation (9) when $\{y_1^m, y_1^p\} = \{y_2^m, y_2^p\}$.

equation (9) when
$$
\{\mathcal{Y}_1^m, \mathcal{Y}_1^p\} = \{\mathcal{Y}_2^m, \mathcal{Y}_2^p\}:
$$

\n
$$
\frac{\partial R_m}{\partial \mathcal{Y}_2^m}\bigg|_{\mathcal{Y}_{m}=\mathcal{Y}_1} = \frac{r_m}{n} \bigg[S'(\mathcal{Y}) + (n - r_m) \frac{f'(\mathcal{Y})S(\mathcal{Y})}{nf(\mathcal{Y})} \bigg], \qquad (10a)
$$

$$
\frac{\partial R_{\rm p}}{\partial y_{\rm p}^{\rm p}}\bigg|_{T_{\rm p}=T_{\rm 1}} = \frac{r_{\rm p}}{n} \left[S'(T) + (n-r_{\rm p}) \frac{f'(T)S(T)}{nf(T)} \right]. \tag{10b}
$$
\n
$$
\text{Subscripts are dropped from } S_{\bullet}(T_{\bullet}) \text{ and } T_{\bullet} \text{ because}
$$
\n
$$
S_{\bullet}(T_{\bullet}) = S_{\bullet}(T_{\bullet}) \text{ when } T = T_{\bullet} - T_{\bullet} \text{ The term within the}
$$

Compression of the 'loudest-voice-prevails' principle (Haig maternally derived alleles are predicted to produce their favoured amount of antagonist at an ESS of the form Put into words rather than equations, both allele Subscripts are dropped from $S_{\bullet}(Y_{\bullet})$ and Y_{\bullet} because $S_{\rm m}(Y_{\rm m}) = S_{\rm p}(Y_{\rm p})$ when $Y_{\rm p} = Y_{\rm m} = Y_{\rm 1}$. The term within the square brackets is larger for equation (10*a*) than equation Subscripts are dropped from $S_{\bullet}(T_{\bullet})$ and T_{\bullet} because $S_{\rm m}(T_{\rm m}) = S_{\rm p}(T_{\rm p})$ when $T_{\rm p} = T_{\rm m} = T_1$. The term within the square brackets is larger for equation (10*a*) than equation (10*b*) except when $r = r$ $S_m(Y_m) = S_p(Y_p)$ when $Y_p = Y_m = Y_1$. The term within the square brackets is larger for equation (10*a*) than equation (10*b*), except when $r_m = r_p$, because $f'(Y) < 0$. Therefore, maternally derived alleles are predicted to prod square brackets is larger for equation (10*a*) than equation (10*b*), except when $r_m = r_p$, because $f'(T) < 0$. Therefore, maternally derived alleles are predicted to produce their favoured amount of antagonist at an ESS of (10*b*), except when $r_m = r_p$, because $f'(T) < 0$. Therefore, maternally derived alleles are predicted to produce their favoured amount of antagonist at an ESS of the form fT^* of Form single paternity $r = r$, the model pr maternally derived alleles are predicted to produce their
favoured amount of antagonist at an ESS of the form
 $\{T^*, 0\}$. For single paternity, $r_m = r_p$, the model predicts
a continuum of ESSs of the form $\{x^*, x^*\}$, whe favoured amount of antagonist at an ESS of the form $\{T^*, 0\}$. For single paternity, $r_m = r_p$, the model predicts a continuum of ESSs of the form $\{y^*, y^*\}$, where $v^* + v^* = T^*$. The unimprinted strategy $\{T^*, T^*\}$ lie a continuum of ESSs of the form $\{y_m^*, y_p^*\}$, where { Y^* , 0}. For single paternity, $r_m = r_p$, the mo
a continuum of ESSs of the form { y^*_{m} ,
 $y^*_{m} + y^*_{p} = Y^*$. The unimprinted strategy { $\frac{1}{2}Y^*$,
the midnoint of this continuum model predicts
 $y_{\text{m}}^{*}, y_{\text{p}}^{*}$ }, where
 $\frac{1}{2}T^{*}, \frac{1}{2}T^{*}$ } lies at a continuum of ESSs of the $y_m^* + y_p^* = T^*$. The unimprinted st
the midpoint of this continuum.
A necessary condition for mate $+y_p^* = T^*$. The unimprinted strategy $\{\frac{1}{2}T^*, \frac{1}{2}T^*\}$ lies at e midpoint of this continuum.
A necessary condition for maternally derived alleles to your non-zero, production, of the antagonist is that

for the midpoint of this continuum.
A necessary condition for maternally derived alleles to favour non-zero production of the antagonist is that $(10a) > 0$ when evaluated for $\gamma = 0$. That is,

(10*a*) > 0 when evaluated for
$$
\hat{T} = 0
$$
. That is,
\n
$$
\frac{S'(0)}{S(0)} > -\left(\frac{n - r_m}{n}\right) \frac{f'(0)}{f(0)} = -\left(\frac{n - 1}{2n}\right) f'(0).
$$
 (11)

The left-hand side of this inequality represents the proportional increase in the pool of resources caused by proportional increase in the pool of resources caused by expressed in the mother favoured even higher levels and
the first small increment in antagonist. The right-hand took over all production. However, if the possibilit proportional increase in the pool of resources caused by
the first small increment in antagonist. The right-hand
side is the corresponding decrease in a B_2B_1 offspring's
level of demand multiplied by the offspring's a the first small increment in antagonist. The right-hand
side is the corresponding decrease in a B_2B_1 offspring's
level of demand multiplied by the offspring's average
subjective frequency of RR , sibs (who produce zer side is the corresponding decrease in a B_2B_1 offspring's
level of demand multiplied by the offspring's average
subjective frequency of B_1B_1 sibs (who produce zero
antagonist) For a litter of two this translates in level of demand multiplied by the offspring's average
subjective frequency of B_1B_1 sibs (who produce zero
antagonist). For a litter of two, this translates into a subjective frequency of B_1B_1 sibs (who produce zero
antagonist). For a litter of two, this translates into a
requirement that the proportional increase of the pool be
greater than a quarter of the offspring's decrease antagonist). For a litter of two, this translates into a
requirement that the proportional increase of the pool be
greater than a quarter of the offspring's decrease in
demand For large litters condition (11) specifies tha requirement that the proportional increase of the pool be
greater than a quarter of the offspring's decrease in
demand. For large litters, condition (11) specifies that the
proportional increase in the pool must exceed hal greater than a quarter of the offspring's decrease in demand. For large litters, condition (11) specifies that the proportional increase in the pool must exceed half the decrease in demand demand. For large litt
proportional increase
decrease in demand. **(c)** *Competition within and between litters*

(c) **Competition within and between litters**
The model presented above excludes effects on future
 $\frac{1}{2}$ isolate, the theoretical consequences of (c) **Competition within and between litters**
The model presented above excludes effects on future
offspring to isolate the theoretical consequences of
scramble competition This limits the kinds of gene action E The model presented above excludes effects on future
offspring to isolate the theoretical consequences of
scramble competition. This limits the kinds of gene action
that are favoured by natural selection to those that offspring to isolate the theoretical consequences of
scramble competition. This limits the kinds of gene action
that are favoured by natural selection to those that
enhance individual fitness. In particular, the model scramble competition. This limits the kinds of gene action
that are favoured by natural selection to those that
enhance individual fitness. In particular, the model
cannot represent gene actions that reduce individual that are favoured by natural selection to those that
enhance individual fitness. In particular, the model
cannot represent gene actions that reduce individual
fitness for the benefit of future offspring. For many real enhance individual fitness. In particular, the model
cannot represent gene actions that reduce individual
fitness for the benefit of future offspring. For many real
organisms, competition within litters can have consecannot represent gene actions that reduce individual
fitness for the benefit of future offspring. For many real
organisms, competition within litters can have conse-
quences for future litters, but few models have attempte fitness for the benefit of future offspring. For many real
organisms, competition within litters can have conse-
quences for future litters, but few models have attempted
to combine single- and multi-straw competition prob organisms, competition within litters can have consequences for future litters, but few models have attempted
to combine single- and multi-straw competition, probably
because such models are messy and lack simple generaliquences for future litters, but few models have attempted
to combine single- and multi-straw competition, probably
because such models are messy and lack simple generali-
zations because such models are messy and lack simple generalizations.
A model that considers both kinds of interaction has zations.

zations.
A model that considers both kinds of interaction has
been presented by Haig (1996). In his model, increased
production of a nutrient-enhancing bormone results in A model that considers both kinds of interaction has
been presented by Haig (1996). In his model, increased
production of a nutrient-enhancing hormone results in
increased resources available to a litter at the cost of been presented by Haig (1996). In his model, increased
production of a nutrient-enhancing hormone results in
increased resources available to a litter at the cost of
decreased resources available for future siblings. The production of a nutrient-enhancing hormone results in
increased resources available to a litter at the cost of
decreased resources available for future siblings. The
multi-straw component of the model is particularly increased resources available to a litter at the cost of
decreased resources available for future siblings. The
multi-straw component of the model is particularly
simple because all members of a litter release the decreased resources available for future siblings. The
multi-straw component of the model is particularly
simple because all members of a litter release the
hormone into a common pool (the maternal circulation) multi-straw component of the model is particularly
simple because all members of a litter release the
hormone into a common pool (the maternal circulation)
and all obtain an equal share of the resulting resources simple because all members of a litter release the hormone into a common pool (the maternal circulation) and all obtain an equal share of the resulting resources (from which each member subtracts her own costs of production).

production).
In this model, multiple paternity within litters had
opposite effects to changes of paternity between litters.
Production of the bormone by offensing was of communal In this model, multiple paternity within litters had
opposite effects to changes of paternity between litters.
Production of the hormone by offspring was of communal
henefit within litters, but had an individual cost Thus peoposite effects to changes of paternity between litters.
Production of the hormone by offspring was of communal
benefit within litters, but had an individual cost. Thus, an
increase in the number of fathers within litter Production of the hormone by offspring was of communal whether the offspring inherits the allele. That is, if genes
benefit within litters, but had an individual cost. Thus, an in parents are uninformed about which offspri benefit within litters, but had an individual cost. Thus, an increase in the number of fathers *within litters* increased the free-rider problem for paternally derived alleles—but not for maternally derived alleles—and con increase in the number of fathers *within litters* increased
the free-rider problem for paternally derived alleles—but
not for maternally derived alleles—and consequently
reduced the level of hormone favoured by paternally the free-rider problem for paternally derived alleles—but
not for maternally derived alleles—and consequently
reduced the level of hormone favoured by paternally
derived alleles (This effect is present in the current not for maternally derived alleles—and consequently
reduced the level of hormone favoured by paternally reduced the level of hormone favoured by paternally
derived alleles. (This effect is present in the current
model and accounts for the higher level of antagonist
favoured by maternally derived alleles). However derived alleles. (This effect is present in the current
model and accounts for the higher level of antagonist
favoured by maternally derived alleles.) However,
increased resources obtained by the current litter Imodel and accounts for the higher level of antagonist

Infavoured by maternally derived alleles.) However,

increased resources obtained by the current litter occurred at the expense of future litters. As a conseincreased resources obtained by the current litter occurred at the expense of future litters. As a consequence, increased turnover of fathers *between litters* caused paternally derived alleles to favour higher levels of occurred at the expense of future litters. As a consequence, increased turnover of fathers *between litters* caused paternally derived alleles to favour higher levels of hormone production but had no effect on the level quence, increased turnover of fathers *between litters* caused
paternally derived alleles to favour higher levels of
hormone production but had no effect on the level
favoured by maternally derived alleles (Effects on futu paternally derived alleles to favour higher levels of
hormone production but had no effect on the level
favoured by maternally derived alleles. (Effects on future
offspring are absent from the current model) hormone production but had no effect on
favoured by maternally derived alleles. (Effects
offspring are absent from the current model.)
The placental-hormone model did no Fracentally derived alleles. (Effects on future

Spring are absent from the current model.)

The placental-hormone model did not predict

printed expression of the hormone by maternally

offspring are absent from the current model.)
The placental-hormone model did not predict
imprinted expression of the hormone by maternally
derived alleles of offspring for any combination of The placental-hormone model did not predict
imprinted expression of the hormone by maternally
derived alleles of offspring for any combination of
multiple paternity within litters and changes of paternity imprinted expression of the hormone by maternally
derived alleles of offspring for any combination of
multiple paternity within litters and changes of paternity
between litters because it included the possibility that derived alleles of offspring for any combination of multiple paternity within litters and changes of paternity between litters because it included the possibility that multiple paternity within litters and changes of paternity
between litters because it included the possibility that
alleles expressed in the mother (as well as in offspring)
could release bormone into the common pool. As a between litters because it included the possibility that alleles expressed in the mother (as well as in offspring) could release hormone into the common pool. As a result, whenever maternally derived alleles of offspring f alleles expressed in the mother (as well as in offspring)
could release hormone into the common pool. As a result,
whenever maternally derived alleles of offspring favoured *Phil. Trans. R. Soc. Lond.* B (2000)

greater production than paternally derived alleles, alleles
greater production than paternally derived alleles, alleles greater production than paternally derived alleles, alleles
expressed in the mother favoured even higher levels and
took over all production. However, if the possibility of greater production than paternally derived alleles, alleles
expressed in the mother favoured even higher levels and
took over all production. However, if the possibility of
production by the mother had been excluded, the m expressed in the mother favoured even higher levels and
took over all production. However, if the possibility of
production by the mother had been excluded, the model
would have predicted imprinted expression of the took over all production. However, if the possibility of
production by the mother had been excluded, the model
would have predicted imprinted expression of the
hormone by either maternally derived or paternally production by the mother had been excluded, the model
would have predicted imprinted expression of the
hormone by either maternally derived or paternally
derived alleles depending on details of the mating would have predicted imprinted expression of the hormone by either maternally derived or paternally derived alleles, depending on details of the mating system system. derived alleles, depending on details of the mating
system.
The placental-hormone model illustrates some of the

system.
The placental-hormone model illustrates some of the
complexities of the interaction between competition
within and between litters but is not a general treatment The placental-hormone model illustrates some of the complexities of the interaction between competition within and between litters, but is not a general treatment of this problem. Other possibilities that remain to be complexities of the interaction between competition
within and between litters, but is not a general treatment
of this problem. Other possibilities that remain to be
formally modelled include a demand factor that increases within and between litters, but is not a general treatment
of this problem. Other possibilities that remain to be
formally modelled include a demand factor that increases of this problem. Other possibilities that remain to be
formally modelled include a demand factor that increases
an offspring's share at the expense of current and future
offspring, or a demand-factor antagonist that takes formally modelled include a demand-factor that increases
an offspring's share at the expense of current and future
offspring, or a demand-factor antagonist that takes from
the current litter to give to future litters an offspring's share at the expense of cur
offspring, or a demand-factor antagonist
the current litter to give to future litters. **1.12. The current litter to give to future litters.**
3. PUBLIC GOODS AND COLLECTIVE ACTION

The model of scramble competition presented in this paper can be interpreted as an illustration of the The model of scramble competition presented in this
paper can be interpreted as an illustration of the
economic principle that groups tend to underprovide
public goods because a public good (by definition) is paper can be interpreted as an illustration of the economic principle that groups tend to underprovide public goods because a public good (by definition) is available to all whether or not an individual contributes economic principle that groups tend to underprovide
public goods because a public good (by definition) is
available to all, whether or not an individual contributes
to its provision (Olson 1961) From this perspective the public goods because a public good (by definition) is available to all, whether or not an individual contributes to its provision (Olson 1961). From this perspective, the available to all, whether or not an individual contributes
to its provision (Olson 1961). From this perspective, the
pool of resources shared by the members of a litter is a
public good that is underprovided at evolutionar to its provision (Olson 1961). From this perspective, the pool of resources shared by the members of a litter is a public good that is underprovided at evolutionary equili-
brium. The size of the pool would be larger and e pool of resources shared by the members of a litter is a
public good that is underprovided at evolutionary equili-
brium. The size of the pool would be larger, and each sib
would receive more, if all sibs demanded less, bu public good that is underprovided at evolutionary equilibrium. The size of the pool would be larger, and each sib would receive more, if all sibs demanded less, but unibrium. The size of the pool would be larger, and each sib
would receive more, if all sibs demanded less, but uni-
lateral restraint by a subset of sibs would reduce their own
share for the benefit of sibs who do not show r would receive more, if all sibs demanded less, but unilateral restraint by a subset of sibs would reduce their own
share for the benefit of sibs who do not show restraint.
Such inefficiencies are a general feature of model lateral restraint by a subset of sibs would reduce their own
share for the benefit of sibs who do not show restraint.
Such inefficiencies are a general feature of models of sib
comnetition competition. Such inefficiencies are a general feature of models of sib competition.
In contrast with models in which genes expressed in

In this model, multiple paternity within litters had the good. This is because the effect on offspring of an expressed in a shared parent determine the distribution of In this model, multiple paternity within litters had t competition.
In contrast with models in which genes expressed in
offspring determine the distribution of a collective good
among sibs efficient outcomes are predicted if genes In contrast with models in which genes expressed in
offspring determine the distribution of a collective good
among sibs, efficient outcomes are predicted if genes
expressed in a shared parent determine the distribution of offspring determine the distribution of a collective good
among sibs, efficient outcomes are predicted if genes
expressed in a shared parent determine the distribution of
the good. This is because the effect on offspring o among sibs, efficient outcomes are predicted if genes
expressed in a shared parent determine the distribution of
the good. This is because the effect on offspring of an
allele expressed in a parent is (usually) independent expressed in a shared parent determine the distribution of
the good. This is because the effect on offspring of an
allele expressed in a parent is (usually) independent of
whether the offenring inherits the allele. That is the good. This is because the effect on offspring of an allele expressed in a parent is (usually) independent of whether the offspring inherits the allele. That is, if genes in parents are uniformed about which offspring i allele expressed in a parent is (usually) independent of
whether the offspring inherits the allele. That is, if genes
in parents are uninformed about which offspring inherit
which alleles the best they can do is to maximiz which alleles, the best they can do is to maximize the in parents are uninformed about which offspring inherit
which alleles, the best they can do is to maximize the
combined fitness of offspring considered as a group (cf.
Harsanyi 1953) The extra information available to gene which alleles, the best they can do is to maximize the
combined fitness of offspring considered as a group (cf.
Harsanyi 1953). The extra information available to genes
in offensing—that an allele is definitely present in combined fitness of offspring considered as a group (cf.
Harsanyi 1953). The extra information available to genes
in offspring—that an allele is definitely present in the
offspring in which it is expressed—prevents these g Harsanyi 1953). The extra information available to genes
in offspring—that an allele is definitely present in the
offspring in which it is expressed—prevents these genes
from achieving an efficient outcome. It is not alway in offspring—that an allele is definitely present in the
offspring in which it is expressed—prevents these genes
from achieving an efficient outcome. It is not always
better to be better informed offspring in which it is expresent
from achieving an efficient of
better to be better informed.
In The logic of collective action In the final and achieving an efficient outcome. It is not always
better to be better informed.
In *The logic of collective action*, Olson (1961) argued that

the larger to be better informed.

In *The logic of collective action*, Olson (1961) argued that

the larger a group, the greater the shortfall from optimal

provision of public goods, other things being equal. If the In *The logic of collective action*, Olson (1961) argued that
the larger a group, the greater the shortfall from optimal
provision of public goods, other things being equal. If the
analogy between sib competition and econo the larger a group, the greater the shortfall from optimal
provision of public goods, other things being equal. If the
analogy between sib competition and economic models is
to be extended, one must ask who or what in the provision of public goods, other things being equal. If the analogy between sib competition and economic models is to be extended, one must ask who or what in the multianalogy between sib competition and economic models is
to be extended, one must ask who or what in the multi-
straw model takes the place of the rational self-interested
individual of economics. The unit of strategic innov to be extended, one must ask who or what in the multi-
straw model takes the place of the rational self-interested
individual of economics. The unit of strategic innovation
in our model is not an individual sib—or even an straw model takes the place of the rational self-interested
individual of economics. The unit of strategic innovation
in our model is not an individual sib—or even an indivi-
dual copy of a gene within a sib—but rather an individual of economics. The unit of strategic innovation
in our model is not an individual sib—or even an indivi-
dual copy of a gene within a sib—but rather an 'allele', in in our model is not an individual sib—or even an individual copy of a gene within a sib—but rather an 'allele', in
the collective sense of all identical-by-descent copies of a
DNA sequence within a litter (compare the disc dual copy of a gene within a sib—but rather an 'allele', in
the collective sense of all identical-by-descent copies of a
DNA sequence within a litter (compare the discussion of
the 'strategic gene' in Haig (1997b)) By this the collective sense of all identical-by-descent copies of a
DNA sequence within a litter (compare the discussion of
the 'strategic gene' in Haig (1997*b*)). By this definition,
the expected number of maternally derived al DNA sequence within a litter (compare the discussion of
the 'strategic gene' in Haig $(1997b)$). By this definition,
the expected number of maternally derived alleles in a
litter (two) is smaller than the expected number the 'strategic gene' in Haig $(1997b)$). By this definition,
the expected number of maternally derived alleles in a
litter (two) is smaller than the expected number of pater-
nally derived alleles (more than two if there the expected number of maternally derived alleles in a
litter (two) is smaller than the expected number of pater-
nally derived alleles (more than two if there is some

BIOLOGICAL
SCIENCES

THE ROYAL

PHILOSOPHICAL
TRANSACTIONS

possibility of multiple paternity). That is, maternally possibility of multiple paternity). That is, maternally
derived alleles comprise a smaller group than paternally
derived alleles and are therefore predicted to contribute possibility of multiple paternity). That is, maternally
derived alleles comprise a smaller group than paternally
derived alleles and are therefore predicted to contribute
more to the provision of public goods. Conversely p derived alleles comprise a smaller group than paternally
derived alleles and are therefore predicted to contribute
more to the provision of public goods. Conversely, pater-
nally derived alleles are predicted to invest mor derived alleles and are therefore predicted to contribute
more to the provision of public goods. Conversely, pater-
nally derived alleles are predicted to invest more in the
acquisition of selfish benefits that reduce the more to the provision of public goods. Conversely, paternally derived alleles are predicted to invest more in the acquisition of selfish benefits that reduce the supply of public goods nally derived alleles are predicted to invest more in the acquisition of selfish benefits that reduce the supply of public goods.
Multiple paternity within litters is not the only reason quisition of selfish benefits that reduce the supply of
blic goods.
Multiple paternity within litters is not the only reason
w alleles of different parental origin might interact in

public goods.
Multiple paternity within litters is not the only reason
why alleles of different parental origin might interact in
groups of different sizes. For example, consider a species Multiple paternity within litters is not the only reason
why alleles of different parental origin might interact in
groups of different sizes. For example, consider a species
that forms social groups of matrilineal female why alleles of different parental origin might interact in
groups of different sizes. For example, consider a species
that forms social groups of matrilineal female kin whose
reproduction is monopolized (temporarily) by ea groups of different sizes. For example, consider a species
that forms social groups of matrilineal female kin whose
reproduction is monopolized (temporarily) by each of a
series of unrelated males. Offspring born during th that forms social groups of matrilineal female kin whose reproduction is monopolized (temporarily) by each of a
series of unrelated males. Offspring born during the
reproductive tenure of any given male would typically
possess fewer paternally derived alleles than maternally series of unrelated males. Offspring born during the
reproductive tenure of any given male would typically
possess fewer paternally derived alleles than maternally
derived alleles especially at X-linked loci If so one reproductive tenure of any given male would typically
possess fewer paternally derived alleles than maternally
derived alleles, especially at X-linked loci. If so, one
might expect the expression of alleles of paternal ori possess fewer paternally derived alleles than maternally
derived alleles, especially at X-linked loci. If so, one
might expect the expression of alleles of paternal origin to
favour greater cooperation between individuals derived alleles, especially at X-linked loci. If so, one
might expect the expression of alleles of paternal origin to
favour greater cooperation between individuals of similar
age than would the expression of alleles of ma might expect the expression of alleles of paternal origin to
favour greater cooperation between individuals of similar
age than would the expression of alleles of maternal
origin (Trivers & Burt 1999; Haig 2000). favour greater cooperation between individuals of similar

Robert Trivers and two anonymous referees have commented
helpfully on the manuscript Robert Trivers and two anor
helpfully on the manuscript.

REFERENCES

REFERENCES
DeChiara, T. M., Robertson, E. J. & Efstratiadis, A. 1991
Parental imprinting of the mouse insulin-like growth factor II **PARTENCES**
Pare[ntal imprinting of](http://gessler.ingentaselect.com/nw=1/rpsv/cgi-bin/linker?ext=a&reqidx=/0092-8674^28^2964L.849[aid=537600,csa=0092-8674^26vol=64^26iss=4^26firstpage=849,nlm=1997210]) the mouse insulin-like growth factor II
gene Cell 64, 840–850 eChiara, T. M., Robert
Parental imprinting of th
gene. *Cell* **64**, 849–859.

- Haig, D. 1992 Genomic imprinting and the theory of parent^ offspring conflict. *Semin. Dev. Biol.* 3, 153-160. Haig, D. 1992 Genomic imprinting and the theory of parent-
offspring conflict. *Semin. Dev. Biol.* 3, 153-160.
Haig, D. 1996 Placental hormones, genomic imprinting, and
maternal fetal communication $\frac{7}{2}$ Find, Biol. 9
- offspring conflict. *Semin. Dev. Biol.* **3**, 153–160.

aig, D. 1996 Placental hormones, genomic imprinting,

maternal-fetal communication. *J. Evol. Biol.* **9**, 357–380.

aig. D. 19974. Parental antagonism, relatedness. Haig,D. 1996 Placental hormones, genomic imprinting, and
maternal-fetal communication. *J. Evol. Biol.* 9, 357–380.
Haig, D. 1997*a* Parental antag[onism,](http://gessler.ingentaselect.com/nw=1/rpsv/cgi-bin/linker?ext=a&reqidx=/0962-8452^28^29264L.1657[aid=535596,nlm=9404029]) relatedness asym-
metries and genomic imprinting *Proc. R. Sec. Lan*
- maternal–fetal communication. *J. Evol. Biol.* **9**, 357–380.
aig, D. 1997*a* Parental antagonism, relatedness asymmetries, and genomic imprinting. *Proc. R. Soc. Lond.* B 264,
1657–1662. metries,and genomic imprinting. *Proc. R. Soc. Lond.* B 264,
1657–1662.
Haig, D. 1997*b* The social gene. In *Behavioural ecology*, 4th edn
(ed. J. R. Krebs & N. R. Davies) pp. 284–304. Oxford UK:
- 1657–1662.
aig, D. 1997b The social gene. In *Behavioural ecology*, 4th edn
(ed. J. R. Krebs & N. B. Davies), pp. 284–304. Oxford, UK:
Blackwell Scientific aig, D. 1997*b* The socker
(ed. J. R. Krebs & N.
Blackwell Scientific.
aig. D. 2000 Genomi (ed. J. R. Krebs & N. B. Davies), pp. 284–304. Oxford, UK:
Blackwell Scientific.
Haig, D. 2000 Genomic imprinting, sex-biased dispersal, and
social behavior *Ands NY Acad Sci* **907** 140–163
- Blackwell Scientific.
aig, D. 2000 Genomic imprinting, sex-biased dis
social behavior. *Annls NY Acad. Sci.* **907**, 149–163.
arganyi, J. C. 1953 Cardinal utility in welfare esc Haig, D. 2000 Genomic imprinting, sex-biased dispersal, and
social behavior. Annls NY Acad. Sci. **907**, 149–163.
Harsanyi, J. C. 1953 Cardinal utility in welfare economics and
in the theory of risk-taking. 7 Polit Econ 61,
- social behavior. *Annls NY Acad. Sci*. **907**, 149–163.
Harsanyi, J. C. 1953 Cardinal utility in welfare economics and
in the theory of risk-taking. *J. Polit. Econ.* **61**, 434–435. Harsanyi, J. C. 1953 Cardinal utility in welfare economics and
in the theory of risk-taking. J. Polit. Econ. 61, 434–435.
Macnair, M. R. & Parker, G. A. 1979 Models of parent-
offenring conflict. III. Intra-brood conflict.
- in the theory of risk-taking. *J. Polit. Econ.* **61**, 434–435.
acnair, M. R. & Parker, G. A. 1979 Models of parent-
offspring conflict. III. Intra-brood conflict. *Anim. Behav.* **27**,
1202–1209. offspring conflict. III. Intra-brood conflict. Anim. Behave 27, 1202-1209.
Maynard Smith, J. & Price, G. R. 1973 The logic of animal conflict. Nature 246, 15-18
- 1202–1209.
aynard Smith, J. & Price,
conflict. *Nature* **246**, 15–18.
atcalf R. A. Stamps, J. A. Maynard Smith, J. & Price, G. R. 1973 The logic of animal
conflict. *Nature* **246**, 15–18.
Metcalf, R. A., Stamps, J. A. & Krishnan, V. V. 1979 Parent-offspring conflict that is not limited by degree of kinship. 7
- conflict. *Nature* **246**, 15–18.
etcalf, R. A., Stamps, J. A. & Krishnan, V. V. 1979 Parent–
offspring conflict that is not limited by degree of kinship. *J.*
Theor Biol **76**, 99–107. *Theor. Biol.* **76**, *R. A., Stamps, J.

<i>Theor. Biol.* **76**, 99–107.
 Rightaria **19.** Takeda **Y.** offspringconflict that is not limited by degree of kinship. \tilde{J} .
Theor. Biol. **76**, 99–107.
Mochizuki, A., Taked[a, Y. & Iwasa, Y. 1996](http://gessler.ingentaselect.com/nw=1/rpsv/cgi-bin/linker?ext=a&reqidx=/0016-6731^28^29144L.1283[aid=537602,csa=0016-6731^26vol=144^26iss=3^26firstpage=1283,nlm=8913768]) The evolution of
genomic immeriation *Cenetics* **144** 1983–1995
- *Theor. Biol.* **76**, 99–107.
ochizuki, A., Takeda, Y. & Iwasa, Y. 1996 T
genomic imprinting. *Genetics* **144**, 1283–1295.
ock. D. W. & Parker G. A. 1997. The evolution
- Mock, D. W. & Parker, G. A. 1997 *The evolution of sibling rivalry*. Oxford University Press. Mock, D. W. & Parker, G. A. 1997 *The evolution of sibling rivalry.*
Oxford University Press.
Olson, M. 1961 *The logic of collective action. Public goods and the*
theory of graphs. Cambridge MA: Harvard University Press.
- Oxford University Press.

son, M. 1961 *The logic of collective action. Public goods and theory of groups*. Cambridge, MA: Harvard University Press.

Straits R. & Burt. A. 1999 Kinship and genomic immedition Olson, M. 1961 *The logic of collective action. Public goods and the theory of groups*. Cambridge, MA: Harvard University Press.
Trivers, R. & Burt, A. 1999 Kinship and genomic imprinting.
In *Genomic imprinting*, An *inte*
- *theory of groups.* Cambridge, MA: Harvard University Press.
ivers, R. & Burt, A. 1999 Kinship and genomic imprinting.
In *Genomic imprinting. An interdisciplinary approach* (ed. R.
Oblsson) pp. 1–91 Berlin: Springer ivers, R. & Burt, A. 1999 Kinship a
In *Genomic imprinting. An interdiscip*.
Ohlsson), pp. 1–21. Berlin: Springer.
ilson D. S. 1977 Structured demes and In *Genomic imprinting. An interdisciplinary approach* (ed. R. Ohlsson), pp. 1–21. Berlin: Springer.

Tilson, D. S. 1977 Str[uctured demes and the](http://gessler.ingentaselect.com/nw=1/rpsv/cgi-bin/linker?ext=a&reqidx=/0003-0147^28^29111L.157[aid=528920]) evolution of group-

advantageous traits. Am. Nat. 111, 157–185.
- Wilson, D. S. 1977 Structured demes and the evolution of group-

BIOLOGICAL CIENCES

THE ROYAL

PHILOSOPHICAL
TRANSACTIONS