



Parental Investment and Family Conflicts



Parental Investment

- Robert Trivers (1972) defined it as: any investment by the parent in an individual offspring that increases the offspring's chance of surviving (and hence reproductive success) at the cost of the parent's ability to invest in other offspring
- Can include any investment that benefits eggs and/or young
 - Provisioning of gametes
 - Provisioning nest, burrow, or territory
 - But unclear if also related to mating effort
 - Care of eggs or young without providing resources outside of egg (protection)
 - Provisioning young before and/or after hatching or birth
 - Care of offspring after nutritional independence (many primates)
- Parental effort = sum of parental investment in all offspring during parent's lifetime
- Finite amount of resources can result in conflict and trade-offs

Parental care and family conflicts

- Three conflicts can shape the amount a parent invests in its offspring
 1. Between parents over how much care each should provide
 2. Between siblings over how much care each should demand
 3. Between parents and offspring over the supply and demand for care

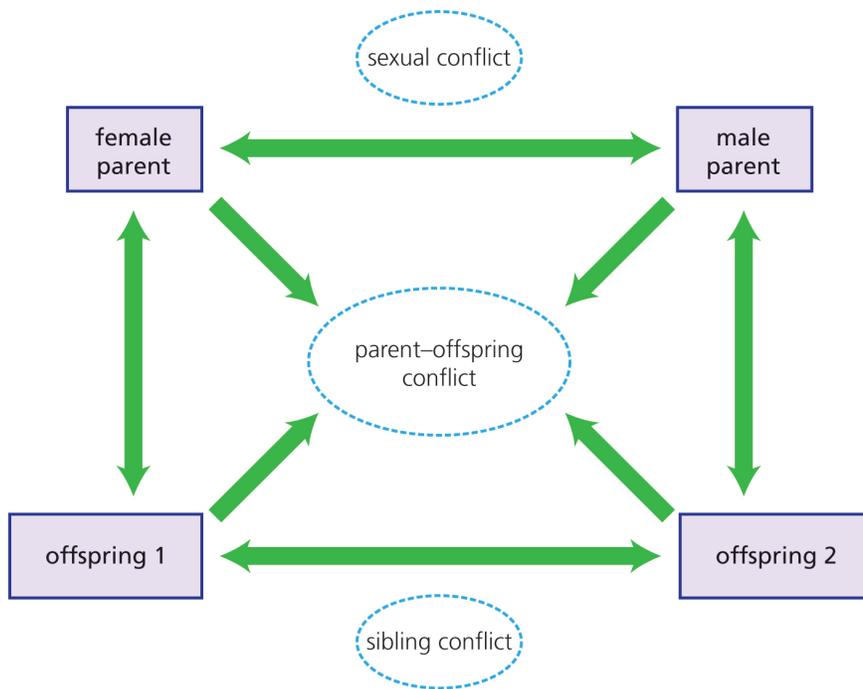


Fig. 8.1

The three types of intra-familial conflict discussed in this chapter. Male and female parents are in conflict over who should invest and how much. Siblings compete over the investment from parents. Offspring have different interests from their parents over supply and demand of investment. From Parker *et al.* (2002).

An Introduction to Behavioural Ecology, Fourth Edition. Nicholas B. Davies, John R. Krebs and Stuart A. West.
© 2012 Nicholas B. Davies, John R. Krebs and Stuart A. West. Published 2012 by John Wiley & Sons, Ltd.

Proximate Constraints on Parental Care

- Basic differences in physiology and life histories (when to reproduce, how many and what size of offspring) can account for differences in parental care and mating systems
- Both sexes selected to maximize their reproductive success, potentially at expense of partner

Table 8.1 Sex roles in parental care (Kokko & Jennions, 2008)

Taxon	Parental care	References
Invertebrates	Uncommon, but when it occurs mainly female only. Biparental care uncommon. Male-only care rarer.	Zeh & Smith (1985); Tallamy (2000).
Fish	Ratio of genera with male-only: biparental: female-only care is 9:3:1.	Reynolds <i>et al.</i> (2002).
Amphibians	Female-only care and male-only care equally common. Low frequency of biparental care.	Beck (1998); Summers <i>et al.</i> (2006).
Reptiles	Either female alone or both parents.	Reynolds <i>et al.</i> (2002).
Birds	In 90% species, biparental care (including 9% where helpers assist), but females often invest more in care. Females care alone in majority of the remaining species. Male-only care is rarer.	Lack (1968); Cockburn (2006).
Mammals	Females care in all species. In 95% species, the female cares alone. In 5% the male helps too. No cases of male-only care.	Clutton-Brock (1991).

Sexual Selection, Mating and Parental Investment

- Trivers argued that the relative parental investment of the sexes in their offspring governs the operation of sexual selection
- Differences between species in parental care associated with differences in mating systems
- Monogamy: male and female form a pair bond, either short or long term. Often both parents care for eggs and/or young.
- Polygyny: male mates with several females, while females mate with only one male. Simultaneous: mates with several females at once; or successive: multiple females over a single breeding season. Usually maternal care.
- Polyandry: females mate with several males either simultaneously or successively. Typically paternal care.



Female vs. male investment in offspring

- Two general reasons females typically invest more than males:
 - Females mate multiply (polyandry)
 - Sexual selection leads to skewed male mating success
- Males must weigh return for providing care vs. attempting to obtain other mates
- Even social monogamy doesn't mean genetic monogamy
 - Little benefit of staying to help raise other male's offspring
- Males have a greater potential reproductive rate
 - However, average actual reproductive rate of all males must be same as females if sex ratio is 1:1
 - Successful males gain more from deserting than females do and therefore have a greater cost of caring
 - As females provide more care, sexual selection on males intensifies
 - Creates positive feedback, making it even less likely males will provide care

Sexual conflict over care

- Ecological factors determine the costs and benefits of whether a parent should stay and care or desert
- Proximal constraints also influence which sex has the opportunity to desert
- Best decision for one sex will depend on the strategy adopted by the other sex
- Game theory can be used to determine the evolutionary stable strategies for male and female care

Sexual conflict over care

- Assume that the more females invest in eggs, the less they invest in care, and vice versa
- P_0 , P_1 , and P_2 = probability of egg survival when cared for by neither, one, or both parents respectively; $P_2 > P_1 > P_0$
- A male that deserts has chance p of mating again
 - Later refinement to model indicated extra matings come from females that deserted male care-givers or from deserting males stealing paternity from care-giving males (ensures average reproductive rate of males=females)
- A female that deserts lays W eggs and one who cares lays w eggs; $W > w$
- Model assumes each parent decides independently whether to care or desert

Sexual conflict over care

- Pay-offs for males and females depending on caring or deserting

		Female	
		Care	Desert
Male	Care	wP_2	WP_1
	Desert	wP_1	WP_0
		Female gets	Male gets
		wP_2	$wP_1(1+p)$
		WP_1	$WP_0(1+p)$

Table 8.3 An ESS model of parental investment (Maynard Smith, 1977). Each sex has the possibility of caring or deserting. The matrix gives the reproductive success for males and females (see text for details)

Sexual conflict over care

- Female's pay-off calculated in # of eggs she can produce and the probability of offspring survival
- Male's pay-off calculated in probability of additional matings he can obtain and probability of offspring survival
- ESS 1: both female and male desert. Requires $WP_0 > wP_1$, or female will care, and $P_0(1+p) > P_1$ or male will care
- ESS 2: female deserts and male cares. Requires $WP_1 > wP_2$ or female will care and $P_1 > P_0(1+p)$ or male will desert
- ESS 3: female cares and male deserts. Requires $wP_1 > WP_0$ or female will desert and $P_1(1+p) > P_2$ or male will care
- ESS 4: both female and male care. Requires $wP_2 > WP_1$ or female will desert and $P_2 > P_1(1+p)$ or male will desert

Sexual conflict over care

- Who will care and who will desert?
- Assume:
 - $W=5$; $w=3$
 - $P_0=.1$; $P_1=.4$; and $P_2=.9$
 - $p=.1$
- ESS 1 (no parental care): requires $WP_0 > wP_1$, or female will care, and $P_0(1+p) > P_1$ or male will care
 - $WP_0(.5) > wP_1(1.2)$? **NO**
 - $P_0(1+p)(.11) > P_1(.4)$? **NO**
- ESS 4 (biparental care): requires $wP_2 > WP_1$ or female will desert and $P_2 > P_1(1+p)$ or male will desert
 - $wP_2(2.7) > WP_1(2)$? **YES**
 - $P_2(.9) > P_1(1+p)(.44)$? **YES**
- Altering parameters will determine if a parent is expected to care or predicted to desert

Sexual conflict over care

- ESS 2 is favored if the female can lay many more eggs if she does not invest in caring and one parent is better than none, but two parents are not much better than one
- ESS 3 is a probability if the male has a high chance of mating again, as in some birds and mammals
- ESS 4 is likely when two parents can raise twice as many young as one or if the chance of mating again is small. This is common in many species of passerine birds

Sexual conflict over care

- Parents can also disagree over how much care to provide
- How do cooperating parents agree over how hard each should work?
 - A partner may be tempted to do less than its fair share by relying on compensation by the other partner
- At ESS of parental effort, each parent invests a fixed level of effort that maximizes its own fitness, given the effort of its mate
- If one parent reduces its effort, other is predicted to increase its effort, but to not enough to fully compensate
 - Incomplete compensation leads to stable biparental care
 - If partner fully compensated then other parent could desert

Altering investment levels in relation to costs and benefits

- Trade-offs between current and future broods occur because parents need to allocate resources to maximize *lifetime* reproductive success
- At certain point benefit of increased investment in each offspring decreases
- Optimum amount to invest per offspring is when benefits minus cost are at a maximum

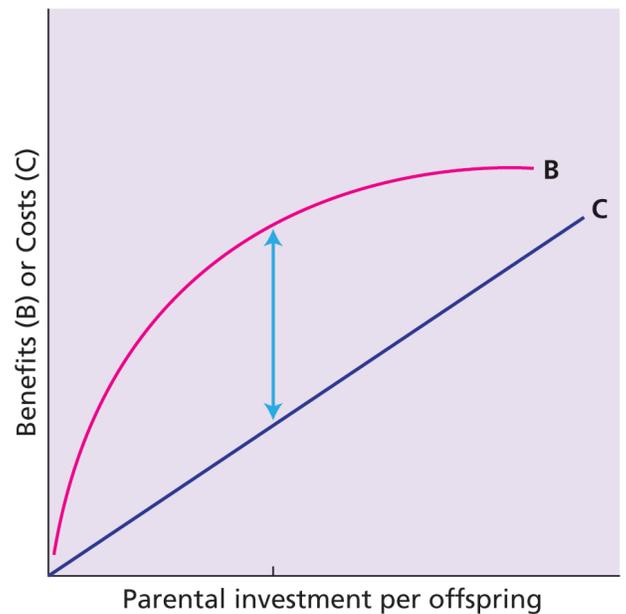


Fig. 8.2 The optimal parental investment per offspring from a parent's point of view is where the Benefits minus Costs are at a maximum. Increasing investment brings diminishing benefits as the offspring's needs become saturated, but costs continue to increase because every unit of continued investment deprives other offspring (current and future) of a parent's limited lifetime resources for care.

Altering investment levels-quality vs. quantity

- Trade-off within broods can take form of quantity versus quality of young
- Optimal brood size will maximize productivity per brood
- Most great tit pairs lay 8-9 eggs but can successfully incubate more
 - But unable to feed large broods as well and nestlings weigh less when they fledge
 - Heavier chicks survive better so a parent leaves less offspring if it lays the maximum number of eggs
- Female color morph determines quantity vs. quality trade-off in side-blotched lizards
 - Orange females produce many small eggs
 - Yellow females produce few large eggs
 - Each strategy does better under different population densities and color morph of neighboring females

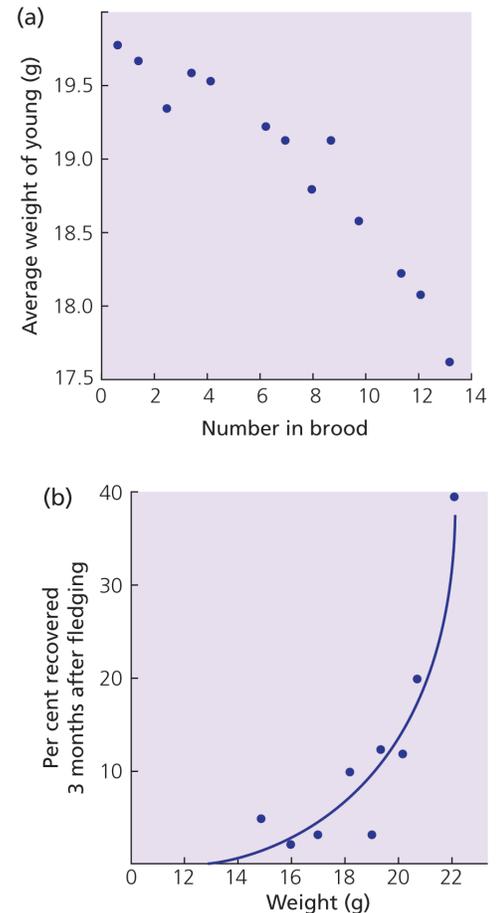


Fig. 1.6 Experimental manipulation of brood sizes in great tits. (a) In larger broods of great tits the young weigh less at fledging because the parents cannot feed them so efficiently. (b) The weight of a nestling at fledging determines its chances of survival; heavier chicks survive better. From Perrins (1965).

Altering investment levels-probability of breeding again

- In N. America birds have shorter life spans and lay larger clutches compared to S. America relatives
- N. American species reduce visits to nest in response to a nestling predator (minimize risk to their offspring)
- S. American species reduce visits to nest due to an adult predator (minimize risk to themselves)
- Balancing value of current brood against expectation of reproducing again results in different strategies

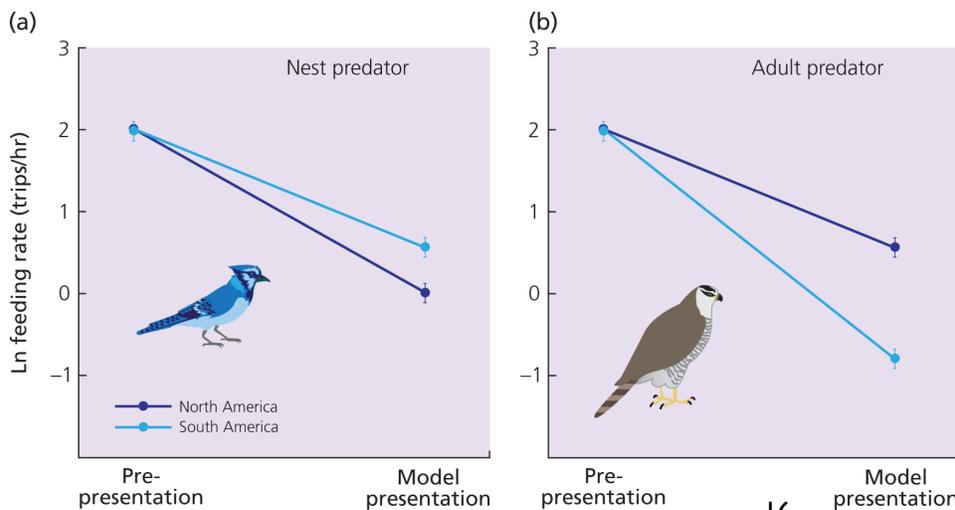


Fig. 8.3 Responses of North American and South American songbird parents to presentations of: (a) a nest predator (experimental playback of calls of a jay) and (b) a predator of adults (presentation of taxidermic mount of a hawk). Responses measured as reduction in feeding visits to a brood of nestlings. South American parents value their own lives (future broods) more (stronger response to adult predator) while North American parents value their current brood more (stronger response to nest predator). From Ghalambor and Martin (2001). Reprinted with permission from AAAS.

Altering investment levels-probability of breeding again

- Parents can also respond with a flexible strategy in response to current brood demands
- Nectar-feeding bird, the hihi (*Notiomystis cincta*) increased feedings to nestlings fed extra carotenoids (indicated healthier young, worth more investment)
- But if adults also provided with extra food parents didn't increase amount fed to nestlings
 - Allowed parents to produce a second brood that season
- Parent's likelihood of breeding a second time within same season determined whether they allocated more resources to offspring



Altering investment levels-probability of breeding again

- Galilee St. Peter's fish (*Sarotherodon galilaeus*) are mouth-brooding cichlids and have either male-only, female-only, or biparental care
- The likelihood of male or female desertion depends on the sex ratio
 - When female-biased, males more likely to desert
 - When male-biased, females more likely to desert
- Small males more likely to desert when paired with larger females
 - Small males able to carry fewer eggs and fry
 - Biparental care brings fewer additional benefits compared to uniparental care

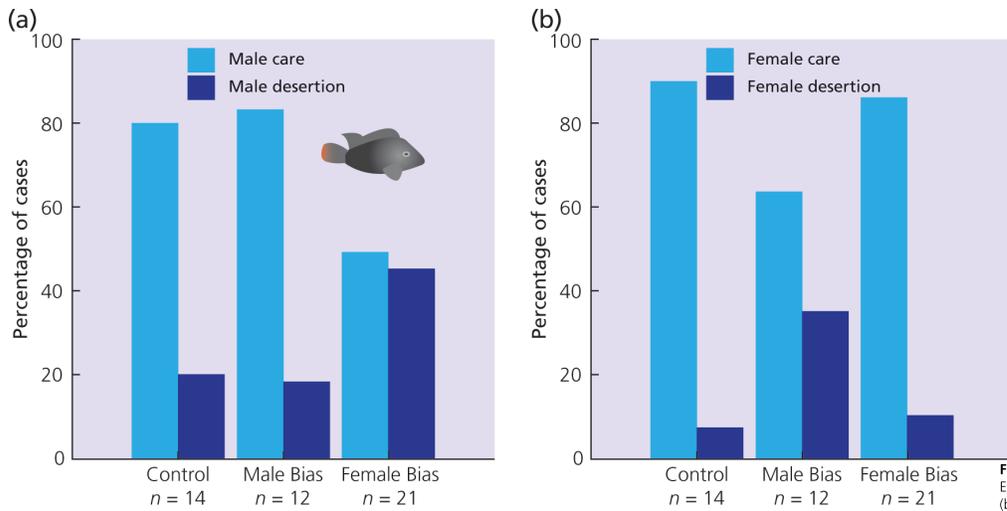


Fig. 8.4 St Peter's fish: a mouth brooder. Photo and drawing © Sigal Balshine. Experiments to test how opportunities for further matings influence: (a) male care and (b) female care in St Peter's fish. Three conditions are tested: Control (2 male, 2 females); Male bias (3 males, 1 female); female bias (1 male, 3 females). Available females increases male desertion (a), while available males increases female desertion (b). From Balshine-Earn and Earn (1998).

Altering investment levels-quality of mate

- Parents should invest more when paired with a mate of better phenotypic or genetic quality (Differential allocation hypothesis, Burley 1986)
 - Capitalize on enhanced potential benefits of current breeding attempt
- Attractiveness manipulated in zebra finches by adding colored leg bands (red bands attractive)
- Attractive birds incurred smaller parental expenditures, while unattractive birds had larger ones
- Unattractive birds had higher parental investment per offspring, shorter life spans, and lower long-term reproductive success than same-sex attractive birds
- Trade-off between current and future breeding attempts

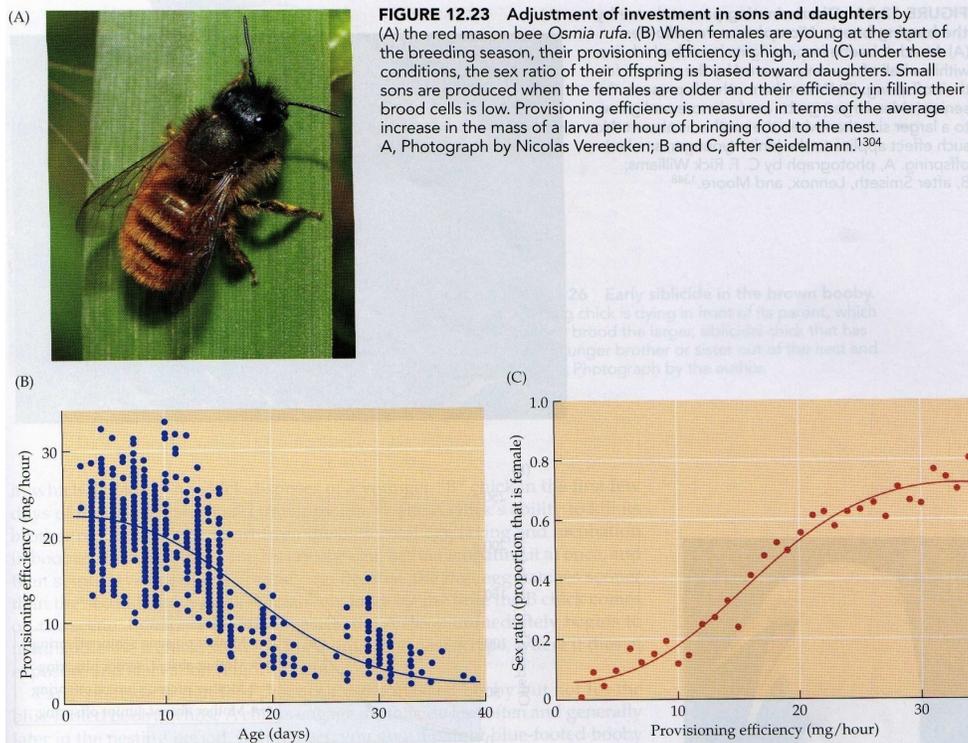
Altering investment levels-quality of mate

- Parents should invest less when they obtain an unattractive mate
 - Lower investment in order to devote more resources to later breeding attempts
- *Pelophylax esculentus* is an interspecific hybrid between *P. lessonae* and *P. ridibundus*
 - Must breed with a parental type to produce viable offspring
- *P. lessonae* females reduce their clutch size when mated to *P. esculentus* males
- Reduction in # of eggs laid results in increased reproduction in later breeding bouts



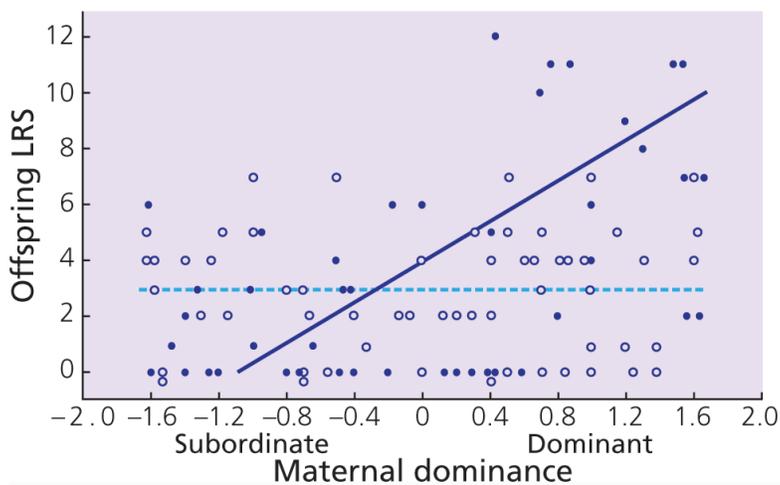
Altering investment levels-maternal condition

- Maternal condition can affect ratio of sons:daughters produced
 - Either within a single breeding season or across multiple breeding events
- Red mason bees produce daughters early in the season, but sons as summer progresses
 - Related to provisioning efficiency



Altering investment levels-maternal condition

- Female condition in red deer determined by rank in dominance hierarchy
- Low-ranking females produce 47% males, while dominant females produce 61% males
- Mother's rank had greater effect on lifetime reproductive success of her sons than that of her daughters
 - Higher ranking females produced heavier offspring
 - Heavier offspring became bigger and higher quality adults
 - Sons gained benefit from increased body size



Sibling rivalry and parent-offspring conflict

- Parent-offspring conflict results from fact that optimal investment from offspring's point of view is different that of parent's point of view
- Parent is related to all of its offspring equally, but each offspring is related (at least) twice as much to itself as it is to its other siblings
 - This results in intrabrood conflict
- Terminating care of the current brood to save investment for future offspring results in interbrood conflict
 - Current offspring more interested in own welfare compared to that of future siblings

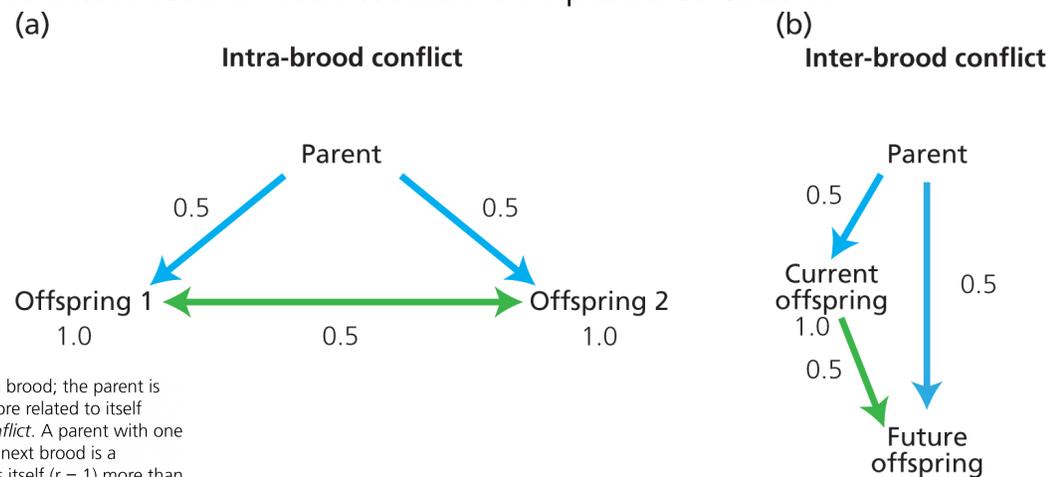


Fig. 8.7 (a) *Intra-brood conflict*. A parent with two offspring in a brood; the parent is equally related to both offspring ($r = 0.5$) but each offspring is more related to itself ($r = 1$) than to its sibling ($r = 0.5$, if full sibling). (b) *Interbrood conflict*. A parent with one offspring per brood. Again it is assumed that the offspring in the next brood is a full-sibling (same father and mother). The current offspring values itself ($r = 1$) more than its future full sibling ($r = 0.5$), whereas the parent is equally related to both offspring ($r = 0.5$).

Sibling rivalry and parent-offspring conflict

- Benefits and costs of providing care from a parent's perspective is same for all offspring
- For offspring, benefit curve is twice the parental benefit curve (it is twice as related to itself compared to the relatedness between parent and offspring)
- For full-siblings, cost curve will be same as parents (offspring related to full-siblings to same degree as parents are to other offspring)
 - If half-siblings, offspring costs are half as much as parents
- Between offspring's optimum and parent's optimum expect conflict over amount of care

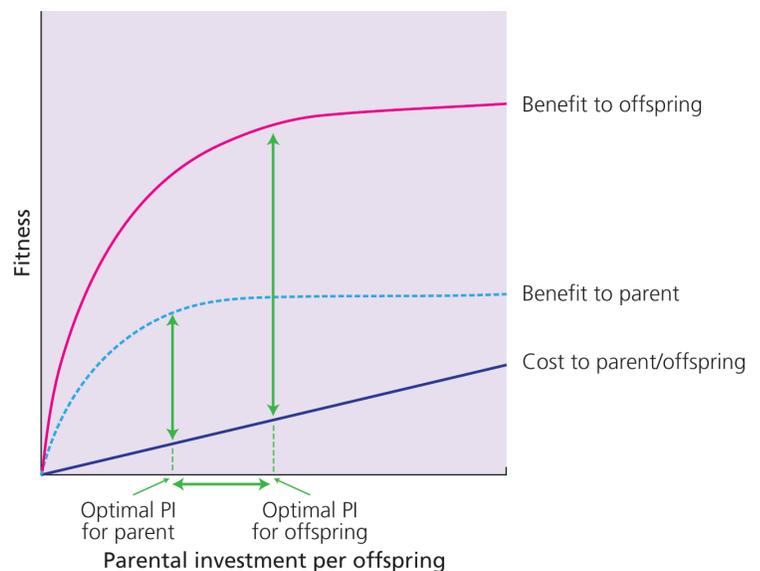


Fig. 8.8 Trivers's (1974) theory of parent-offspring conflict. The benefits and costs from the parent's point of view are the same as for Fig. 8.2. However, an offspring will value its own life ($r = 1$) twice as much as it is valued by its parent ($r = 0.5$), so the benefit curve for the offspring is twice that for the parent. If siblings are full siblings ($r = 0.5$) then the cost curve for the offspring is the same as that for the parent (see text). The optimal parental investment from an offspring's point of view is greater than the parental optimum. From Lazarus and Inglis (1986). With Permission from Elsevier.

Sibling rivalry

Facultative siblicide

- Interbrood conflict
 - Galapagos fur seals give birth to one seal at a time
 - When fish are abundant females can wean pups in 18 months; in poor conditions pups suckle for 2-3 years
 - 23% of pups/year born when older sibling still being nursed
 - Younger pup dies often either from starvation or from direct attacks by older sibling
- Intra brood conflict
 - Blue-footed boobies lay two eggs; incubation begins after the first egg is laid so first egg hatches earlier
 - If elder sibling is 20-25% below its expected weight it attacks sibling
 - Experimentally withheld food a day; older chick attacked younger but stopped once feeding resumed

Sibling rivalry

Obligate siblicide

- In some species of pelicans, boobies, and birds of prey the mother always lays two eggs
- Older sibling always kills younger sibling
- Extra egg can act as an insurance
- Second egg of Nazca boobies survives if first egg fails to hatch
- In both Nazca boobies and American white pelicans reproductive success is reduced if second egg is experimentally removed

Sibling rivalry

Sibling relatedness influences rivalry

- An offspring's demand for parental resources depends also on the cost of depriving siblings from resources
- As relatedness to siblings declines, cost of depriving them of parental care decreases
- Nestlings beg more vigorously in species with higher levels of extra-pair paternity
- In birds with well-lit nests offspring have redder mouths in species with higher rates of extra-pair paternity. Intensity of red in mouth is indicator of chick hunger so offspring try to increase their share of parental resources

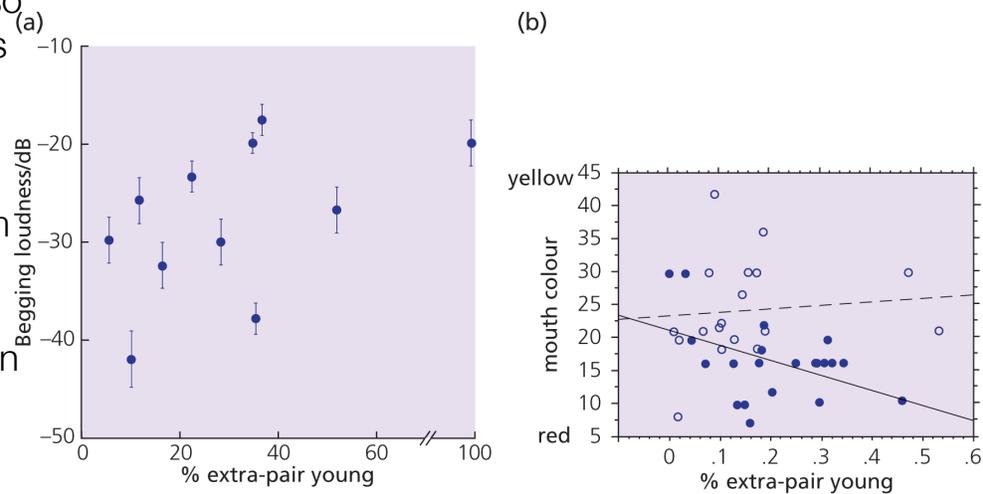
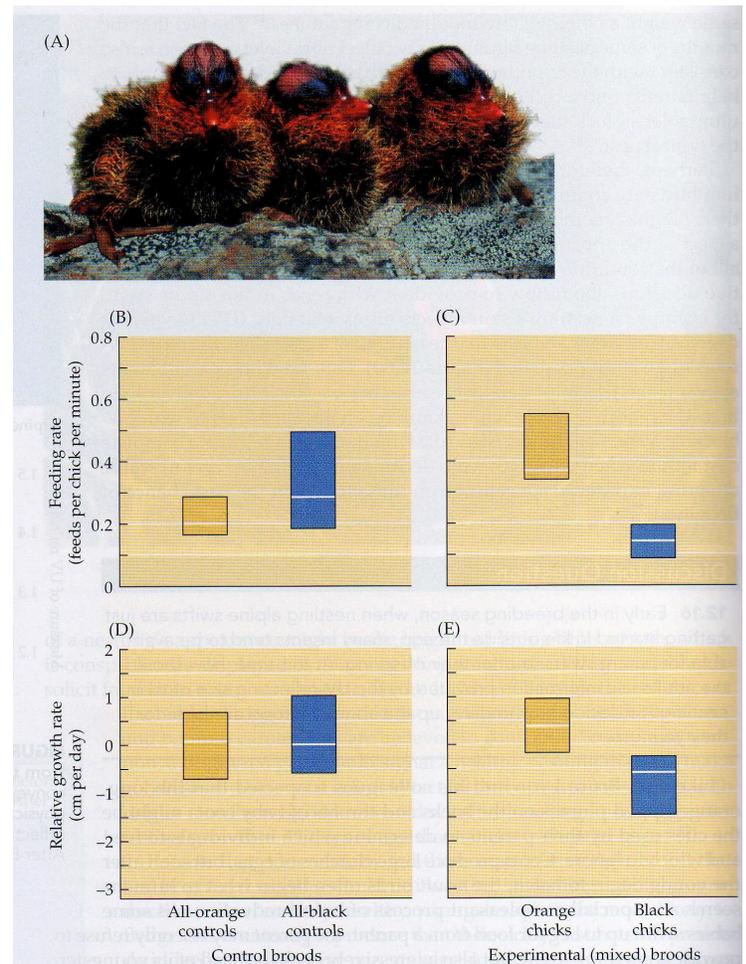


Fig. 8.9 Sibling conflict within broods of nestling birds increases as relatedness declines. (a) Nestlings beg more loudly in species where there is higher extra-pair parentage (i.e. lower average relatedness between siblings). This significant relationship still holds when controlling statistically for phylogeny, brood size and body mass. The species with 100% extra-pair parentage is the brown-headed cowbird, a brood parasite unrelated to the host young (Briskie *et al.* 1994). (b) Nestlings also have redder mouths in species with higher extra-pair parentage, but only in species nesting in open nests (solid symbols; solid line), not in those nesting in dark nests (open symbols: dashed line) (Kilner, 1999).

Sibling rivalry

Offspring cues

- Not all offspring expected to survive to adulthood and reproduction
 - If offspring display cue to indicate future reproductive potential parents may show favoritism
- American coots produce more eggs than they can feed and actively reduce brood size
- Chicks have bright orange-tipped feathers on their backs and throat
- Orange feathers trimmed from 50% of chicks in experimental broods. Control broods either all orange or all trimmed
- Unaltered chicks in experimental broods fed more and grew faster. In both control groups chicks fed at same rate and had similar survival



Parent-offspring conflict

- Parent-offspring conflict harder to prove
 - Previous examples of sibling rivalry could be parent optimizing investment in relation to variable resources
- Parent-offspring conflict can lead to evolution of genomic imprinting
 - Resources invested in current offspring can't be used for future ones
 - Often occurs during pregnancy
 - Imprinted genes behave differently depending on the parent they are inherited from
- In many species a female mates with several males during her lifetime
 - Maternally inherited genes in current offspring more likely to be present in future offspring (mother remains the same)
 - Maternally-derived genes predicted to restrict current embryos' nutrient intake
- Paternally-inherited genes have less of a probability of being in future offspring (future offspring may have different fathers)
 - Paternally-derived genes predicted to demand more maternal resources than maternal genes in the same offspring

Parent-offspring conflict

- Genomic imprinting and antagonistic genes studied in mice
- *Insulin-like growth factor 2 (Igf2)* is expressed only when inherited from the father
 - When expression is experimentally inactivated offspring are 60% of their normal birth weight
 - Inactivation of maternal allele has no effect on birth weight
- *Insulin-like growth factor 2 receptor (Igf2r)* is maternally imprinted
 - Degrades *Igf2* product, reducing resource transfer from mother to offspring
 - Inactivation of allele results in offspring that are 20% larger than normal birth weight
 - Inactivation of paternal allele has no effect on birth weight
- Tug of war between offspring and mother
 - Genes from father try to extract more resources for his offspring than is optimal for mother to give

Summary

- Differences in whether each sex provides parental care reflect differences in life history constraints, in the benefits of care and the costs of missed mating opportunities
- Sexual conflict occurs over which parent should provide care and over how much to provide
- Even though species usually have one type of parental care (maternal, paternal, biparental) many factors can influence the amount each parent invests during a reproductive event
- Individual offspring are selected to demand more care than is optimal from a parent's point of view and can result in intrabrood and interbrood conflict