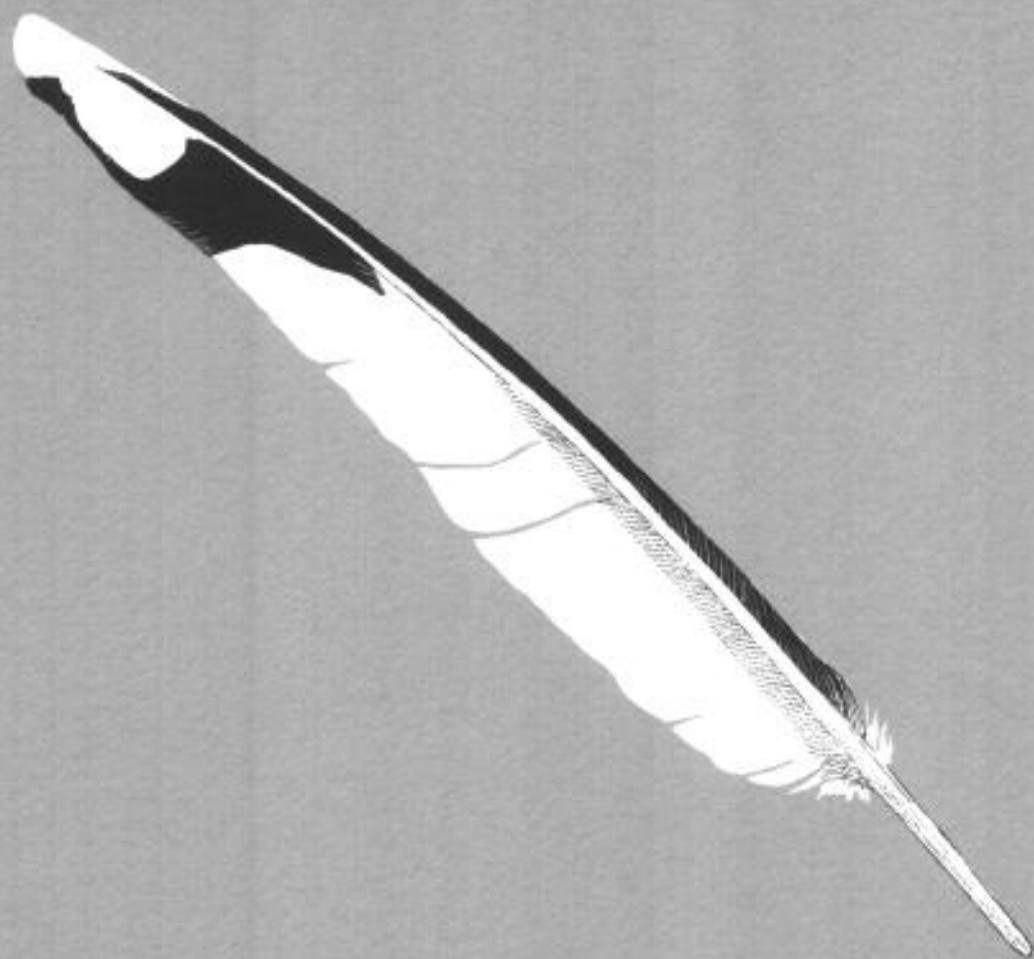# Ornithological Monographs No. 47

Parent–Offspring Conflict and its Resolution
in the
European Starling

by

Elizabeth Litovich and Harry W. Power

PARENT–OFFSPRING CONFLICT
AND ITS RESOLUTION
IN THE
EUROPEAN STARLING

ORNITHOLOGICAL MONOGRAPHS

Edited by

NED K. JOHNSON
Museum of Vertebrate Zoology
&
Department of Integrative Biology
Life Sciences Building
University of California
Berkeley, California 94720

PARENT–OFFSPRING CONFLICT AND ITS RESOLUTION IN THE EUROPEAN STARLING

BY

ELIZABETH LITOVICH and HARRY W. POWER
Department of Biological Sciences
Rutgers University
P.O. Box 1059
Piscataway, N.J. 08855-1059

FOR

EL's children, Jacqueline, Michelle and Jon Alexander Torres

and

HWP's child, Rebecca Power

in the fervent hope that they will be like good little starlings and *not* develop ways to deceive or coerce their parents into capitulating to their demands.

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CHAPTER 1

Basic Concepts and General Methods

A common feature of human experience is conflict between parents and children. Analogues of human parent–offspring conflict abound in other socially advanced species, particularly among birds and mammals. Familiar examples include the common weaning conflicts of mammals and the parallel termination of feeding conflicts of altricial birds.

Trivers (1974) appears to have been the first to have made a full-scale effort to understand intra-family conflict in evolutionary terms. He singled out parents and offspring as very special actors in genetic conflict. He argued that because each parent passes on only one half of its genetic endowment to each offspring, what is in the genetic interests of the parent is not necessarily in the genetic interests of the offspring and vice versa. He also speculated that offspring could be expected to win some of the time, if they have the ability to manipulate their parents.

Manipulation could occur through either coercion or deception (Table 1). Manipulation of offspring through coercion could commonly be done by parents as in the cases of genetic sex determination and hatching order; in both cases, offspring are presented with a *fait accompli* and have no ability to change the outcome of the parental action. Manipulation of parents through coercion by offspring would seem to be difficult outside *Homo sapiens* because in most other species parents appear to control all the essential resources (but see social insects below). Manipulation through deception could occur in many species and be done by either parents or offspring provided that they could communicate with each other. Parents have more opportunities for manipulation (3 out of 4 possibilities in Table 1) than offspring have (only 1 out of 4 possibilities) because parents control resources.

Deception is the more interesting form of manipulation because with deception both parent and offspring can be proactive as well as reactive parties, i.e., both can initiate action as well as respond to the actions of others. This symmetry between parent and offspring, and between action and response, should permit a greater range of strategies and tactics by both parties. The power of offspring to deceive their parents (and so gain more than their fair share of parental resources) lies at the heart of the Trivers-Alexander debate over who wins in parent–offspring conflict. We will review that debate in some detail in Chapter 6 but only briefly summarize it now.

Trivers (1974) used mostly weaning conflict examples from the literature as evidence of his view that offspring can win in at least a partial sense (e.g., a compromise between parent and offspring), and he left open the possibility of total offspring victory on a more than rare basis. Alexander (1974) took the position that offspring victory is highly unlikely in an *evolutionary* (as opposed to a short-term phenotypic) sense because (1) parents control essential resources and can withhold benefits when offspring do not meet parental expectations and (2) today's winning offspring is tomorrow's losing parent. The second objection is potentially the more damaging because although parents control resources, offspring could conceivably manipulate parents into believing that offspring are meeting parental expectations. Later Alexander (1979) made it clear that he agrees

TABLE 1

MANIPULATION AND COMMUNICATION[1]

Communication	Manipulation via	
	Coercion	Deception
A. Parents		
Present	P[2]	P
Absent	P	N
B. Offspring		
Present	N	P
Absent	N	N

[1] From Litovich (1982).
[2] P = Possible; N = Not possible.

that offspring can win in intergenerational time under special circumstances, but only rarely. Thus the Trivers-Alexander debate is about *how frequently* offspring victory can occur, *not whether it can occur.* This point seems generally misunderstood by commentators on the subject who have caricatured Alexander's (1974, 1979) position more than they have addressed it (see *The Parent–Offspring Conflict Debate* in Chapter 6).

Most commentaries and models have sided with Trivers (1974). However, none of them provides a clear-cut empirical test to determine who wins in parent–offspring conflict in real species living in real environments. Thus these treatments cannot be used to determine the frequency of offspring victory. We address that shortcoming in Chapter 6 by proposing a simple empirical test and applying it to our results.

We believe that it is important to understand a fact mentioned in few theoretical treatments, i.e., that the existence of phenotypic conflict is itself not sufficient to prove the existence of genotypic conflict of interest (Alexander 1974; Anderson 1989). Weaning conflicts are examples of this concept. They could as easily represent a "discussion" between parent and offspring over the offspring's true needs as they could represent a condition of true hostility based on the degree of genetic dissimilarity between parent and offspring (R. D. Alexander, personal communication). Thus a distinction between genotypic and phenotypic conflict is in order. Table 2 shows all possible formal cases of such conflict and agreement.

1) Phenotypic and genotypic conflict could simultaneously occur between a parent and its offspring when they each have their own genetic best interests at heart. In such a case, they might be expected to behave in a manner that would have the effect of increasing their own personal fitness, even if this is at the expense of lowering the other's personal fitness (Table 2, Type A).

2) Genotypic conflict and phenotypic agreement (Table 2, Type B) could occur as in the case of altruistic offspring meeting parental expectations without regard for their own genetic self-interest and because of that losing to more selfish offspring. This situation could be expected to be uncommon because these individuals would be selected against.

Another example would be the case where parents coerce their offspring into submitting to their demands even though it is not in the offspring's genetic self-interest to do so (R. D. Alexander, personal communication). This might be common in nature.

TABLE 2

PHENOTYPIC VS GENOTYPIC CONFLICT[1]

Type	Genotypic	Phenotypic	Example
A	Conflict	Conflict	—Offspring fails to persuade parent to give it more food than the parent is favored for giving.
B	Conflict	Agreement	—Offspring deceives parent into giving more food than the parent is favored for giving.
C	Agreement	Conflict	—Offspring begs even though it is so weak that a meal will not save it and it has healthy sibs that would gain from the same meal.
D	Agreement	Agreement	—Offspring is fed by a parent favored for feeding it.

[1] Adapted from Alexander (1974) and Litovich (1982).

3) Phenotypic conflict could occur between a parent and its offspring even when their genetic interests coincide (Table 2, Type C). Failure of communication could be the cause of such an event as when offspring continue to beg despite their parents' efforts to silence them because a predator is near.

Another example would be the case where a parent feeds the wrong kind of food just to silence begging offspring (Tinbergen 1981).

4) Simultaneous genotypic and phenotypic agreement could occur when both parties gain from cooperation (Table 2, Type D), e.g., when young obey their parents' calls to be quiet as a predator approaches. Intuitively, this would appear to be the most common case.

More than anything else, Table 2 shows that parent–offspring conflict is not a simplistic phenomenon that can be fully understood by purely theoretical treatment. It needs an empirical treatment to demonstrate the full array of parent–offspring interactions and their most reasonable interpretations.

In this monograph we seek to reduce the confusion surrounding the subject of parent–offspring conflict by reporting the results of a series of experiments on European Starlings (*Sturnus vulgaris*). This is an appropriate study species for several reasons:

1) It is an outbred, sexually reproducing species. Only a few (n < 10) of the 1,000+ nestlings we have banded have returned to our study area to breed, and none of these has mated with a known relative. This outbreeding creates genetic dissimilarity between parent and offspring, setting the stage for genotypic conflict of interest.

2) It has altricial young subject to starvation during the nestling period. This creates frequent opportunities for phenotypic conflict over the timing and amount of food delivered to nestlings.

3) Potential conflicts of interest between parents and offspring are exacerbated by asynchronous hatching. This creates a frequently lethal competition for food between the last hatched nestling (hereafter the "runt") and its older synchronously hatched nestmates (Stouffer and Power 1990, 1991; this study). It also creates a direct conflict of interest between the runt and the parent in that the parent dispenses food by a rule that disfavors the runt, threatening its life (Chapter 4). One of the most powerful conflicts of interest has to be between individuals that disagree over the value of one of the contestant's lives to the point that one allows the other to die. [Although it is true that situations can exist where the parent

and runt can agree that it is in their joint best interest for the runt to die (O'Connor 1978), runt death at the end of the nestling period is not such a situation (see Chapter 5).]

4) It has complex communication signals (Feare 1984). This is a prerequisite for manipulation through deception.

5) Both male and female parents care for young. This allows observation of potentially different gender-based parental strategies.

6) It nests in dense populations and accepts nest boxes. This enables observation and experimental manipulation of sufficient numbers of individuals and broods to provide answers to difficult questions.

These experiments were conducted between 1979 and 1982 on the Livingston Campus (previously called the Kilmer Campus) of Rutgers University in Piscataway, NJ. The field site, described by Crossner (1977), is a mosaic of old fields, tended lawns, roads, parking lots and scattered buildings.

Between 21 and 113 wooden nest boxes were available annually for this project, depending on year and the needs of competing projects on starling behavior. Nestlings were individually marked by clipping their toenails in a unique pattern shortly after hatching, and by ringing with USFWS numbered aluminum leg bands on days 10 or 11. (Day 1 was the day of hatching.) Nestlings were weighed with Pesola scales every day from days 1–5 and on alternate days from days 10–20. Additionally, some adults were trapped in their nest boxes, and weighed and marked with both color rings and USFWS leg bands.

A total of 17 "viewing boxes" were constructed over the window openings of unused rooms (7) in old office buildings, or over holes (10) cut into the walls of an abandoned poultry shed. These allowed observation of nest interiors and manipulation of nestlings for experimental purposes. Each viewing box had a 5.5 cm diameter circular hole to the exterior to allow birds access to their nests, and a 13 × 17.5 cm rectangular hole to the interior to allow investigators to view nests and manipulate nestlings. The rectangular holes were covered with plywood when not in use. About two days after hatching, the plywood was replaced with a piece of glass. The birds' view of the room or shed interior was blocked by a thick, dark piece of fabric suspended behind the glass. A slit was cut into the fabric to enable insertion of the lens of a black-and-white video camera. The camera was connected to a videotape recorder to allow permanent recording of nest activities. A monitor was used to observe nest interiors when the camera was operating.

However, most nests were watched directly (i.e., without a camera) because it was impossible to distinguish the sexes of the parents, and to a lesser extent individual chicks, with a black and white camera. Whenever the nest was watched through the slit, another piece of cloth, 60 × 100 cm, was placed behind the observer. This prevented birds in the nest from seeing any activity in and around the observer, even when the lights were on.

Each nestling in a viewing box was individually marked within 24 hours of hatching with a collar made from colored plastic flagging material and held together with a thin strip of masking tape. This marking method was found to be better than painting the nestlings themselves because in most cases paint (e.g., ink, magic marker, or watercolors) wore off in less than 24 hours. These collars

did not need to be replaced until the nestlings outgrew them in about 5–8 days. However, paint was used to distinguish nestlings whenever they were videotaped.

In order to prevent adults from watching experimental manipulations, they were excluded from the nest by a piece of cardboard over the entrance until the manipulation was finished. If the birds built a nest with the cup at the end of the viewing box farthest from the observer's point of view, the whole nest was lifted and rotated until the cup was closest to the viewing hole. This prevented the parent from blocking the observer's view while it fed young. Specific methods for individual experiments are detailed in the chapters below.

CHAPTER 2

COMMUNICATION BETWEEN PARENT AND BROOD

In this chapter we present the results of two experiments designed to test whether *entire broods* can influence the behavior of their parents through communication. This is important because parent–offspring conflict can be resolved in favor of offspring only with deception in an altricial species such as starlings where nestlings are entirely dependent upon their parents for the first few weeks of life, and deception is obviously impossible in the absence of communication. Thus it is necessary to show that parents respond to communication from their offspring. Communication between parent and entire brood is simpler than communication between parent and individual offspring because it does not require recognition of individuals and their separate needs. (The question of communication between parents and *individual offspring* will be considered in the next chapter.)

Before describing the experiments, it is worthwhile to consider whether "deception" is a useful concept in animal behavior. Some people are uncomfortable with its application to non-humans because they perceive the term as anthropomorphic and laden with moral connotations. We intend no such interpretation. To us, non-humans are entirely amoral and "deception" is a useful term because it simply means a trick, stratagem, ruse or subterfuge to fulfill a purpose or to obtain an advantage (Stein and Urdang 1969). The ideas of purpose and advantage have long proven useful in analyzing animal behavior (Williams 1966). Deception by adult humans clearly has moral content but there is no reason to suppose that deception by animals and very young children is anything other than an operational device without moral meaning.

Although important topics, we are not here concerned with either the philosophical or psychological dimensions of "deception." Nor are we concerned with its evolution within the Animal Kingdom. Every monograph must set its limits lest it become endless, and these limits are among ours. Readers interested in these broader questions are referred to the paper collections in Mitchell and Thompson (1986), and Byrne and Whiten (1988).

The concept of deception has proven useful in the study of birds. Munn (1986) found that members of the sentinel species *Lanio versicolor* and *Thamnomanes schistogynus* use false alarm calls to stimulate individuals of other species within mixed species flocks of the Amazon forest into evasive behavior, and thereby enhance their own chances of capturing arthropods flushed by fooled individuals. Møller (1988) similarly found that Great Tits (*Parus major*) use false alarm calls in order to increase their chances of obtaining access to concentrated food sources monopolized by other species, or by more dominant members of their own species. And Møller (1987) found that House Sparrows (*Passer domesticus*) use throat patch size to signal dominance status but that they frequently challenge each other to fights because throat patch size can be a deceptive signal, i.e., a bird's fighting ability may not be as high as its throat patch is large.

Classical ethologists have usually assumed that communication occurs in order to make information available to others, or to reduce ambiguity about the internal state of the signaler (Tinbergen 1964; Zahavi 1979). However, evidence of deception is too overwhelming to ignore. Consider cryptic coloration, or cryptic morphology, or Batesian or Mullerian mimicry, or mimicry in the beetle *Atemeles*

pubicollis, which obtains food and grooming from wood ants by faking its host's signals (Holldobler 1971) or mimicry in the firefly *Photuris versicolor* where the females attract male prey of other firefly species by distinctively flashing back the responses of the prey species' own females (Lloyd 1975). Evidence of intraspecific deception, although harder to obtain, is also compelling. Male ten-spined stick-lebacks (*Pygosteus pungitius*) adopt cryptic female coloration and gain access to nests of other territorial males. Although the purpose of this deception is still being investigated (Morris 1952; Otte 1974; Rohwer 1978), there is no doubt that the available evidence refutes the notion that communication involves only the provision of information.

Dawkins and Krebs (1978) believe that communication is always an attempt by the signaler to manipulate the signalee. They state that to view communication as a simple exchange of information is naive. In our opinion, the correctness of their view depends on the meaning of "manipulation."

If by "manipulation," "deception" is really meant, then all communication cannot be manipulation. A bird giving an alarm call is not necessarily deceiving its neighbors; it may be merely informing them of imminent danger. And a hungry nestling begging for food is not necessarily deceiving its parents; it may be genuinely informing them that it is hungry. Indeed, if deception were always involved, then the receiver would be selected to discount at least the intensity with which the signal was given and thus communication would deteriorate, perhaps even dissolve.

But if by "manipulation," "management or influence to suit one's advantage" (Stein and Urdang 1969) is really meant, then even fully truthful communication could have a goal of manipulation because telling the truth could stimulate the receiver to benefit the signaler as in the nestling begging example. We accept Dawkins and Krebs' (1978) interpretation with the understanding that "manipulation" has this latter meaning of influence for the purpose of gaining advantage; sometimes this may involve deception but not by definition.

THE EXPERIMENTS

DESIGN

In order to determine whether entire broods can influence their parents' behavior, begging behavior was looked at because it is the dominant form of communication between nestlings and parents. Its consequences for nestlings are potentially life-threatening if a parent chooses to ignore its nestlings, or phenotypically and genotypically rewarding if a parent benefits them.

The potential for conflict of interest is great in begging behavior because each "player" has power. The parents control the food and have the ability to clean nests while the offspring control information about the status of the parents' genetic investment because only they know their own physiological condition. It is in just such a system that one could expect to find both communication and attempts at manipulation by parents and offspring.

Experiment 1 tested the null hypothesis (H_0): the frequency of begging by the brood does not affect the number of parental feeding visits to the nest.

Experiment 2 tested the H_0: the frequency of begging by the brood does not affect fecal sac removal by parents.

The alternative to both H_0's is that the frequency of begging stimulates the frequencies of feeding and of fecal sac removal, respectively.

Nine viewing boxes and one trail box were used to perform these experiments. Only one trail box was used because of the need to monitor nestlings. Since it was not possible to see inside a trail box, it was difficult to determine the effects of experimental treatments. Nevertheless, results from this one trail box are included because begging by nestlings could be heard.

The two hypotheses were tested by decreasing the frequency of begging by drugging nestlings with alcohol. Raisins were soaked in brandy or whiskey for at least 24 hours, and then fed to each nestling in a nest. If just enough were administered, nestlings calmed down but did not go to sleep. Because each nestling's alcohol tolerance was found to be different, an initial dose of one raisin/chick was given, followed by subsequent doses of ¼–½ raisin each until begging behavior was obviously affected. This was usually evident in 5–8 minutes.

"Boosters" were also administered throughout the experimental period whenever any chick's begging intensity appeared to return to normal. Usually not more than ½ raisin per vigorous chick was necessary as a booster during any given period.

Raisins not soaked in alcohol were used as a control for alcohol-soaked raisins. A non-alcohol raisin was administered to each nestling before control observations started. Control observations were made on either the day before or the day after experimental observations in no particular order; this prevented habituation or associative learning effects.

In order to minimize interference and to increase a nestling's acceptance of raisins, raisins were administered just after parents had left the nest. This was because every time a parent left the nest there was a period of a few seconds when the nestlings were still feverishly begging in a sort of "feeding frenzy." A pair of long forceps was quickly slipped through a gap purposely left open between the glass pane and the box roof and a morsel was offered. Nestlings often appeared to be so caught up in begging that they did not know what they swallowed. This was another advantage of using viewing boxes.

Each of the 10 broods was observed for one hour at the same time of day for two consecutive days for a total of 20 contact hours.

The experiment was begun between days 12 and 14 at each nest. The time, sex of parent, begging score of each nestling (see Chapter 3), and the identity of the nestling fed were noted each time a parent visited the nest. Removal of fecal sacs was also noted.

RESULTS

Figures 1 and 2 are decision graphs summarizing the results of Experiments 1 and 2. Each is bisected by a 45° line of equality. The area above that line is the region where nestlings under the influence of alcohol (said to be "drunk" as a convenient shorthand for their slowed begging behavior) invoked a greater parental response than did nestlings not under the influence of alcohol (said to be "sober"). The area below the 45° line is the region where sober nestlings invoked a greater parental response than did drunk nestlings. The 45° line itself is the place where sober and drunk nestlings invoked equal parental responses. The curved line on each graph simply envelops the data points.
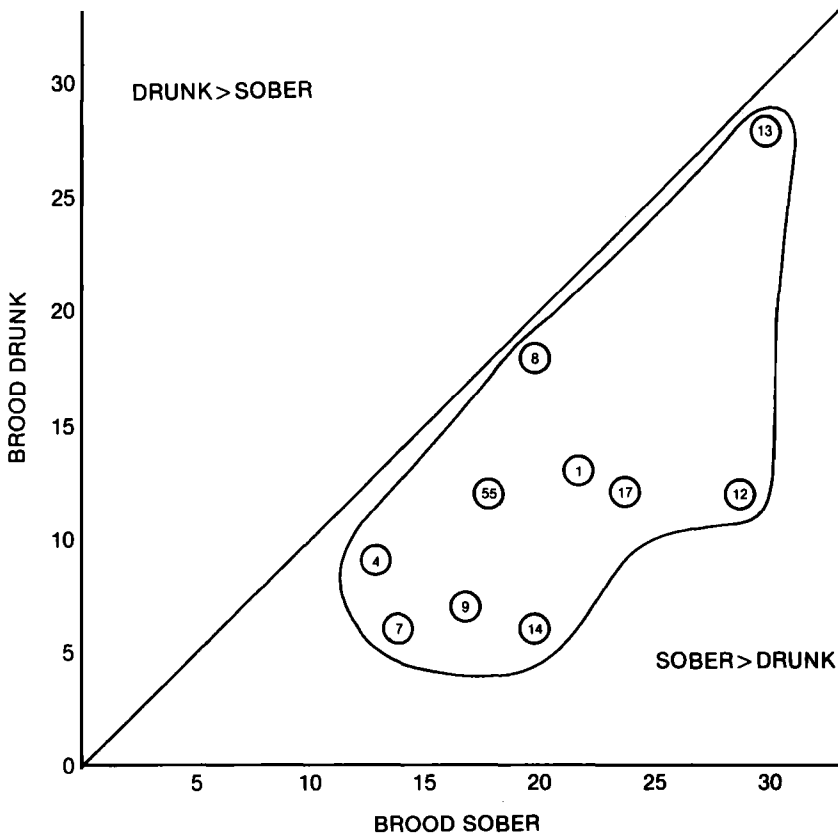
FIG. 1. Communication between a parent and its brood: feedings/hour. x-axis, parental feeding rate when brood was sober/hungry; y-axis, parental feeding rate when brood was fed alcohol-soaked raisins or was sated. Circled numbers refer to individual nests.

The parental response in Figure 1 is the number of times a parent fed its brood per hour when its brood was sober (x-axis) and when it was drunk (y-axis). The parental response in Figure 2 is the number of fecal sacs a parent removed per visit under the same conditions.

Each point on both graphs is the parental response at a single nest, e.g., at nest 12 there were 29 feedings per hour when the brood was sober but only 12 when it was drunk (x,y = 29, 12 in Fig. 1), while there were equal numbers of fecal sacs removed per visit when the brood was sober and drunk (x,y = 0.31, 0.031 in Fig. 2).

Figure 1 shows that broods garnered more feedings per hour from their parents when they were sober than when they were drunk. This difference is highly statistically significant (Wilcoxon Signed Rank Test, $T^+ = 0$, $P < 0.001$) and disproves the H_0 for experiment 1. Figure 2 shows that broods experienced no difference in parental cleaning behavior when they were drunk or sober ($T^+ = 13$, $P < 0.2$). Thus the H_0 is accepted for Experiment 2.

These results suggest that parents use begging behavior by the brood as a whole as a cue in deciding how often to feed young but not in how often to clean nests.
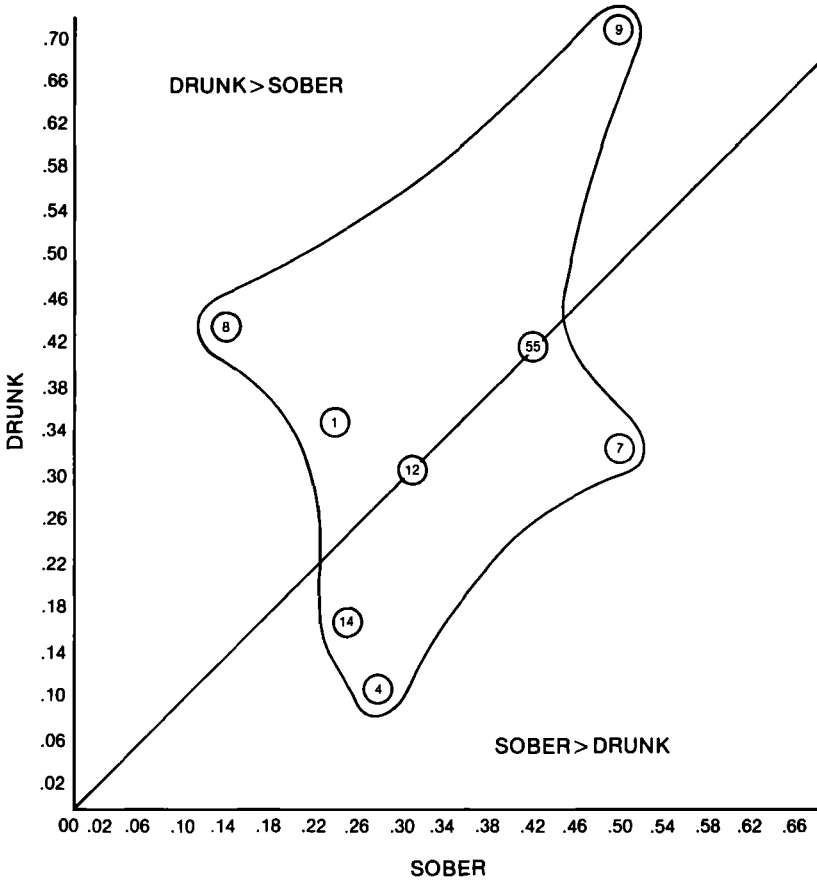
FIG. 2. Communication between a parent and its brood: fecal sac removals/hour. Coordinates and circled numbers are analogous to those in Figure 1.

DISCUSSION

These results are consistent with those of Tinbergen (1981). Observing 3 pairs of starlings, he found that both nestling hunger and number of young affected the frequency of parental visits to the nest. He also found that nestling hunger influences prey choice. Females feeding very hungry nestlings take lower quality prey found in greater abundance in an apparent effort to maximize energy over time while females feeding satiated young appear to maximize prey quality.

Communication between entire broods and their parents has also been shown in other species. Von Hartman (1953) showed that six hungry nestling Pied Fly-catchers (*Ficedula hypoleuca*) calling from a hidden compartment stimulated parents to feed a single offspring more than twice as much as they normally would. Henderson (1975) found that the parent's foraging rate is apparently regulated by the brood's cumulative calling rate in Glaucous-winged Gulls (*Larus glaucescens*). Muller and Smith (1978) found that visual cues were more important than vocalizations in young nestling Zebra Finches (*Taeniopygia guttata*), but that when offspring reached 12–16 days of age recorded calls were sufficient to stimulate

feeding by parents. Miller and Conover (1979) found that brood vocalizations were critical in Ring-billed Gulls (*Larus delawarensis*) only for the first three days after hatching; thereafter parental care proceeded normally even when the whole brood was muted. Harris (1983) found that parent Atlantic Puffins (*Fratercula arctica*) brought more food to their nesting burrows under 2 experimental conditions: (1) when older chicks were replaced by younger chicks, and (2) when taped begging calls were played from the roofs of nesting burrows. Presumably younger chicks were fed more than older ones because the latter were at an age ($\bar{X} = 31$ days) when the feeding rate normally declines. Taped begging calls simply added to those given by the chicks. Bengtsson and Ryden (1983) found that parent Great Tits fed their broods more often (1) when begging calls were played during feeding visits, and (2) after an experimental period of 4 hours of food deprivation. They also found an enhanced feeding rate when the heaviest nestlings in broods were temporarily removed, but we find this result difficult to interpret. Nevertheless, their first 2 results clearly show communication between brood and parent, i.e., their first result directly connects begging calls with feeding frequency and their second indirectly connects them in that hungrier young could be expected to beg more intensely.

That parental feeding behavior was influenced by the begging behavior of nestling starlings in our study, but that parental removal of fecal sacs was not, is consistent with the idea that the begging threshold of a nestling should be lower when only one individual is rewarded by an act of parental care (e.g., feeding of individual young) than when several or all young are rewarded (e.g., nest sanitation). This is because the cost of remaining silent when nest mates are begging is to go hungry in the context of parental feeding (see next chapter), but is probably nothing at all in the context of nest sanitation because the parent will clean the nest even if some young are silent.

Of course, the difference in parental feeding and nest sanitation behaviors is also consistent with the idea that parents do not use offspring begging as a cue in deciding when to clean nests. They probably use the presence of fecal sacs as the cue that cleaning is needed.

Hussell (1988) published a model of interaction between parents and broods that would have influenced our design had it been available before our experiments. Even so, interesting comparisons can be made between his model and our results. Hussell's (1988) model is based on microeconomic theory. It generated predictions consistent with the results of a field experiment on wild broods of Tree Swallows (*Tachycineta bicolor*) at Long Point Bird Observatory in Ontario. The model posits separate supply and demand functions interrelating hunger signals by young and feeding rate by parents. The supply function is the response of the parents to the hunger signals of their young. The demand function is the hunger signal response of the young to the feeding rate of their parents.

Because our experiments were completed before Hussell's (1988) model was published, we did not design them to show the possible existence of 2 or more supply functions nor did we measure feeding rate and hunger signals in the same manner as Hussell (1988). But our experiments did produce results consistent with the idea that there are at least 2 demand curves, one for sober broods and the other for drunk broods. Thus our results are qualitatively similar to Hussell's

(1988) Figure 8 except that the variable affecting demand in his study was brood size while it was brood alertness in ours. Even the rough support for Hussell's (1988) model provided by our study suggests that his model has value and should be rigorously tested in several species.

CHAPTER 3

COMMUNICATION BETWEEN PARENT AND INDIVIDUAL OFFSPRING

In this chapter we present the results of two experiments designed to test whether individual offspring can influence the feeding behavior of their parents. The first tests whether parents respond differently to individual offspring on the basis of differences in begging behavior both within and between individuals. The second tests whether parents differ in their response to offspring on the basis of parental gender.

The first experiment is important because individual offspring can win in parent–offspring conflict only if their individual behavior can influence their parents' response to them. It is also important because differences in the behavior of individual offspring could be used by parents to manipulate their offspring in order to produce parental victory in parent–offspring conflict, e.g., by rewarding only those offspring whose behavior conforms to the parents' best interests. The second experiment is important because offspring could potentially manipulate their parents more easily if their parents respond differently to them as individuals, i.e., if male parents respond differently to individual offspring than female parents do (e.g., by responding to different cues), then individual offspring might be able to deceive their parents into giving them more food (or other resources) than is in their parents' best interests by "telling" one parent one thing and the other parent another thing.

THE EXPERIMENTS

DESIGN

Experiment 3 tested the H_0: differences in the individual begging behavior of nestlings do not influence parental feeding behavior. The alternative hypothesis was that more intense begging behavior stimulates more frequent feeding behavior.

To test this hypothesis it was necessary to score begging behavior and to manipulate its intensity.

Begging behavior was scored according to the scheme in Table 3. Although begging has many components, no attempt was made to isolate them or to determine their relative importance because we were interested in their cumulative effect. However, a higher score reflected the use of a greater number of components. Thus a score of 3 was assigned to a chick when it opened its bill but did not peep while a score of 4 meant peeping while opening the bill. If a nestling stood out in the brood (either because its vocalizations were clearly louder than its sibs' or because its head stuck out the farthest), that nestling was assigned a score 0.5 points higher than it otherwise would have earned. In the previous example, the nestling would have gotten a 3.5 rather than a 3 if its actions made it stand out while it was silently opening its bill. Similarly, whenever a nestling weakly performed all the actions that categorize a given level, it was assigned a score 0.25 points lower than its behavior otherwise indicated. [Gottlander (1987) independently developed a similar scheme for recording begging intensity in nestling Pied Flycatchers several years after this study was completed (Litovich 1982).]

Scoring was based only on behavior displayed from the time the parent showed up in the nest until it began feeding. Behaviors before or after that were not

TABLE 3

ETHOGRAM OF NESTLING BEGGING BEHAVIOR

Code	Description
1	Sleeping, or chirping with eyes and bill closed
2	Awake but not begging
3	Lifts head and opens bill; no vocalizations
4	Head up and chirping
5	Head up and facing parent while standing up and chirping
*	First one to beg
**	Loudest, or head stands out

considered because they were irrelevant to determining whether nestlings could individually communicate with their parents since their parents weren't there. Because it was impossible to watch all nests at the same time of day, observation periods were standardized by watching until a parent fed its brood 32 times or until two hours had elapsed, whichever came first. Thirty-two is representative of the number of trips a parent makes to its nest in the morning.

To obtain baseline feeding data for experimental nestlings, each was observed at the same time of day either the day before or the day after the experimental observations were made.

Only viewing boxes were used in these experiments. All nestlings were individually marked. The experimental nestling was chosen indiscriminately from its brood except that nestlings that had already been tested were not used again.

The time of day, identity of nestling fed, and begging score of all nestlings in a brood were noted every time a parent visited the nest.

Begging behavior was manipulated in different ways in different years. In 1980 it was manipulated by providing extra food (1–2 cm long sausage-shaped portions of ground beef); in 1981 it was manipulated by providing alcohol-soaked raisins (see Chapter 2). Both procedures reduced begging scores relative to the control procedures of no extra food (hungry nestlings) or provision of non-alcohol raisins (sober nestlings). Thus the data for both years were pooled and are presented jointly in the results below. Drugging with alcohol proved to be a better manipulation than sating with meat because alcohol was easier to administer, faster to act, and more economical to provide. We recommend it for future studies.

As in Experiment 1, artificial feeding was performed right after parents left the nest when most nestlings were still begging.

Experiment 4 tested the H_0: there is no sexual dimorphism in parental feeding response to nestlings.

This hypothesis was tested by noting the gender of the parent providing food during the experimental manipulations described above, and comparing the results for male and female parents.

RESULTS

Figure 3 is a decision graph that compares the response of parents to individual nestlings when those nestlings were either sober/hungry or drunk/sated. The x and y values are proportions, e.g., the vertically highest point represents a nestling that was fed on 0.33 of the feeding trips to the brood when it was sober/hungry (x-value), and on 0.22 of the feeding trips to the brood when it was drunk/sated
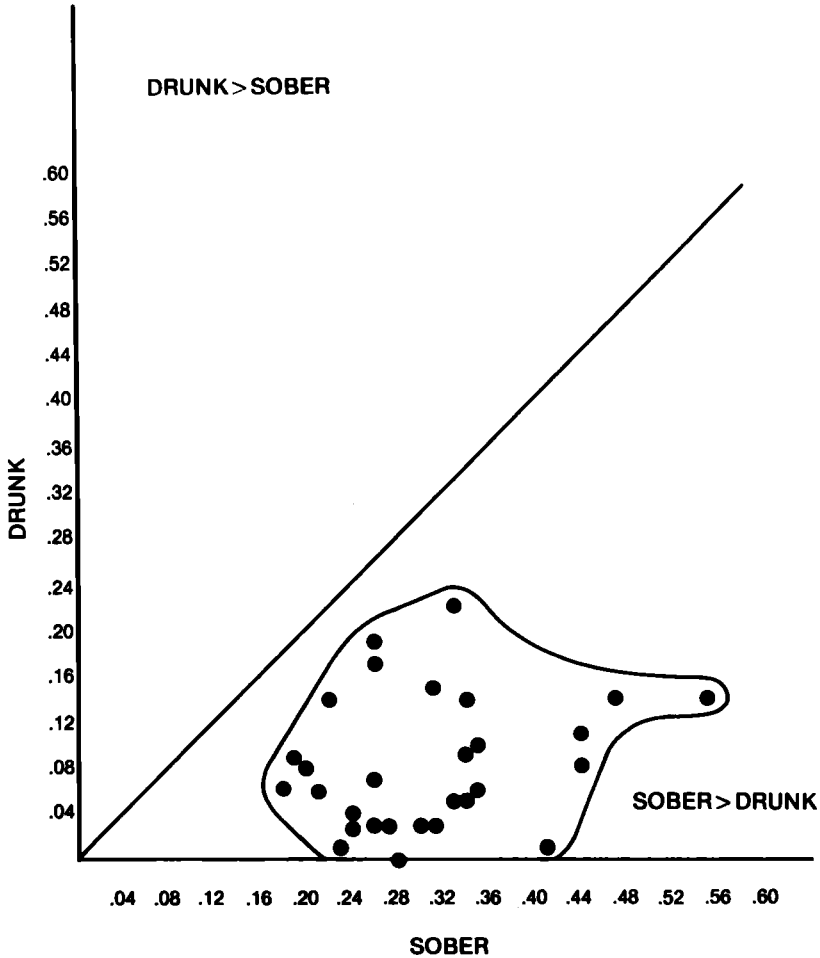
FIG. 3. Communication between a parent and individual offspring. The number of times an individual nestling was fed when it was sober (x-axis) vs when it was treated with alcohol-soaked raisins (y-axis) as a proportion of the number of times its entire brood was fed.

(y-value). Figure 3 shows that individual nestlings were always fed more when they were sober/hungry than when they were drunk/sated (Wilcoxon Signed Rank Test, $T^+ = 0$, $P < 0.002$).

Figure 4 graphs the feeding response of parents to their nestlings in relation to those nestlings' individual begging behavior. It shows that parents almost always fed the nestling with the highest begging score (hereafter the "best beggar") ($r = 0.93$, $r^2 = 0.87$, $P < 0.001$). It may have been that parents did always feed the best beggar but that parental scoring differed from observer scoring because the observer didn't evolve to score nestling begging behavior.

Figures 3 and 4 collectively show that parents fed their nestlings on the basis of their nestlings' individual behavior. Figure 3 shows this in the context of within-individual begging behavior (sober/hungry vs drunk/sated), and Figure 4 shows it in the context of between-individuals begging behavior (best beggar vs its nest mates). Thus the null hypothesis for Experiment 3 is rejected and the alternative
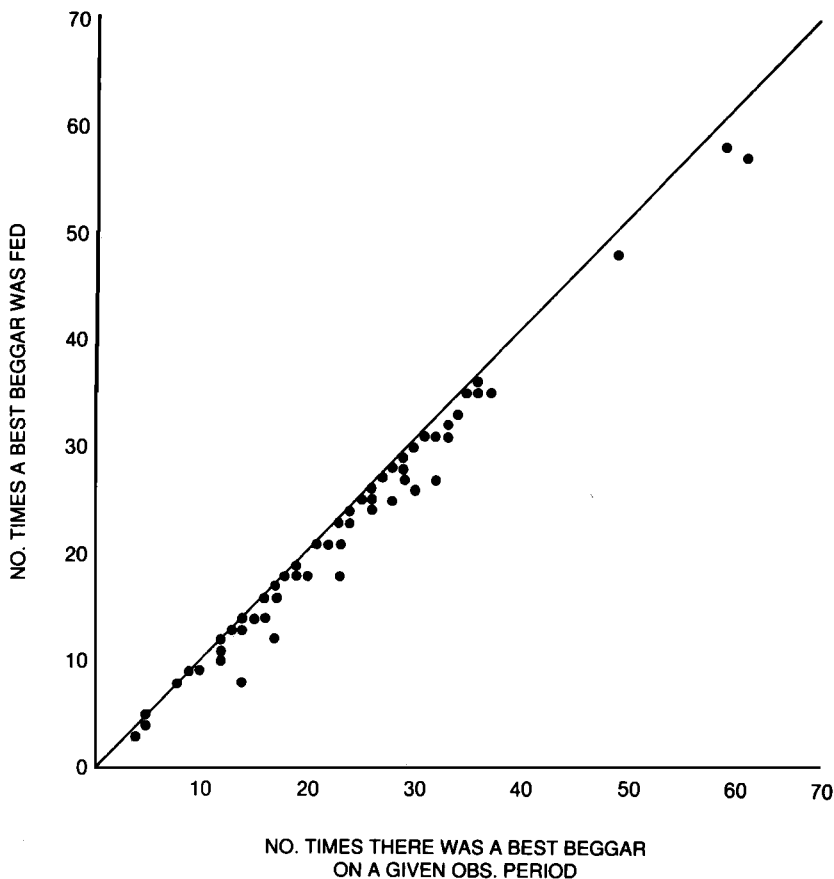
FIG. 4.   The feeding success of "best beggars." Each point refers to a single observation period and relates the number of times a best beggar was detectable (x-axis) to the number of times that the best beggar was fed (y-axis). Points fall along the 45° line when the best beggar was the only nestling fed, but fall below that line when other nestlings were fed.

hypothesis is accepted, i.e., that more intense begging stimulates more intense parental feeding. Jointly these figures show that offspring can individually communicate with their parents.

Figure 5 compares the feeding response of male and female parents when all the members of their broods begged with equal intensity. Since this did not happen often (there was usually a best beggar), the sample is small. Figure 5 is restricted to cases of equal begging intensity by all members of a brood in order to give it the potential to reveal any parental preference other than that for the best beggar.

Figure 4 already implies that both sexes preferred the best beggar. If that were not true, the correlation in Figure 4 could not have been as high as it is because many nestlings besides the best beggar would have been fed, driving the correlation down.

Figure 5 is based on the proportion of all deliveries to a brood by a particular parent that went to an individual nestling. It shows that there was no sexual dimorphism in parental feeding response under the relevant circumstances (Wilcoxon Rank Sum Test, $W = 263$, $P > 0.1$).
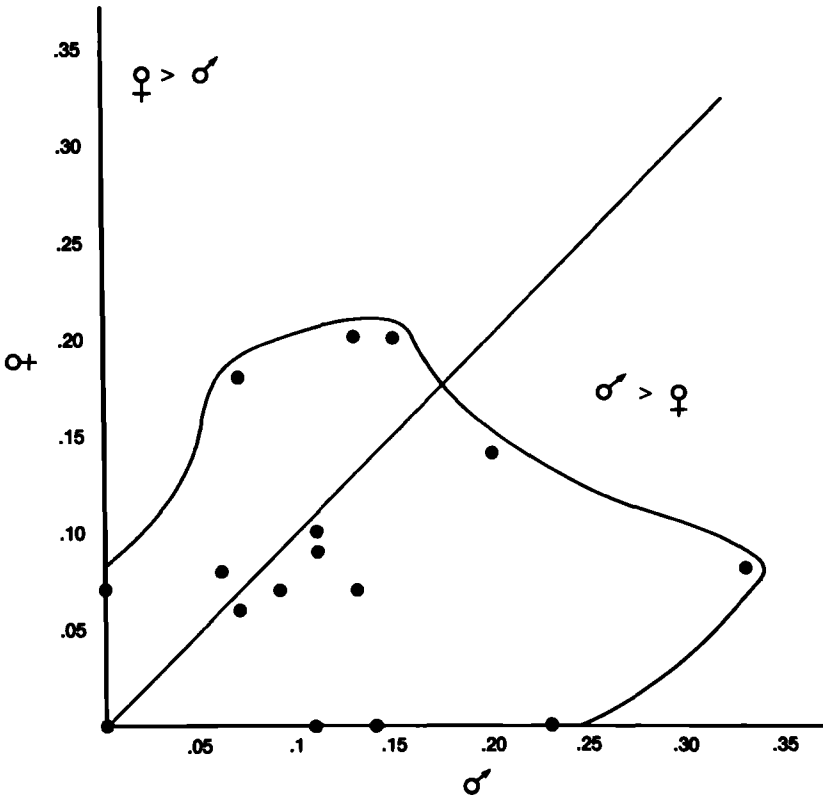
FIG. 5. Sexual dimorphism in parental feeding during the nestling period. The coordinates map the number of times an experimental nestling was fed by a given parent over the number of times that that same parent fed the brood during an observation period for male and female parents, respectively.

The pattern in Figure 5 that would most clearly have shown sexual dimorphism (if it had existed) would have been a significant *negative* correlation. Such a pattern could have resulted from each parent specializing in different young, e.g., from the male caring for one-half of the brood and the female for the other half, or the male caring for sons and the female for daughters. However, such specialization would require that parents feed the best beggar in their portion of the brood rather than the best beggar in the entire brood. We shall see in the discussion that such a response would not be as adaptive as feeding the best beggar in the entire brood.

Because Figure 4 implies that both parents preferred the best beggar and Figure 5 shows that no sexual dimorphism existed in parental feeding response when all nestlings begged equally, the H_0 for Experiment 4 is accepted, i.e., that there is no sexual dimorphism in parental feeding response to individual nestlings.

DISCUSSION

The demonstration that individual nestlings can communicate with their parents affirms the possibility that they might be able to manipulate their parents. However, the fact that parents almost always feed the best beggar suggests that parental victory is almost certain. This is because the parent's interests are always

served by feeding the best beggar but the offspring's interests are not. This conclusion is made clear by exploring the interests of the two parties separately.

1) *The parent's interests.* Feeding the best beggar means investing in the most robust offspring, the ones most likely to survive and hence to reproduce, i.e., those with the highest reproductive value (*sensu* Fisher 1930). This conclusion assumes that begging in the context of a best beggar competition is ultimately an honest signal, i.e., that while nestlings may be able to deceive their parents into "thinking" that they are the best beggar at the time of a single feeding, they cannot consistently deceive them over the course of the nestling period, and that the best beggars really are the most robust offspring. (The more general question of *The Honesty of Begging as a Signal* will be considered in Chapter 6 in the discussion of the parent–offspring debate.)

Nestlings could not long successfully deceive their parents about their own vigor in a best beggar competition: the truly best beggar will be obvious in time while a faker will collapse from exhaustion. Thus offspring *inevitably* tell their parents the truth about their own vigor, and hence investment potential, in a best beggar competition.

Exaggeration in the effort to be perceived as the best beggar is not lying. This is because exaggeration means working harder to get a higher score, and working harder inevitably reveals the true condition of the beggar since the harder it works the less long it will be able to sustain a lie. Thus exaggeration in begging evolves not through successful offspring lying but through parental rewarding of the best beggar.

Feeding the best beggar serves the parent's interests as well as or better than any of its obvious alternatives:

a) *The laissez-faire policy* (Mock 1987). This reduces to feeding the young highest in the nestling hierarchy and letting them work out the hierarchy on their own. [A form of this (feeding the hole-blocker) that occurs late in the starling nestling period will be described below.] Actually, the best beggar on any given feeding is the momentarily highest ranking offspring, and the individual that is most frequently the best beggar is, *ipso facto,* the highest ranking nestling in general. The only difference between feeding the best beggar and the laissez-faire policy is that the latter was first described in siblicidal species where parents feed the older, larger and consistently dominant chick even though that contributes to the death of the younger, smaller and subordinate chick, whereas feeding the best beggar frequently permits the survival of all of the synchronously hatched young and sometimes the survival of the last hatched young. The best beggar policy can be thought of as a more general form of the laissez-faire policy Mock (1987) described for siblicidal species. (The question of siblicide will be returned to in Chapter 6 in the section on *Siblicide and the Best Beggar Rule*.)

b) *The feed-all-equally policy.* This would result in all nestlings being fed equally irrespective of their begging effort or place in the nestling hierarchy. This policy would not serve the parent's interests as well as the best beggar policy because it would invest as much in uncompetitive young as in young potentially winning in reproductive competition. Moreover, if food were in-

sufficient for all young, each would receive the same, inadequate share, potentially dooming the entire brood.

c) *The feed-in-proportion-to-need policy.* This would result in the weaker receiving more attention than the stronger, and would be difficult to implement when there was not enough food for all nestlings because all young would then need more than they could get. This policy would endanger the entire brood when food was scarce. A version of this policy seems to be used by female, but not male Budgerigars (*Melopsittacus undulatus*) (Stamps et al. 1985), and to a lesser extent, by female but not male Pied Flycatchers (Gottlander 1987) (see below). (The feed-in-proportion-to-need policy will be revisited in the *Honesty of Begging as a Signal* section of Chapter 6.)

In essence, feeding the best beggar is equivalent to the laissez-faire policy in some contexts. It serves the parent's interests as well as the feed-all-equally and feed-in-proportion-to-need policies when food is sufficient for all young, and serves the parent's interests better than the latter 2 policies when food is insufficient because only it directs investment in proportion to reproductive value.

2) *The offspring's interests.* The offspring's interests are served by the best beggar rule only when it is the best beggar. At other times it would profit more from the feed-in-proportion-to-need policy except when its needs were unmeetable (e.g., it was ill and could not consume food), and it was favored for "suicide" in the O'Connor (1978) model. The offspring suffering most from the best beggar policy would be those that could gain from being fed but were consistently denied best beggar status by their more competitive nestmates. We shall consider them in detail in the next chapter.

Just as every other adaptation has costs as well as benefits, parental selection of the best beggar has a cost. A high one: the occasional loss of broods to predators attracted to nests by loud, frequent begging calls. Thus selection for parental victory can be limited by the loss of the parent's offspring.

Presumably the best way for a parent to avoid brood loss through predation would be to feed its young so often that they would not attract predators by loud begging. Although this would not help individual nestlings deceive their parents into getting more than their appropriate share of the food relative to their nestmates, it could conceivably enable an entire brood to get more than its fair share relative to future broods, i.e., by deceiving the parents into exhausting themselves on the current brood and so having less than the optimal amount for subsequent broods. Apparently this does not happen in starlings. Power et al. (1989) and Stouffer (1989) found that neither current clutch size nor current brood size affect future clutch size or reproductive success in the study population. Thus it appears that neither individual nestlings nor entire broods can *deceive* their parents into acting against their parents' own best interests.

But begging is not the only way that nestlings get fed. Beginning about day 15, nestlings hop around the nest and block the entrance hole (Ricklefs 1979; this study). The nestling blocking the hole and extending its head through the hole is the one that usually gets fed. When this happens, the other nestlings reduce their begging intensity and attempt to wedge their way into the hole.

If the goal is offspring victory, monopolizing the hole is a better way for a

nestling to operate than begging because the hole-blocking nestling eliminates its parent's ability to choose the offspring to be fed, and makes that choice itself. Nevertheless, moving the operational decision of whom is to be fed from the parent to the offspring does not result in offspring victory in this case because the parent's interests are not hurt even though the offspring's interests are served.

The parent's interests are not hurt because the effect of feeding the hole-blocker is the same as that of feeding the best beggar. Only the most vigorous offspring can succeed at either tactic. Thus the parent feeds the best investment in both cases.

Gottlander's (1987) results for Pied Flycatchers are similar to our hole-blocker results. She found that parents almost exclusively fed those nestlings that were closest to them when they arrived at the nest box (i.e., those young they could reach without stretching their necks), and that nestlings vied for the position that placed them closest to the parent upon its next visit. Greater weight enhanced a nestling's ability to achieve this optimal position.

In the Results we reported that male and female parents do not divide their broods into portions with males specializing in feeding one part and females the other. Instead, both feed whichever nestling is the best beggar in the entire brood at the time of their feeding visit. Both parents feeding the best beggar in the entire brood has these advantages:

1) It avoids the so-called Concorde Fallacy (Dawkins and Carlisle 1976). Good investment does not follow bad. If the best beggar for only a portion of the brood were fed on each visit, good investment would follow bad because the best beggar for the entire brood would often go temporarily unfed.

2) It creates no opportunity for young to play one parent against the other. By having no "favorites" except the current best beggar of the brood, the parents cannot be manipulated by offspring making special claims upon them, e.g., by sons making special claims upon their father even when their begging performance is less than that of some or all of their sisters.

3) It avoids the otherwise inevitable loss of a portion of the brood following the death or desertion of the parent in charge of that portion. The remaining parent continues to provision all young on the basis of their best beggar status. If there are too many young for one parent to rear, it should still be able to fledge at least half of them, the half containing the best beggars in the brood.

Our results differ dramatically from those of Stamps et al. (1985) on domesticated Budgerigars. They found that female parents do not feed the best beggars, but instead preferentially feed the smallest nestlings and often discriminate against their larger, more vigorously begging young. Male parents, however, are similar to starlings in that they feed the most vigorously begging nestlings, particularly late in the nestling period.

A similar but less pronounced preference for smaller nestlings is shown by female but not male Pied Flycatchers (Gottlander 1987). The difference between Budgerigars and flycatchers is that maternal intervention to counteract sibling competition is effective in the former but apparently not in the latter. Thus we shall not discuss this aspect of the flycatcher case further as its results do not differ from those in the starling case, i.e., the best beggar is favored in both.

We believe that some of the difference in feeding strategies of starlings and Budgerigars lies in the difference in their degree of hatching asynchrony. Hatching

asynchrony is taken to an extreme in Budgerigars with incubation beginning with the first of an average of 6.16 eggs and hatching occurring over an average of 8.1 days (Stamps et al. 1985). By contrast, hatching asynchrony usually involves only the last of a modal clutch of 5 eggs in starlings (Stouffer and Power 1990). Were Budgerigars to feed only the best beggar, they could conceivably fledge only a single nestling per clutch because all younger nestlings might be unable to compete with the first-hatched nestling. But in starlings only the last hatched nestling is at special risk when the best beggar is preferred, and these young have the ability sometimes to overcome the handicap of their birth order (see Chapter 4). Why the degree of hatching asynchrony is so much greater in Budgerigars than starlings is outside the scope of this monograph.

Undoubtedly differences in the life histories of Budgerigars and European Starlings account for the presence of sexual dimorphism in parental feeding behavior in the former but not the latter. However, the nature of these life history differences is obscure to us. Intuitively it appears that starlings have a pattern of parental feeding behavior that will be found common in songbirds. Parrots are very different from songbirds and perhaps it should not be surprising that they have different parental behavior.

Stamps et al. (1987) found that male Budgerigars preferentially feed broods with female-biased sex ratios. Female parents have a similar but much weaker tendency. If such a phenomenon exists in starlings it is beyond our ability to detect since we are unable to determine the gender of nestlings despite several efforts to do so.

To the best of our knowledge, this study is the first experimental demonstration that there is communication between individual nestlings and their parents. Other studies have focused on communication between entire broods and parents (Chapter 2), or on when parents recognize nestlings as their own offspring (Davies and Carrick 1962; Peek et al. 1972; Buckley and Buckley 1972; Burtt 1977; Shugart 1977; Beecher, Beecher, and Lumpkin 1981; Beecher, Beecher, and Nichols 1981; and van Elsacker et al. 1988). Parental recognition of their own young is not the same as parental communication with individual offspring because parents could conceivably recognize young as their own without responding to their *individual* signals and needs (instead, treating all members of a brood identically), and adults could conceivably respond to the signals of individual young that were not their own offspring. Parental recognition of their own young is an important question because parental failure to discriminate between their own and other's young could result in altruistic errors. The two questions are interrelated because parental recognition of their own offspring is made easier if those offspring can individually communicate with their parents. This is because parental recognition is likely to be based on factors that are unique about their young (e.g., development, odor, visual appearance or vocalizations), and although parents should be able to discover this uniqueness without the help of their offspring, individual communication from offspring should hasten the process.

Parental recognition of offspring as their own appears to occur later in the nesting cycle than communication between parents and individual offspring. Davies and Carrick (1962) suggested that parent–young recognition develops just prior to the onset of brood mobility. Beecher, Beecher and Lumpkin (1981) postulated that such recognition is not required if parents correctly identify their

own nests and their young remain in them. Work by Davies and Carrick (1962), Peek et al. (1972), Buckley and Buckley (1972), Burtt (1977), Beecher, Beecher, and Lumpkin (1981), Beecher, Beecher, and Nichols (1981), and van Elsacker et al. (1988) has been consistent with these hypotheses (but see Shugart 1977).

Communication between parents and individual offspring apparently occurs right after hatching in starlings since parents always seem to prefer to feed the best beggar, and there is a best beggar from day 1 of the nestling period. However, parental recognition of their own nestlings does not appear early in the nestling period in starlings. As part of experiments on different subjects, Crossner (1977), and Stouffer and Power (1991) transferred nestlings between broods early in the nestling period in our study population and found that all were accepted by their foster parents: none was discriminated against and no parents deserted. Moreover, starlings are unable to recognize their own eggs in our population (Stouffer et al. 1987) despite selective pressure to do so generated by conspecific brood parasitism affecting at least one-third of all early nests (Kennedy et al. 1989), the ones most important in fledgling production (Power et al. 1989).

Recognition of individual nestlings develops before fledging in our starling population. "Alien" fledglings that were almost indistinguishable to the observer from resident nestlings close to fledging age visited viewing boxes but were always evicted by parents returning to their nests to feed their young. Had parents been unable to distinguish the aliens from their own young, they would have fed the aliens instead of evicting them. van Elsacker et al. (1988) performed a cross-fostering experiment and found that parent starlings do not definitively recognize young as their own until their young reach 20 days of age. They believe that vocalizations are the important cue.

To the best of our knowledge, this study is also the first experimental demonstration that parents choose which nestling to feed on the basis of which is the best beggar at the time of a feeding visit. In a sense this is trivially obvious: "everybody knows" that "the squeaky wheel gets the grease." Lay people have told us that they have seen "best beggars" being fed in their backyards, and several theoretical studies of parent–offspring conflict have assumed something like a "best beggar" in their discussions (see Chapter 6). But our result is not trivial because we *defined* what a best beggar is through our ethogram (Table 3), and we developed the importance of best beggar competition to the outcome of parent–offspring conflict over the feeding of nestlings, i.e., inevitable parental victory (see above and *Who Wins in Parent–Offspring Conflict in Starlings* in Chapter 6).

Some other studies have suggested that the largest, most aggressive, most active or most hungry nestling is the one usually fed (Gabrielson 1913 cited in Reed 1981; Lockie 1955; Lack 1956; Ricklefs 1965; Maxwell and Putnam 1971; Henderson 1975; Skutch 1976; Drummond et al. 1986) but offered only anecdotal evidence in support of their suggestions.

Yet other studies have been more explicit in their evidentiary basis but did not conclude that parents favored the best beggar in a brood. Muller and Smith (1978) examined the relationship between lateral tongue movement in nestling Zebra Finches and feeding frequency but concluded that they were not causally related. Ryden and Bengtsson (1980) analyzed begging behavior in one brood each of European Blackbird (*Turdus merula*) and Fieldfare (*T. pilaris*), and found that neck extension, beak to beak distance between parent and nestling, and onset of

begging were all positively related to parental feeding response. However, they treated these variables separately rather than as components of begging intensity and seemed to overlook their inter-relationships. They then analyzed the feeding frequency of two broods of Great Tits in relation to position in the nest and begging frequency (as opposed to intensity), but could not distinguish between them in terms of effect. They did find that nestlings farthest from their parents tended to beg less frequently and were fed less often. Bengtsson and Ryden (1983: 249) concluded that "the effective stimulation of the youngs' begging behavior (in Great Tits) that governs the parental feeding rate is the average intensity of their begging calls" and that this intensity is not affected by "the non-vocal components of the begging response (stretching and gaping)." Bengtsson and Ryden's (1983) study, however, was not designed to test the effect of the non-vocal components of begging since they made no observations of them.

Although size, aggressiveness, activity, hunger, tongue movement, neck extension, distance between parent and nestling, onset of begging, position in the nest, and begging frequency may all affect best beggar status (and do so differently in different species), they individually are only factors contributing to it, not a complete description of it. The holistic approach of Table 3 is a better way to discover what parents respond to in nestling begging behavior than the component approach of other studies because the holistic approach is more complete. The tight correlation of Figure 4 implies that the ethogram in Table 3 is a sufficient explanation of what parents respond to in nestling begging behavior. We recommend that future studies take the holistic approach.

Unlike this study or any cited, Reed (1981) concluded that parents feed nestlings randomly rather than in response to nestling stimulus factors. If this were true, then communication would not exist between parents and offspring, and offspring victory through either truth-telling or deceit would be impossible. Moreover, the very function of nestling begging behavior itself would be obscure. However, we believe that Reed's (1981) conclusion is an artifact of his study design.

Reed (1981) studied a single nest of Song Sparrows (*Melospiza melodia*) during the last three days before fledging. He tested the hypothesis that parents preferentially feed the hungriest nestling. He assumed that this would result in rotational feeding, i.e., that each nestling would be fed in turn so that every n^{th} feeding would go to the same nestling in a brood of $n - 1$ nestlings. When he found no such pattern he accepted the null hypothesis of random feeding.

We do not accept Reed's (1981) assumption that non-random feeding requires a rotational sequence of meals among nestlings. Such a sequence could be expected only if all meals were identical, and the physiological (and perhaps even psychological) needs of all nestlings were equal. If either assumption were violated, the most recently fed nestling would not necessarily be the least hungry, and the most distantly fed nestling would not necessarily be the most hungry. In fact, both assumptions are routinely violated in nature. Meals are various in size and quality (e.g., the difference between a caterpillar and a fly), and nestlings differ in size and thus apparent need.

In rejecting Reed's (1981) assumption, we also reject his conclusion of random feeding. Apparent randomness in his study is an artifact of failing to measure the critical parameter: begging behavior. Common sense says that the appearance of a random pattern can be expected whenever the critical parameter in a given

phenomenon has not been identified or measured, e.g., eclipses would appear to occur randomly to an observer who did not take into account the alignment of the sun, moon and earth, but they would be fully non-random and predictable to one who did.

CHAPTER 4

THE SPECIAL CASE OF RUNTS

We call the last hatched nestlings in starling broods "runts" because they are smaller than their older nestmates throughout most or all of the nestling period. This is because they hatch 1 to 2 days later than their nestmates on account of the fact that starlings initiate incubation midway through laying (Power et al. 1981; Romagnano et al. 1990) resulting in asynchronous hatching (Stouffer and Power 1990). Because they are smaller, runts have difficulty competing with their nestmates and consequently suffer a greater mortality: only 59% of all runts (n = 34) fledged in this study while 90% of all synchronously hatched nestlings (n = 115) fledged (χ^2 = 15.85; d.f. = 1; P < 0.0005). [In a later study (Stouffer and Power 1990) runt survivorship was even less: only 49% of runts (n = 72) fledged whereas 91% of synchronously hatched nestlings (n = 218) fledged (χ^2 = 58.43; d.f. = 1; P < 0.00005).]

The special difficulty of runts should favor them for trying particularly hard to manipulate their parents into giving them better treatment than their rank in the nestling hierarchy warrants, provided that their condition is below the threshold in O'Connor's (1978) model where they would be favored for "suicide" (or at least passive acquiescence to their own death from starvation). [They would be favored for suicide when their death promoted survival of the remaining brood above a threshold probability (O'Connor 1978). This complication will be dealt with in the next chapter.] However, parents may resist the overtures of runts because it may not be in the parents' interests to give any offspring, no matter what its needs, more than its investment potential (as indicated by its place in the brood hierarchy) warrants. Thus parent–runt relations should be the situation where parent–offspring conflict is most intense and most noticeable.

In order to determine the outcome of parent–runt relations, we performed a pair of experiments.

THE EXPERIMENTS

DESIGN

Experiment 5 tested the H_0: runts are not fed preferentially despite their greater need.

This hypothesis was tested by re-analyzing the data from experiment 3 in order to see whether parents used different criteria for feeding runts than other nestlings.

Experiment 6 tested the H_0: runts are unable to extricate themselves from the predicament that their mothers place them in at the time of laying. The predicament is that they start out behind their nestmates in development and survival ability and therefore run the risk of remaining behind.

This hypothesis was tested by comparing the fledging weights and times of runts with their older, synchronously hatched nestmates to determine whether surviving runts fledged in poorer or equivalent condition when compared to their nestmates.

RESULTS

Figure 6 compares the feeding frequencies for runts and their largest nestmates. If runts were fed preferentially, then we would expect them to be fed as often as
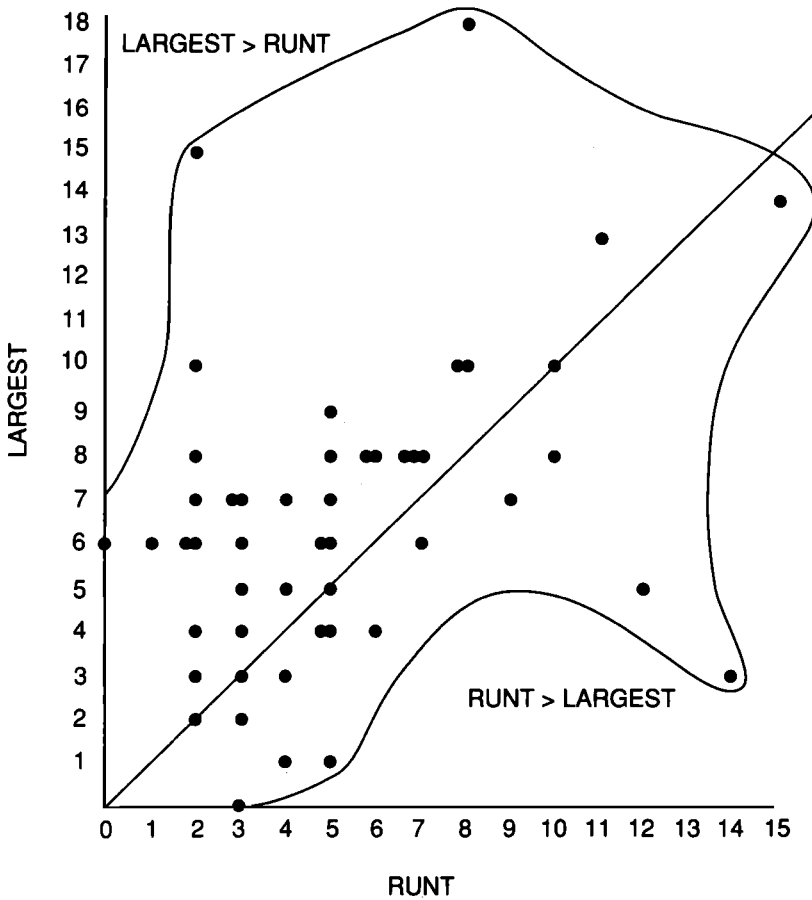
FIG. 6. Feeding of runts vs feeding of their largest nestmate, per observation period.

their largest nestmates on the assumption that those in greatest need should be fed at least as much as those in least need. This would require parents to break the best beggar rule because the smaller size of runts makes it more difficult for them to be the best beggars. This is because smaller nestlings cannot extend their heads as high or their beaks as wide, or stand as tall, or chirp as loudly as their largest nestmates when nestlings beg competitively. However, Figure 6 shows that the largest nestling in each brood was fed significantly more often than the runt (n = 13 broods; Student's t = 2.0; d.f. = 12; P < 0.05).

Figure 7 compares the feeding frequencies of runts when all of their nestmates were sober/hungry vs when one of their nestmates was drunk/sated. If runts were fed preferentially, then we would expect them to be fed no more often when one nestmate was drunk/sated than when all were sober/hungry. This is because preferential treatment for runts should not depend upon the behavior of their nestmates; it should depend upon their needs. But if runts were fed according to the same rules as their nestmates (i.e., the best beggar or hole blocker gets fed), then runts should be fed more often when their competition is reduced by alcohol/food since runts would then get a higher relative begging score. Figure 7 shows that runts were fed significantly more often when one of their nestmates was
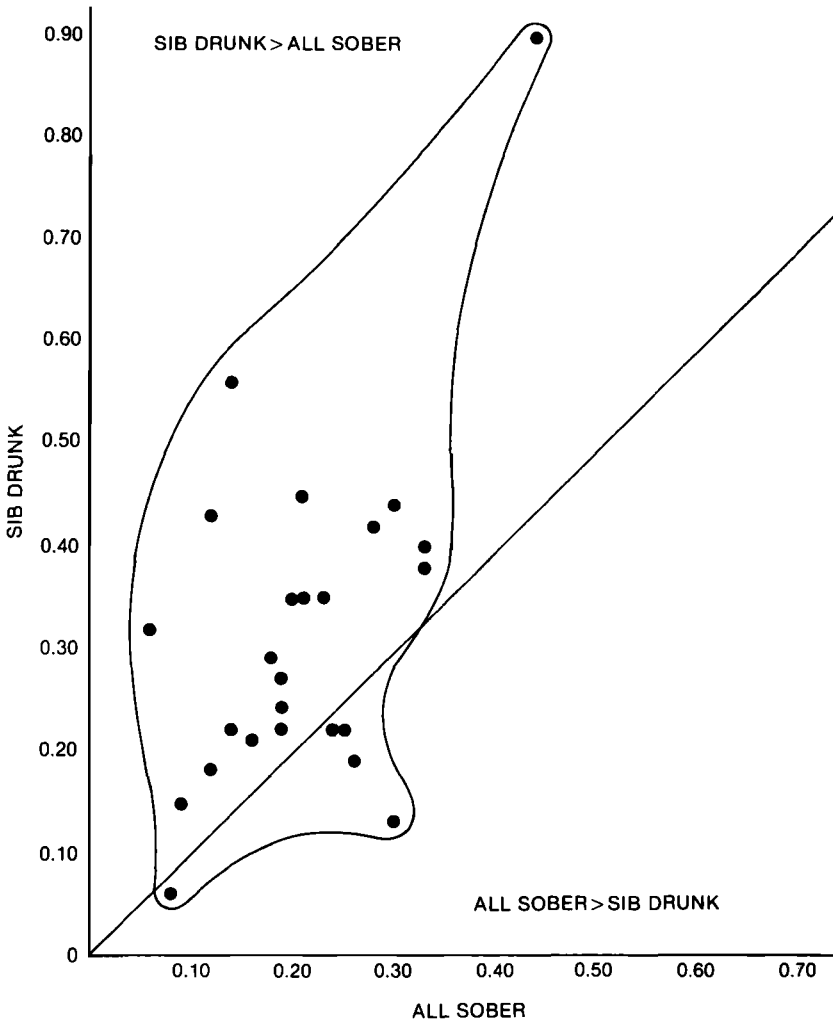
FIG. 7.   Feeding of runts when their nestmates were sober or drunk. The proportion of feedings to the entire brood obtained by the runt when all of its nestmates were sober/hungry (x-axis) vs when one of its nestmates was treated with alcohol-soaked raisins or sated (y-axis).

drunk/sated than when all were sober/hungry (n = 15 broods; Wilcoxon Signed Rank Test, T^+ = 271.5; P < 0.0002). ["Sibs" is used as short hand in Figs. 7 and 8 for "nestmates." The latter is a better term because the high frequency of conspecific brood parasitism in our population frequently results in nestmates that are not siblings (Power et al. 1989; Romagnano et al. 1990). This fact does not affect our results because parasitism increases rather than eliminates the genetic basis for parent–offspring and nestmate–nestmate conflict.]

That Figures 6 and 7 show, respectively, that the largest nestling was fed significantly more often than the runt, and that runts were fed significantly more often when one of their nestmates suffered from diminished begging capacity leads us to accept the H_0 for *Experiment 5*, i.e., runts are *not* fed preferentially despite their greater relative need (shown by their higher mortality). Thus parents use the same criteria for feeding all young irrespective of their relative needs.
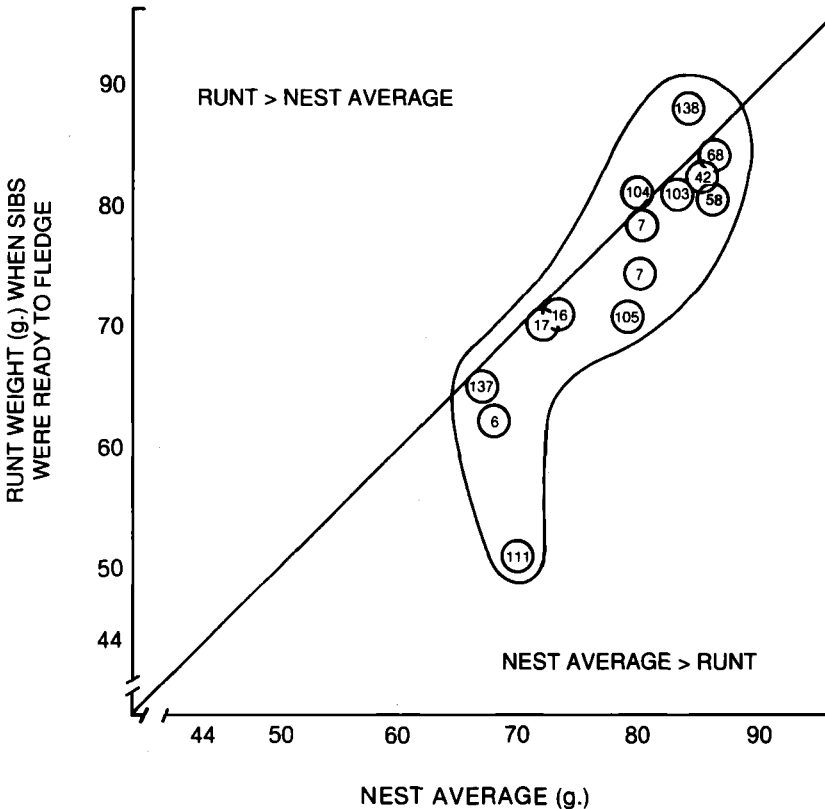
FIG. 8. Weights of runts compared to their larger nestmates. A comparison between the average nestling weight and the runt's weight when its older nestmates were ready to fledge. Circled numbers refer to individual nests.

Figure 8 compares the weights of runts with the average weights of their nestmates at the time that the nestmates were ready to fledge. It shows that runts were significantly lighter than their nestmates (Wilcoxon Signed Rank Test, $T^+ = 14$, $P < 0.01$).

Figure 9 compares the weights of runts with the weights of the lightest of their older, synchronously hatched nestmates at the time that their nestmates were ready to fledge. It shows that runts were on average as heavy as these older nestmates (Wilcoxon Signed Rank Test, $T^+ = 24$, $P > 0.05$).

Figures 8 and 9 jointly imply that by the time their nestmates were ready to fledge, runts had made up much but not all of the difference that existed between themselves and their nestmates at the time of their own hatching. [At the time of hatching, runts weighed only ⅔ as much as their older nestmates (Stouffer and Power 1991).] One way that runts could make up even more of the difference would be to delay their own fledging until they were as developed as their nestmates at the time that their nestmates were ready to fledge.

Table 4 is a comparison between the temporal spread in hatching and the temporal spread in fledging, separating older nestlings from runts. It shows that the spread in fledging was as great as that in hatching (Student's t-test, $t = 1.35$,
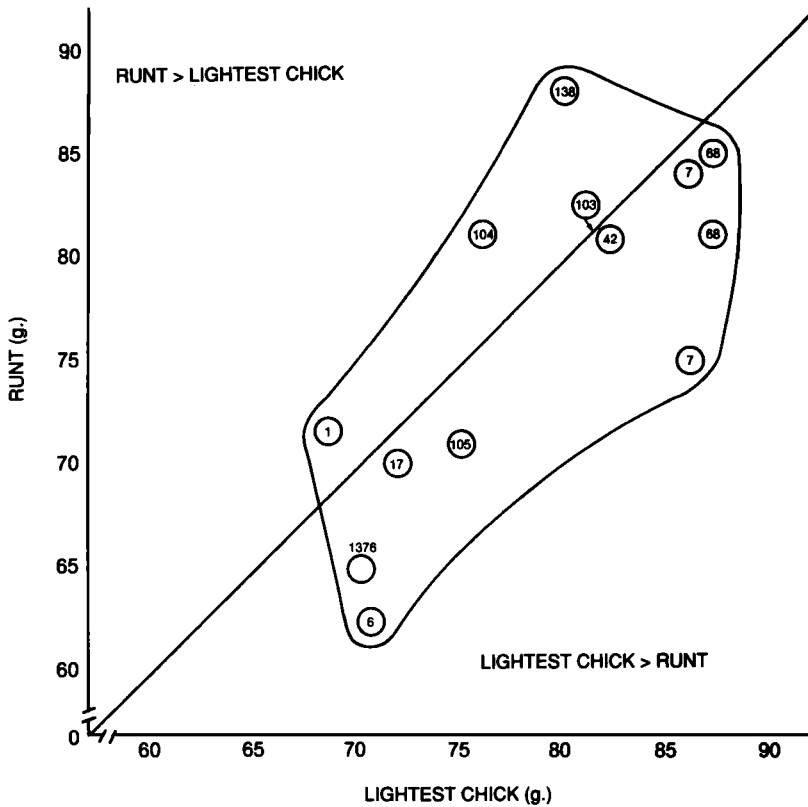
FIG. 9. Weights of runts compared to the lightest of their older nestmates. A comparison of the runt's weight to the weight of the lightest of its synchronously hatched nestmates at the time the oldest nestmate was ready to fledge. Circled numbers refer to individual nests.

$P > 0.2$), e.g., at nest 79-VB4, 3 older nestlings hatched and fledged 1 day before the runt, creating a temporal spread of 1 day in each case (1 older nestling died). This implies that runts were able to delay fledging after their nestmates were gone by enough to give themselves the same total duration in the nest as their nestmates had enjoyed.

Although parents were observed feeding runts after the older nestlings had fledged, it is not known whether runts actually reached the fledging weights of their older nestmates. This was because runts were not weighed on their expected day of fledging (anytime from 20 days after hatching) in order to prevent premature fledging. Premature fledging would have precluded harvesting the data needed to build Table 4. Instead of weighing runts on or after day 20, they were weighed on day 19 and their fledging weights were projected to day 20.

Projected fledging weights were based on the assumption that runt growth rate was constant from days 14–15 to 20. This was a conservative assumption because nestlings had already reached $95 \pm 5\%$ of their fledging weight by days 14–15 (Table 5). Consequently, nestlings were well past their period of rapid growth by fledging age (Crossner 1977). While the assumption of constant rate of growth does not take into account the weight recession sometimes seen in nestlings (Cross-

TABLE 4
HATCHING VS FLEDGING PATTERN

Nest	Hatching temporal pattern	Spread (days)	Fledging temporal pattern	Spread (days)
79-VB4	3 + 1	1	2 + 1	1
80-VB1	3 + 1	1	1 + 3	1
80-VB3	1 + 4	1	3 + 1	1
80-VB5	2 + 2 + 1	2	2	0
80-VB11	3 + 1	1	2	0
80-VB15	2 + 1	1	1 + 1	1
80-VB17	4 + 1	1	4 + 1	1
80-111	3 + 2	1	3 + 1	1
81-VB1	3 + 1	1	3 + 1	1
81-VB55	1 + 2 + 1	2	1 + 2 + 1	2
81-VB77	3 + 3	1	2 + 4	1
		$\bar{x} = 1.18 \pm 0.40$		$\bar{y} = 0.91 \pm 0.54$

ner 1977), weight recession does not seem to be very important in starlings. Ricklefs and Peters' (1979) data do not show it, and Kessel's (1957) are equivocal. More importantly, projected fledging weights for runts were calculated from actual weights taken before any of their nestmates had fledged and thus at a time when their potential for weight gain was lower than it became after competition for food within the nest had ended or been reduced by the fledging of all or some of their nestmates (Table 4). Thus projected fledging weights for runts should be conservative.

Runt fledging weights were projected by calculating their average daily weight gain from days 14–15 to 19 using actual measurements, then adding that gain to their day 19 weights.

Figure 10 compares the projected day 20 weights of runts with the average day 20 weights of their older nestmates. It shows that there was no significant difference between the two groups of fledging weights (Wilcoxon Signed Rank Test, $T^+ =$ 13, $P > 0.1$). Thus runts were able to make up the difference in fledging weight between themselves and their older nestmates by remaining in the nest after some or all of their nestmates had fledged, assuming that the projected weights are approximately correct, which seems conservative.

Because some runts were able to make up the difference in weight between themselves and their older nestmates by remaining in the nest past the fledging time of some or all of their nestmates, we reject the H_0 of *Experiment 6* and accept its alternative, i.e., that runts are at least sometimes able to extricate themselves from the predicament of poor competitive ability created by asynchronous hatching due to asynchronous onset of incubation.

DISCUSSION

Runts pay a dreadful price for their parents' refusal to give them special treatment. Between 41% (this study) and 51% (Stouffer and Power 1990) of the runts in our population died before fledging, most of them in the first 5 days after hatching (Stouffer and Power 1991), many of them probably without having been fed even once (this study) because they were too weak and puny ever to be the

TABLE 5
Nestling Weights (g)[1]

Day 14 or 15	Day 20	D15/D20%
91.0	87.0	105
89.5	89.0	100
85.0	81.0	105
86.5	85.0	102
73.0	80.0	91
76.0	85.0	89
77.0	81.0	95
74.0	81.0	91
76.0	79.0	96
77.5	79.0	98
78.0	83.0	94
74.0	76.0	97
80.0	81.0	99
77.5	82.0	94
70.5	75.0	94
73.0	83.0	88
81.5	87.0	94
70.5	78.0	90
80.0	83.0	96
77.0	82.0	94
77.5	87.0	89
78.5	88.5	89
74.0	80.5	92
74.0	86.0	86
74.0	80.0	92
78.0	83.0	94
79.0	86.0	92
78.0	82.0	95
80.0	88.0	91

[1] $n = 29$, $\bar{X}\% = 95 \pm 0.05$.

best beggar. The runts that did fledge, did so by conforming to their parents' rigid rule of food dispensation: be either the best beggar or the hole-blocker at the time of a feeding visit. Even the ability of runts to extend their stay in the nest beyond the fledging time of some or all of their nestmates did not represent special treatment by their parents because that extended time only gave them the same length of nestling period as that of the first-fledging of their nestmates.

These results are inconsistent with an hypothesis of offspring victory by runts. Runts that fledged did so (in essence) by proving that they were as worthy of parental investment as their nestmates, not by coercing or deceiving their parents into giving them more resources than indicated by their place in the nestling begging hierarchy. Runts did not even succeed in getting their parents to provide them with enough extra food to allow them to grow to the size and vigor of their older nestmates without having always to be the best beggar or hole-blocker.

The lack of preferential treatment for runts in our study is not surprising given the fate of runts in most other species. Parents typically provide them with no extra food and sometimes allow their older nestmates to kill them. We will not discuss the literature of sibling competition in broods of asynchronously hatched young here because the causes and consequences of asynchronous hatching in our
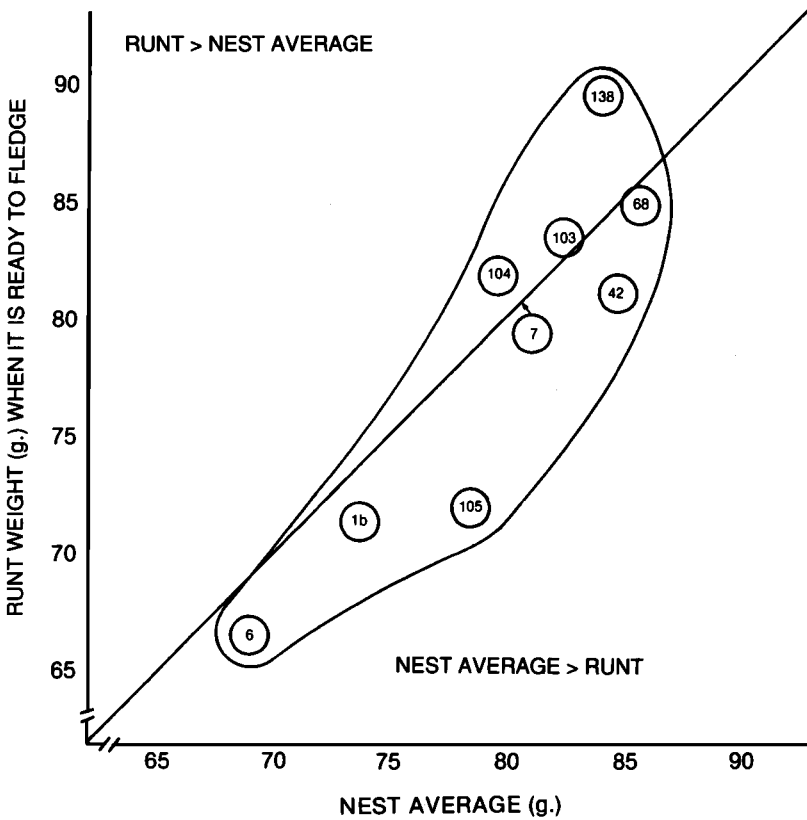
FIG. 10.   Projected fledging weights of runts compared to the nest average fledging weight. Circled numbers refer to individual nests.

population of starlings are the subject of other papers (Stouffer and Power 1990, 1991). We will discuss siblicide in relation to the best beggar rule in Chapter 6.

The great exception to the apparently indifferent treatment of runts by their parents is found in Budgerigars (Stamps et al. 1985). As noted in the previous chapter, female Budgerigars preferentially feed smaller young, often without prior begging vocalizations from them. The maternal tenderness described by Stamps et al. (1985) is more reminiscent of mammalian nursing behavior than the often rough feeding behavior of most described birds. Perhaps the fact that Budgerigars feed by regurgitation rather than by distribution of fresh food is involved. Whatever the cause, Budgerigar runts thrive and fledge at the same ages and at significantly heavier weights than their older siblings. It is almost as if life were more precious in Budgerigars than in starlings and other described species. Yet the success of Budgerigar runts is clearly not due to their having won in parent–offspring conflict. They succeed not by deceiving or otherwise manipulating their parents but by accepting their parents' largesse.

CHAPTER 5

An Experimental Simulation of Offspring Manipulation

The demonstration that runts can delay their fledging by 1–2 days after the departure of the first fledging of their nestmates (Table 4) suggests the possibility that nestlings—as individuals or as broods—may be able to manipulate their parents into providing them with extended care. If this care were extended long enough, it is conceivable that parents might provide more care than the nestlings were worth as investment recipients, e.g., extended care might come at the expense of the parent not having a second brood in the same breeding season. In such an outcome, nestlings could be thought of as winning in parent–offspring conflict, assuming that the nestlings increased their fitness more through extended care than they lost through not having second brood siblings. That is not a difficult outcome to imagine because extended care could conceivably produce more robust fledglings better able to survive and ultimately reproduce, while second brood siblings are of dubious value anyway since second broods in our population fledge very few young (Stouffer 1989) and those that do fledge are significantly lighter than first brood fledglings (Litovich 1982). Moreover, runts are most valuable to their parents as they approach fledging age because they have made up most of the difference between themselves and their older siblings in size and thus approach them in reproductive value. It is for this reason that the O'Connor (1978) model suggests that the prospects for runt victory should be highest at the close of the nestling period, making that the best time to manipulate the circumstances that might produce offspring victory. Thus we thought it would be interesting to simulate experimentally the appearance of offspring refusal to fledge on schedule in order to see how long parental care at the nest could be extended beyond its usual termination. Although we performed this experiment years before his recommendation was published (Litovich 1982), our attempt to protract artificially the period of parental feeding is one of the experiments called for by Drummond (1987) in order to determine who wins in parent–offspring conflict.

The Experiments

Design

Experiment 7 tested the H_0: the number of days that parents tend young in the nest is not increased by simulated delayed fledging.

This hypothesis was tested by dividing subject nests into two experimental groups and one control group, and comparing the results.

1) In the first experimental group (restrictor nests), fledging was prevented by placement of a restrictor over the nest entrance. The restrictor was a square of wood 10 cm on a side and 1.9 cm thick with a 2.5 cm circular hole in the center and a short dowel (0.63 cm × 5 cm) upon which birds could perch. The covered nest entrance was 5 cm in diameter. Thus the restrictor reduced the diameter of the opening to the nest box by 50 percent. It allowed young to poke their heads through the hole and beg for food, and adults to perch on the dowel and feed them.

Restrictors were installed when the oldest nestling in a nest was 20–21 days old. Day 23 was the modal fledging day for unrestricted nestlings, so day 23 was used as the origin day for measuring the length of extended parental care, e.g., if

parents at a restrictor nest fed for 2 days after day 23, then their nest received a score of 2.

The purpose of restrictor nests was to determine the length of the period of extended parental care, if any.

2) In the second experimental group (isolated nests), both fledging and feeding were prevented by covering the nest entrance with wire mesh on day 20–21. Moreover, broods were moved from their nest boxes of origin to empty nest boxes in order to allow their parents to prepare replacement clutches. Isolated broods were allowed to die.

The purpose of isolated nests was to provide a base line of daily weight loss and death weight with which to compare the events in restrictor nests. This information was essential in deciding whether *apparent* extended parental care in restrictor nests was genuine, or only an attempt by parents to induce fledging by teasing young with food as happens in many birds. *A priori,* we decided that extended parental care in restrictor nests would be considered genuine only if restrictor nestlings lost weight at a significantly lower rate than isolated nestlings. The death weights of isolated nestlings were used to indicate when restrictor nestlings were approaching critical starvation weights and thus when to remove restrictors. This allowed us to save lives in the restrictor group.

We regret the necessity of having isolated any nestlings but the restrictor experiment would have been uninterpretable without the isolation group. Fortunately, it was necessary to use only 5 broods. (This experiment was done in 1980 and 1981. There was no federal or Rutgers University requirement to file a research protocol for field work on wild birds until 1985.)

3) In control nests, nestlings were neither restricted nor isolated, but allowed to fledge normally. The purpose of control nests was to establish a base line for normal fledging times, parental feeding frequencies, and nestling weights.

Young in all groups were weighed on days 14–15 and 20. Restrictor nestlings were also weighed 1–3 times each during the restrictor period, depending upon its length, usually on days 24 and 27. Isolated nestlings were weighed every 24 hours from the day of isolation until death.

Behavioral observations were made on either days 15, 16 or 17, and again on day 20 for all groups, and on days 22 or 23 and every other day thereafter at restrictor nests until the experiment was terminated. The experiment was terminated when parents had not been seen feeding for more than 24 hours or nestlings had reached a critical minimum weight (as determined by death weights of isolated nestlings) even when fed by parents.

Only trail boxes were used in Experiment 7 because viewing boxes were needed to perform experiments on communication (Chapters 2 and 3).

RESULTS

Table 6 compares the fledging times of control young with the length of extended care given restricted young. It shows that restricted nestlings were fed at the nest an average of 3.52 ± 4.58 days after day 23 whereas control nestlings fledged 0.03 ± 1.17 days after day 23. This difference in the number of days that parents fed young at the nest is significant (Wilcoxon Rank Sum Test, $W^* = 4.87$, $P < 0.0002$). Data were pooled between years for this test because there was no dif-

TABLE 6
Fledging Time vs Length of Extended Care

	Control		Restricted	
Year	Box	Days after day 23[1]	Box	Days after day 23[2]
1980	104a	1	42a	2
	105	1	7	2
	97	0	6	2
	111	1	138	3
	118	1	1	2
	209	1	103	3
	256	−1	31	3
	113	1	50	11
	102	0	64	2
	253	0	42b	4
	273	−1	32	2
	277	0		
	70	0		
	44	0		
	93a	0		
	104b	−1		
	VB1	1		
	18	−4		
	93b	0		
	113b	0		
	VB4	0		
	105	−2		
1981	29a	0	7a	1
	5	0	7b	10+
	111	2	29b	1
	260	0	42a	1
	138	2	68	3
	VB1	1	701a	3
	137b	0	101b	6
	104b	−1	103	20+
	42b	−1	104a	0
			105	1
			124	0
			137a	−1
		$\bar{x} = 0.03$		$\bar{y} = 3.52$
		s.d. = ±1.17		s.d. = ±4.58

[1] Fledging time relative to day 23.
[2] Number of days on which young were fed relative to day 23.

ference in the results between years, i.e., $P > 0.5$ for control and restrictor nests, respectively, using Wilcoxon Rank Sum Tests.

That the observed feedings given to restricted young were more than just efforts by parents to tease young into fledging is shown by two lines of evidence:

1) Table 7 shows that restricted nestlings lost significantly less weight per day than isolated nestlings (Wilcoxon Rank Sum Test, $W^* = 5.6$, $P < 0.0002$). This was true not only for restricted nestlings as a group, but for each of them as individuals, i.e., the restricted nestling with the greatest rate of weight loss (#40) had a lower rate of loss than the isolated nestling with the lowest rate of weight loss (#2). This shows that parents did not simply starve nestlings.

TABLE 7

WEIGHT CHANGES OF ISOLATED VS RESTRICTED NESTLINGS

	Restricted				Isolated	
Nestling	Slope of weight loss line (g/dy)	Nestling	Slope of weight loss line (g/dy)		Nestling	Slope of weight loss line (g/dy)
1	−4.1	23	−0.5		1	−10.0
2	−3.5	24	+2.0		2	−8.3
3	−3.2	25	−1.1		3	−9.7
4	−2.2	26	−7.0		4	−9.4
5	−2.6	27	−5.8		5	−13.5
6	−0.8	28	−7.3		6	−13.8
7	−6.1	29	−5.9		7	−14.0
8	−2.3	30	−3.5		8	−13.0
9	−2.6	31	−5.0		9	−11.0
10	−3.4	32	−4.3		10	−9.6
11	−5.3	33	−3.3		11	−11.0
12	−2.8	34	−0.8		12	−13.5
13	−7.0	35	−6.0		13	−14.0
14	−7.3	36	−3.0		14	−12.9
15	−6.0	37	−3.3			
16	−6.7	38	−4.0			
17	−3.3	39	−8.0			
18	−4.6	40	−8.1			
19	−2.8	41	−6.9			
20	−3.8	42	−7.5			
21	−2.6	43	−7.8			
22	−2.8					

2) Table 8 shows that while restricted nestlings were fed significantly less often after the restrictor was installed (Wilcoxon Signed Rank Test, $T^+ = 0$, $P < 0.0001$), the actual number of visits per hour was considerable, i.e., the number of visits per hour was greater than the number of nestlings per brood in all but the last two cases. Such a high rate of feeding would not be expected if parents were only using food to inveigle young at the nest entrance since a single food item could serve that purpose. (The significance of the lower rate of feeding after installation of the restrictor will be considered in the Discussion.)

Because restricted young were fed at the nest for significantly more days than control young (Table 6), and they were fed above terminal starvation level (Table 7) at a meaningful rate (Table 8), the H_0 for *Experiment 7* is rejected and its alternative accepted, i.e., the number of days that parents tend young in the nest is increased by simulated delayed fledging. Thus there is no reason to suppose that it would not also be increased by delayed fledging initiated by nestlings themselves.

DISCUSSION

DELAYED FLEDGING AND OFFSPRING VICTORY

The fact that parents responded to simulated delayed fledging by prolonging the period of feeding at the nest suggests that offspring *might* be able to use delayed fledging as a means to extract more investment from their parents than they were worth as vehicles of their parents' fitness. But before it can be concluded that offspring would be favored for delaying fledging in order to win in parent–offspring

TABLE 8
FEEDING FREQUENCIES

		X̄ Feeding Freq. (visits/hr.)		
Box	n[1]	Before restrictor[2]	n	After restrictor
7a	2	31	1	11
7b	1	30	10	18
29b	1	48	3.5	16
42a	2	26	2	15.5
68	2	12	2	11.5
101a	2	14.5	2	14.5
101b	1	28	5.45	20
103	2	13.5	11	9.5
104a	2	33	1	6
105	2	21	1	8
124	2	11	2	3
137a	2	31.5	1	3

[1] n = hours of observation.
[2] During last week before restrictor.

conflict, it must be shown that (1) the offspring would be better off than if they had fledged on schedule, and (2) the parents would be worse off than if they had terminated feeding at the nest at the usual time. Neither requirement is met:

1) Young whose fledging was delayed by a restrictor lost weight (Table 7) and were fed less often than during the normal nestling period (Table 8). Thus, delayed fledging was not advantageous to them. There is no reason to believe that normally fledging young would have fared so badly; if they had, they would normally be in a greatly weakened condition, perhaps close to death, at the end of the fledgling period. Such a pattern of injurious parental care could not evolve because of its destructive consequences for parents as well as young.

2) Although parents continued to feed young whose fledging was delayed (Table 6), they clearly spent less effort doing so than they had prior to the normal time of fledging (Table 8). Moreover, the average duration of extended care (3.52 days) was very close to the fledgling period reported for starlings in our own and other populations.

Litovich and Donald Caccamise were able to radio track one nestling for 4 weeks after it fledged prematurely (Litovich 1982). As near as they could determine, it was not fed by its parents during that time, suggesting that it was able to feed itself from the time of fledging. In 1981, 5 boxes were monitored to determine the interval between fledging of the last nestling of the first brood, and laying of the first egg of the second brood. This interval was 5.0 ± 0.71 days. Unless parents continued to feed first brood fledglings while they prepared their second broods, it is unlikely that first brood young were fed much more than 5 days after fledging. Continuing to care for first brood young into the second brood would have been costly to females because they were busy forming and laying eggs, and would have been costly to males because they guard their mates closely during laying in order to prevent their own cuckoldry (Power et al. 1981). Therefore it is probable that feeding of first brood fledglings did not extend into the second brood.

Kessel (1957) reported that starlings in her Ithaca, New York population had a very short fledgling period, probably not longer than 4 days in most cases. She

found that fledglings were able to do some foraging for themselves as soon as they left the nest, implying that the fledgling period became progressively less expensive for parents with every post-fledging day.

Feare (1984) reported that fledglings wait in trees for their parents to feed them for the first few days after fledging in England, then spend more and more time following their parents around the feeding grounds, begging for food and making exploratory pecks at the ground until they can feed entirely by themselves. He believes this process does not require more than 10–12 days.

van Elsacker et al. (1988) found that the fledgling period varied from 3–12 days in Belgium with variation in duration within as well as between broods. She did not report whether prolonged period of post-fledging care within broods correlated with runt status.

These reports of the length of the fledgling period jointly imply that the 3.52 days average duration of extended care in our experiment was not greater than the normal period of post-fledging care in starlings. Thus there is no reason to believe that delayed fledging initiated by nestlings would cause parents to be worse off than if young fledged at the normal time.

Since neither the requirement of improved offspring welfare nor the requirement of diminished parental welfare were met by the results of our delayed fledging experiment, we conclude that no grounds exist for evolving offspring victory through delayed fledging.

THE VARIABILITY OF EXTENDED CARE

The most striking result in Table 6 is the variability in the length of extended care that occurred among restrictor nests. Extended care ranged from 0 days (nestboxes 1981 #104a and #124) to more than 20 days (nestbox 1981 #103), and the standard deviation exceeded the mean. Why was there such great variability?

One possibility is that the novelty of restriction confused parents and they individually chose different responses because there was no pattern of response in their evolutionary past that consistently produced a greater fitness than its alternatives. For this possibility to be correct, the analogue of restriction, genuine delayed fledging, must be virtually unknown in the evolutionary history of starlings. Given the poor reward of simulated delayed fledging (Tables 7–8), an absence of genuine delayed fledging as anything but a rare event is most conceivable.

Another possibility is that different parents responded differently based on their individually different costs and benefits of providing extended care. While this possibility is almost inevitably correct as a truism, it can only be tested by learning the details of the cost-benefit schedules of each parent. We were unable to do this despite closed-circuit television, banding and many hours in the field. Few songbirds provide the opportunity to gather such detailed and intimate information.

While we do not know the cause of variability in extended care, extended care itself has been reported in other species, suggesting that it may be a common response when parents "judge" that specific offspring or broods are worth extra care. Lack (1956) found that the second nestling in the Swift (*Apus apus*) usually fledges 1–2 days later than the first (like runts in starlings), but that when weather is unusually wet and thus food difficult to find, the second nestling may delay its fledging by 5–8 days after that of the first nestling. Norton-Griffiths (1969) found

that parent Oystercatchers (*Haematopus ostralegus*) feed their broods for different lengths of time depending upon the habitat in which they nest: feeding is prolonged in rocky shore habitat where young are fed on metabolically expensive bivalves and crabs relative to dune, meadow and mudflat habitats where young are fed on easier to digest annelids. Harris (1969) used chick replacement in the Audubon's Shearwater (*Puffinus lherminieri*) to extend parental feeding of young from its normal 75 days to up to 120 days. Harris (1983) also used chick replacement in Atlantic Puffins and found that adults in the experimental group (older chicks replaced by younger chicks) fed for an average of 51.6 days while adults in the control group (chicks of approximately the same age exchanged between nests) fed for an average of only 39.1 days. Perhaps the most striking case of extended care was found in the House Sparrow (*Passer domesticus*). Summers-Smith (1963) observed a pair feed a nestling caught in a tangle of thread in the nest throughout an entire fall and winter.

Extended care is not the only way that dependent young can garner extra parental resources in birds. Its contrary—early fledging—sometimes works. Graves et al. (1991) found that runt chicks in Herring Gulls (*Larus argentatus*) leave the nest before their larger sibs. Similarly, Lemel (1989) found that the first nestling to fledge in Great Tits was the one in poorest physical condition. Since parent tits prefer to feed fledglings over nestlings, early fledging gives young in poor condition a temporary advantage over their healthier nestmates. That advantage is lost as soon as the nestmates fledge, reconstituting the brood hierarchy.

How effective the tactic of early fledging works depends on how well it provides individual attention to young in need. Although it appears to work in some species, the facts that runt starlings do not fledge before their larger nestmates and gain weight by delaying their fledging suggest that early fledging would not be as adaptive as delayed fledging in starlings.

CHAPTER 6

THE RESOLUTION OF PARENT–OFFSPRING CONFLICT

In this chapter we review those results that are directly relevant to the parent–offspring conflict debate, compare them with the theoretical literature of that debate, provide a simple empirical method to determine who wins in parent–offspring conflict, apply that method to starlings, and close with thoughts on the nature of the debate and where we think behavioral ecology ought to go in the future on this topic.

SUMMARY OF RELEVANT RESULTS

1) *The brood as a whole can communicate with its parents.* In principle this could allow a form of group deception to occur that could cause a brood to obtain more parental investment (PI) (*sensu* Trivers 1972, 1974) than it is worth at the expense of later broods. However, Power et al.'s (1989) and Stouffer's (1989) results show that later broods are unaffected by PI in current broods, i.e., neither clutch size nor brood size nor degree of hatching synchrony affect the probability of return of parents to have future clutches within the same year or in future years, or the interval between clutches, or the size or success of future clutches. Therefore there is no evidence of damage to later broods by the begging activities of earlier broods, and thus no evidence of successful deceit by the brood as a whole.

2) *Parents feed the best beggar or hole-blocker.* This precludes successful offspring deceit over the nestling period as a whole because a liar will collapse from exhaustion over the course of the nestling period. Exaggeration in the effort to be perceived as the best beggar is not lying because it requires working harder to get a higher score and that inevitably reveals the true condition of the beggar since the harder it works the shorter it will be able to sustain a lie.

3) *Feeding the hole-blocker does not hurt the parent's interests even though it moves the operational decision of whom gets fed from the parent to the offspring.* This is because the effect of feeding the hole-blocker is the same as that of feeding the best beggar: only the most vigorous offspring gets fed in either case.

4) *Lack of sexual dimorphism in parental feeding criteria precludes offspring victory through either (a) offspring playing parents against each other, or (b) offspring successfully meeting the potentially different and specialized feeding criteria of male and female parents when they were not the best beggars or hole-blockers.* Possibility (a) could occur with different parental criteria because different criteria for each of two parents automatically means more criteria for a family as a whole, and more criteria create the opportunity for more confusion and thus successful deception. Possibility (b) would probably frequently occur if parents used different feeding criteria in order to specialize on different parts of the brood. Thus lack of sexual dimorphism in feeding criteria keeps feeding decisions simple and thus little subject to successful offspring manipulation.

5) *Runts are not fed preferentially despite their greater need.* In order to be fed, they have to be the best beggar or hole-blocker. Thus they have to conform to the same rules as their older and larger nestmates. They cannot win in parent–offspring conflict either by (a) deceiving their parents into giving them more than they are worth as investment recipients, or (b) persuading their parents into giving them enough extra food to make up the difference between themselves and their

larger nestmates, i.e., into feeding them when they are not the best beggars (or hole-blockers) until they can be the best beggars (or hole-blockers) as often as their larger nestmates. This is a particularly significant result because it means that even the category of offspring under the greatest selective pressure to win in parent–offspring conflict cannot win.

6) *The ability of runts to delay fledging does not imply offspring victory because runts spend no more time in the nest than their older nestmates do without delayed fledging.* Yet again there is no evidence of successful runt deception leading parents into giving them more than they are worth to the parents.

7) *Experimentally simulated delayed fledging gives no reason for believing that offspring under natural conditions could use delayed fledging to get more PI than they would normally get if they fledged on schedule.* Parents seemed to be in control of their PI schedule because (a) they provided food during the period of delayed fledging for no more days than they would have if their young had fledged on schedule, and (b) they provided significantly less food during the period of delayed fledging than they had previously provided during the normal nestling period. Moreover, offspring lost weight during the period of experimentally delayed fledging.

THE PARENT–OFFSPRING CONFLICT DEBATE: AN OVERVIEW

The parent–offspring conflict debate has been argued in the context of many genetic systems, including asexual reproduction, sexually reproducing diploid organisms, and haplodiploid eusocial insects. We shall concentrate on sexually reproducing diploid organisms simply because that is what birds are, and the genesis of the debate lay in such species. We shall focus on the question of who wins in parent–offspring conflict because that question stimulated our study. We shall begin with a chronological overview of the debate to show its direction, then briefly consider two issues of special significance to our study: the honesty of begging as a signal and avian siblicide.

As noted in Chapter 1, Trivers (1974) began the debate. He presented intuitively compelling graphical models that show differences between parent and offspring over the duration and amount of PI that parents should give. The basis for this difference is the non-identity of genetic interests between parent and offspring generated by sexual reproduction. This non-identity of interests results in full sibs being related on average by a coefficient of relatedness of $\bar{r} = \frac{1}{2}$, and in half sibs being related on average by only $\bar{r} = \frac{1}{4}$ (Hamilton 1964). Since a selfish offspring is fully related to itself but only partly related to its sibs, it values itself 2–$4\times$ more highly than it does its sibs. But a parent will value all of its offspring equally in terms of r. Thus a parent would like all of its offspring to cooperate with each other whereas each of its selfish offspring would like to gain more than $1/n$ of the PI offered the brood (where n = brood size).

In Trivers' (1974) models, benefit (B) is measured for both parents and offspring by the probability of offspring becoming adults, and cost (C) is measured in lost offspring for the parent and lost sibs for the offspring. Lost offspring (and sibs) can occur in the same brood as does an offspring in conflict with its parent, or in a future brood.

In terms of duration of PI, Trivers' argument (1974) holds that a parent is favored for continuing PI only as long as $B/C > 1$, but an offspring is favored for

taking PI as long as B/C > ½ (for full sibs) or B/C > ¼ (for half sibs). B/C > ½ (or ¼) always occurs later in the period of PI than does B/C > 1 because B reaches a maximum while C continues to climb as long as PI is given, i.e., when B reaches its maximum but C continues to climb, B/C drops. Thus offspring are always favored for demanding PI after the time when parents are favored for discontinuing it.

In terms of amount of PI at any given moment, Trivers' (1974) argument holds that a parent is favored for providing that amount of PI that maximizes B − C (i.e., net B for the parent), but a selfish offspring is favored for taking that amount of PI that maximizes B − ½C (for full sibs) or B − ¼C (for half sibs), i.e., net B for the offspring. Because of the shape of Trivers' (1974) B curve (an asymptotic approach from minimum to maximum value), maximum B − ½C (or maximum B − ¼C) always occurs at a higher amount of PI than does maximum B − C. Thus the offspring always demands more PI than the parent is favored for giving.

Obviously parent–offspring conflict over PI would not be very interesting to the behavioral ecologist if the parent always won. Therefore Trivers (1974) sought ways that offspring might win. He decided that offspring victory through deceit was possible and suggested weaning conflicts in mammals and their analogues in birds as examples of intense parent–offspring conflict where offspring sometimes win. Unfortunately he did not specify how we are to know who wins or whether the conflict results in a compromise. As we shall see, this is a failing common to all those who have sided with Trivers in the parent–offspring conflict debate. Remember that in Chapter 1 we showed that the mere existence of weaning conflicts and their analogues is not sufficient evidence to decide any outcome of parent–offspring conflict, or even to know that bonafide genotypic conflict is occurring. Weaning-type conflicts might only mean intense communication between parent and offspring over the offspring's true needs (Zahavi 1977, 1981, 1985; Godfray 1991).

Alexander (1974) considered the subject of parent–offspring conflict in a large paper that also considered the evolution of a panoply of other social behaviors. For obscure reasons, many citations of his paper seem to imply that he was only concerned with parent–offspring conflict and that he made a mistake, the mistake of concluding that offspring can *never* win in conflict with their parents. Strictly speaking this is not true. Alexander (1974) *never actually said* that offspring victory was impossible but his remarks on p. 340 and in Figure 1 of his paper seem to suggest this. These treatments allow offspring victory only in a phenotypic sense, not in a genotypic sense through evolutionary time. They imply that offspring victory is ultimately impossible because the genes enabling offspring victory lead to parental defeat in the same genetic line in subsequent generations. Alexander believed that selection focuses on the parent and therefore that parental defeat is more destructive to the long term survival of a genetic line than offspring defeat.

Later Alexander (1979:39) clarified his stand by stating that the idea that offspring can *never* win is wrong, but reiterated his position that offspring victory is *infrequent*. A major reason for Alexander's (1979) clarification seems to have been Blick's (1977) model showing the possibility of offspring victory in sexually reproducing species. But he clung to the idea that offspring victory is *infrequent*.

Blick (1977) built and published his model with Alexander's encouragement [acknowledged in Blick (1977)]. His 1-locus, 2-allele model shows formal circum-

stances where bona fide offspring victory *could* occur as envisioned by Trivers (1974). This happens through the probability of survival to adulthood being higher in selfish than so-called altruistic offspring. [The use of "altruistic" in this context is unfortunate because it suggests that *normal* offspring are genuinely altruistic. Of course they are not because true altruism is extremely difficult to evolve and almost impossible to maintain (Williams 1966). What authors on the subject of parent–offspring conflict from Trivers (1974) onward have really meant is not "altruism" but "cooperation." So we should really be talking about selfish vs cooperative offspring. Unfortunately the term "altruism" is so deeply embedded in the literature that we feel obligated to continue using it. Now back to Blick's (1977) argument.] The fact that selfish offspring sometimes have fewer surviving offspring of their own than altruistic offspring have is irrelevant because this outcome occurs through the death of the altruistic offspring in the broods of selfish individuals, not of the selfish offspring. More importantly, the higher probability of survival to adulthood of selfish offspring means that they are more likely to have any grand offspring at all. Thus selection *can* result in more carriers for genes for selfishness than for altruism. However, nothing in Blick's (1977) model requires that selfishness always be favored.

Metcalf et al. (1979) also developed a 1-locus, 2-allele model that shows that genes for offspring selfishness can prevail in competition against genes for offspring altruism. Other aspects of this paper will be considered below.

Dawkins (1976) appears to have been the first to have publicly sided with Trivers (1974) and against what *he stated* to be Alexander's (1974) position, i.e., the idea that offspring can *never* win. His argument is particularly relevant here because he presumed that birds always feed what we call the best beggar although he cited no references or evidence for his presumption, nor did he understand the implications for resolution of parent–offspring conflict when parents always feed the best beggar (see Relevant Result #2 above).

Dawkins (1976) criticized Alexander (1974) almost to the point of ridicule for supposing that parents always win. Dawkins (1976) was correct in concluding that the parent doesn't *always* win, but his argument leading to this conclusion is more rhetorical than scientific because it rests upon an erroneous assumption. This assumption is that since there is no *genetic* difference between the same individual when it is a parent and when it is an offspring, there is no *fundamental* asymmetry between parent and offspring leading to parental victory. This assumption is erroneous because the lack of a fundamental asymmetry [as Dawkins (1976:146–147) contextually defines it] is unnecessary to produce parental victory. Dawkins (1976) admits the existence of a *practical* asymmetry between parent and offspring based on the parent's greater size, experience and control of resources. But he does not seem to understand that *this practical asymmetry is all that is necessary for parental victory most of the time.* How else can we interpret his statement (Dawkins 1976:149), "There is, then, no general answer to the question of who is more likely to win the battle of the generations. What will finally emerge is a compromise between the ideal situation desired between the child and that desired by the parent"? [For a purely mathematical deflation of Dawkins' (1976) rhetorical attack upon Alexander (1974), see Harpending (1979:628).]

Dawkins (1989) did not correct his misstatement of Alexander's (1974) position in the second edition of his book. Rather than acknowledging that Alexander

(1974) *never* actually said that offspring victory was impossible—a fact pointed out to him in correspondence from Alexander (R. D. Alexander, personal communication) which he could have confirmed by re-reading Alexander (1974)— Dawkins (1989:298) compounded his original misstatement in an endnote by misstating Alexander's (1979) later position, "Alexander had generously conceded ... that he was wrong to argue that parental victory in parent–offspring conflict follows inevitably from fundamental Darwinian assumption." Alexander (1979) made no such concession because he made no such claim originally. While legitimate debate between scientists promotes the process of discovery, criticizing other scientists for extreme positions that they never took promotes only discord.

Parker and Macnair wrote a series of papers on parent-offspring conflict (Macnair and Parker 1978, 1979; Parker 1985; Parker and Macnair 1978, 1979) that are perhaps the most important since the original Trivers (1974) and Alexander (1974) papers because their models are more mathematically sophisticated than most of their predecessors and, judging from their frequency of citation, they have had a greater impact on the subsequent literature than any other set of papers since Trivers (1974) opened the debate [see the textbook-level reviews in Krebs and Davies (1991), and Clutton-Brock (1991)]. Moreover, they said they were modelling the kind of conflict exemplified by parents feeding in response to offspring squawkings, making their models directly relevant to our study.

Parker and Macnair presented several 2-locus models and evaluated them by means of computer simulations. One locus determined the degree of offspring solicitation while the other determined how parents retaliated against selfish offspring.

The most relevant models are the uniparental intrabrood conflict model (Parker and Macnair 1979), and the biparental intrabrood conflict model (Parker 1985). Only intrabrood conflict models are applicable since we looked at parent–offspring interactions at the intrabrood level, and there are no apparent interbrood effects of nesting in our starling population (Relevant Result #1), as would be required for application of their interbrood models.

The models cannot be applied without modification because at least one of their assumptions is not met in our population. This assumption is that the amount of PI is fixed at the beginning of the period of parental care. When that is true, offspring compete with one another over allocation of the fixed total amount and individuals are paid in direct proportion to their relative solicitation levels.

This assumption is not met in starlings and may not be met in any species of bird with begging young. But modification of this assumption to fit starling natural history may not affect the outcome of the models.

This assumption is not met because *Experiment 1* showed that starlings feed their broods in proportion to *brood* solicitation, i.e., broods that begged more (because they were sober/hungry) were fed more. This implies that PI is not fixed but increases with brood demand.

We believe that Parker and Macnair's (1979; Parker 1985) assumption of "fixed PI" should be modified to "fixed *maximum* PI," i.e., that parents will not invest beyond some maximum level but they will vary their PI below that level. Thus they could be expected to give less to drunk or smaller broods than to sober or larger broods.

Our modification is consistent with Power et al.'s (1989) and Stouffer's (1989)

findings that there are no interbrood costs of variation in clutch and brood size or hatching synchrony (see Relevant Result #1 above). Lack of interbrood costs implies that variation in brood demand does not reduce a parent's future PI ability, and therefore that some threshold of damage to parents (the fixed maximum PI) is not exceeded.

At first it would seem that our modification would enrich the Parker and Macnair (1979; Parker 1985) models by allowing an outcome that they disallowed. That outcome was unambiguous offspring victory. They disallowed it on the ground that fixed PI automatically precludes offspring from extracting more than parents are willing to give.

Our modification would at first seem to allow the possibility of offspring victory by giving offspring more potential PI to inveigle their parents out of, viz. the difference between the amount of PI that parents would normally give and the fixed maximum PI that parents would ever give. But upon closer examination it becomes apparent that whether PI is absolutely fixed or there is a fixed maximum PI with flexible amounts of dispensation below that maximum makes no difference. In both cases, the parent refuses to give beyond some pre-set amount and therefore the offspring cannot win in Trivers' (1974) sense of the parent being coerced or deceived into paying a cost that is ultimately bad for it.

Thus only the 2 outcomes of the intrabrood models that Parker and Macnair (1979; Parker 1985) allowed, remain. These are (a) outright parental victory, and (b) a compromise between the demands of parent and offspring. Parker and Macnair (1979) called this compromise a "pro rata ESS" (evolutionarily stable strategy).

Parker and Macnair (1979; Parker 1985) concluded that whether intrabrood conflict results in parental victory or a pro rata ESS depends on how steeply offspring solicitation costs rise. If they rise steeply (because competitive solicitation is suppressed by parents or attracts predators to the nest), then parental victory occurs. But if they rise more gently, a pro rata ESS results.

While these outcomes are intuitively pleasing, Parker and Macnair (1979; Parker 1985) give us no satisfactory way to recognize them in *nature*. Exactly what signifies parental victory vs a pro rata ESS? The argument (Parker and Macnair 1979:1230; Parker 1985:531) that observation of (a) conflicts between parent and offspring at weaning and over the transfer of food before then, and (b) offspring commonly soliciting without being rewarded, constitute evidence that pro rata ESS's are common in nature, is not convincing. This is because such observations do not show that parents are giving more than their optimal amounts. Strictly speaking, they only show that offspring often get less than they demand.

Because no one from Trivers (1974) onward has specified how to detect either a parent's or an offspring's optimal PI in nature (Clutton-Brock 1991), evidence of conflict and unrewarded solicitation is consistent with both a pro rata ESS and a parental victory ESS. In the former case, the offspring is demanding and getting more than the parent wants to give but less than the offspring wants to have. In the latter case, the offspring is merely complaining that it is not getting all of what it wants. Obviously a clear cut empirical test to detect the optimal PI levels of the two players and their relation to the actual PI dispensed is sorely needed in order to test the various models.

Stamps et al. (1978), Metcalf et al. (1979), and Stamps and Metcalf (1980) are similar to the Parker-Macnair series of papers but appear to have been less influ-

ential. They view parent-offspring conflict as a coevolutionary race between alleles expressed in the contending parties, and struggling to spread at each other's expense. They conclude that while various outcomes can be produced by varying the parameters of the models, there is no general solution as to whom wins. They also believe that such behaviors as weaning conflicts, crying and tantrums do not necessarily indicate who is winning.

To us, the most original and interesting part of the Stamps-Metcalf papers is the suggestion at the end of Metcalf et al. (1979:106) that asynchronous hatching in birds might have evolved as a parental tactic to counter offspring selfishness. Their analysis had shown that offspring raised simultaneously would be favored for greater selfishness than offspring raised sequentially. This is because the cost of the selfishness of older offspring *raised in series* would be inflicted on all younger offspring whether they were altruistic or selfish since the younger would be unable to fight back at the already fledged older offspring, but the cost of the selfishness of older offspring *raised simultaneously* would be inflicted solely on their altruistic nestmates since all selfish offspring would be equally competitive. Thus parents would be favored for sequential production of offspring, but factors such as low adult survival probability and scarce, highly contested nest sites would prevent many parents from raising offspring sequentially. A compromise that would "approximate a sequential system without loss of simultaneity is for the parent to produce offspring of different sizes, where size is . . . determined independently of offspring genotype." This would happen with asynchronous hatching in birds.

Although a very stimulating idea, we must reject the Metcalf et al. (1979) hypothesis because (1) it would not be a parental adaptation, and (2) it is inconsistent with the facts of starling biology in our population.

1) To be an adaptation for parental victory in parent-offspring conflict, asynchronous hatching would have to result in either offspring defeat or at least a compromise between parent and offspring. Asynchronous hatching would do neither. Its initial effect would be to increase the time to offspring victory but not prevent that victory. It would increase the time to offspring victory by allowing some altruistic young to "hide" from their selfish sibs by being the oldest offspring in their broods, and by forcing some selfish young to lose in competition with their older, altruistic sibs by being the runts of their broods. But since selfish young would still win when they were not runts and altruistic young would still lose against same-sized selfish nestmates (which would happen whenever broods contained both genotypes), neither extinction of the allele for offspring selfishness nor equilibrium between the alleles for offspring selfishness and offspring altruism would result. Worse yet, trying to contain offspring selfishness through asynchronous hatching would culminate in uniting inevitable offspring victory with lower fledging success. This last outcome would be produced by runt deaths.

2) Asynchronous hatching is an almost universal feature of starling life history that has been studied both observationally and experimentally in our population (Stouffer and Power 1990, 1991). If it evolved to promote parental victory, it is reasonable to suppose that it would increase parental reproductive success relative to its alternative, synchronous hatching, unless excess mortality from asynchronous hatching (i.e., runt death) was largely focused on selfish offspring. However, experimentally synchronized broods produce significantly more fledglings, and no mechanisms could exist that would force selfish offspring to be the runts that

would not also violate Metcalf et al.'s (1979) assumption that size (i.e., hatching order) was independent of offspring genotype. Moreover, any mechanism that related hatching order to offspring genotype would have to recognize genotype before shell formation. Instead of making selfish offspring hatch last, a more adaptive response would be for the mechanism recognizing selfish offspring to terminate them simply by preventing their endowment with yolk prior to shell formation.

The failure of the Metcalf et al. (1979) hypothesis leads to the question, why does asynchronous hatching exist in starlings? Several alternatives were explored in Stouffer and Power (1990, 1991) but none provided a satisfactory answer. Our interest in the Metcalf et al. (1979) hypothesis was in part derived from the hope that it would help us answer an unresolved question. Unfortunately, it does not.

Charnov (1982) entered the parent–offspring conflict debate by presenting a very idiosyncratic model. Like Trivers' model (1974) it is depicted graphically, but unlike Trivers', its underlying logic is explained only telegraphically. Moreover, it is only relevant to the special case where broods contain only a single young, and the cost of offspring victory is measured solely in reduced maternal survivorship. Other models typically measure that cost in reduced sibs for the winning offspring. Charnov (1982) concludes that parent–offspring conflict results in a compromise value heavily weighted against maternal survivorship (his graph shows a 70 percent reduction in maternal survivorship at the equilibrium value relative to the condition of no maternal effort), but intentionally omits the algebra leading to that conclusion. Since the model is so idiosyncratic in its life history assumptions and the proof is deliberately omitted, we conclude that Charnov's (1982) model is too special to be of general value in the parent–offspring conflict debate.

Feldman and Eshel (1982) also challenged the idea that there is a universal answer to the question of who wins in parent–offspring conflict. Using the mathematics of population genetics they found that different outcomes occurred when different asumptions were used. Moreover, they found that other modelers often make implicit assumptions that they are virtually unaware of but which affect the outcome of their models. In our opinion, these technical difficulties of modeling underscore the need for empirical studies.

Harper (1986) extended the Parker-Macnair models to take account of the effects of brood size, and emphasized that parents should respond to the *relative* differences in begging intensity among their young rather than to their *absolute* begging intensity. He claimed that the Parker-Macnair models ignored relative differences but Parker denied this, insisting that such differences were built into both the intra-brood and inter-brood models (Parker et al. 1989). Harper (1986) attempted to support his models by claiming that their predictions were consistent with bird begging behavior. However, the fit between his models and the behavior that he cited (e.g., that chicks should beg harder when starving) is so general and anecdotal that we do not find his claims compelling, i.e., we do not find his models to make predictions sufficiently precise to be considered advances over common sense and everyday observations. Harper (1986) did not answer the question of who wins in parent–offspring conflict.

Lazarus and Inglis (1986) presented a series of parent–offspring conflict models that are sensitive to brood size and the mode of PI. These models take Trivers' (1974) original model as their starting point rather than the Parker-Macnair mod-

els. Thus their consideration of brood size effects is mathematically different from Harper's (1986). Questions of brood size are of limited relevance to our results because brood size was not an experimental variable in our study. The Lazarus-Inglis models do not specify who wins in parent–offspring conflict as a function of brood size.

Perhaps the greatest contribution of Lazarus and Inglis (1986) was their alteration of Trivers' (1974) original graphical model. That model had shown parent–offspring conflict by drawing a benefit line that was the same for both parties but cost lines that were different for each of them. As noted above, cost is different for parents and offspring in the Trivers' (1974) model because $r = \frac{1}{2}$ between them. However, Lazarus and Inglis (1986) showed that there are cases where the cost is the same for parents and offspring but the benefit is different. For example, when benefit is defined in terms of offspring reproductive success, that benefit would be worth twice as much to the offspring as to the parents because the offspring of offspring would be related to the latter by $r = \frac{1}{2}$ but they would be related to the original parents by only $r = \frac{1}{4}$ since they would be the original parents' grandoffspring. The cost would be the same for both parties when it was borne by the parent's future offspring and they were full sibs of the present offspring because $r = \frac{1}{2}$ between those future offspring and both of the presently contending parties. Of course, the cost would be different for parents and offspring when future offspring were not full sibs of present offspring because in that case $r = \frac{1}{2}$ between parent and *all* offspring, but $r < \frac{1}{2}$ between present and future offspring.

Despite the heuristic value of Lazarus and Inglis' (1986) reversal of which parameter (benefit or cost) is variable, the practical effect of their change of the Trivers (1974) model is nil. This is because the offspring still wants more than the parent is favored to give, and the magnitude of that disagreement remains the same in both models because the disagreement is driven by $r = \frac{1}{2}$ between parent and offspring.

Clark and Ydenberg (1990a, b) applied stochastic dynamic programming to parental defense, and the feeding and fledging of young. Their work is an advance over classical life-history theory in that it permits analysis of facultative parental strategies, those that respond to unpredicted events. Previous theory assumed that responses are inflexible.

Clark and Ydenberg (1990b) derived a dynamic ESS model to describe parent–offspring interactions in the context of feeding young seabirds at the nest. Their model treats parent–offspring interactions as a series of alternating decisions: in each time period the parent decides whether or not to continue provisioning the chick, after which the chick decides whether or not to fledge. They apply their model to the Dovekie (*Alle alle*). The result is an ESS diagram, detailing whether the parent should abandon the nest or feed the chick, and whether the chick should remain in the nest or fledge. These decisions are a function of numerous variables, but in the diagram reduce to the relationship between the chick's mass at a given age and its optimal fledging mass.

We find the model a significant improvement over earlier "static" ESS approaches because it uses real values to describe accurately the feeding and fledging behavior of real creatures. Although the model does not directly address the question of who wins in parent–offspring conflict, Ydenberg (personal communication) told us how to read it to answer that question.

In the Clark and Ydenberg (1990b) model, Dovekie chicks are grown enough

to fledge from about 18 days after hatching. It is in the parents' interest for them to fledge at that time because visits to the nest are costly to parents, especially in predation risk. But it is in the chick's interest to remain in the nest for as long as 50 days because they are safer there than at sea. Who wins in parent–offspring conflict can be determined by observing where fledging occurs relative to the preferred fledging dates of the 2 parties. As it turns out, Dovekie chicks fledge about day 18, the parents' optimum, implying that parents win.

The only limitation of the Clark and Ydenberg (1990b) model is that it is restricted to the case of conflict over fledging date. Clearly this is an important case but obviously not the only case.

Pugesek (1990) studied California Gulls (*Larus californicus*) in Wyoming in a test of 3 predictions of Trivers' (1974) model: (1) the amount of parent–offspring conflict should be directly correlated with offspring age and the amount of lapsed time in the period of parental care; (2) the amount of conflict should be inversely correlated with parental age; and (3) the length of the period of parental care should be directly correlated with parental age. Pugesek (1990) obtained results consistent with all 3 predictions: (1) the amount of time parents withheld food from offspring increased with their age; (2) older parents gave food to offspring more quickly than younger parents did; and (3) older parents cared for offspring for a greater number of days than did younger parents.

We applaud Pugesek (1990) for providing empirical results for empirical predictions. As noted above, too many participants in the parent–offspring conflict debate have made imprecise, untestable predictions, thereby depreciating the value of their contribution to the debate. However, we have reservations about the meaning of Pugesek's (1990) results:

1) Although all of the predictions Pugesek (1990) tested came from Trivers (1974), they can also be derived from earlier work on reproductive value. Fisher (1930, 1958) developed the concept of reproductive value from Darwin (1871). Reproductive value is a function of survivorship and fecundity. The first prediction Pugesek (1990) tested reduces to saying that weaning conflicts are expected. This can also be derived from reproductive value theory in that a parent cannot have future broods until care for present broods has been terminated, i.e., without some analogue of weaning, the parents' fecundity component of reproductive value goes to zero, dragging the entire reproductive value to zero along with it. Thus parents have no choice but to terminate parental care at some point.

The second and third predictions Pugesek (1990) tested are implicit in the changing relationship between the reproductive values of parent and offspring. Reproductive value rises early in life, peaks, and then declines. [Graphical depictions of this are given in Fisher (1958:28), and MacArthur and Wilson (1967: 85), the latter based on Lewontin (1965).] The consequence is that offspring become more valuable to parents as parents progress through their reproductive careers because later offspring become increasingly larger shares of their parents' remaining reproductive value until the last offspring represent all of their parents' remaining reproductive value. Thus Pugesek's (1990) second and third results (i.e., that older parents invested more than younger parents did) could be expected for asexual as well as for sexual species, despite the fact that there is no depreciation of genetic relatedness in asexual species, because reproductive value is a function of survivorship and fecundity, not of r. Trivers' (1974) theory of parent–offspring

conflict is based on both reproductive value and depreciation of r as a result of sexual reproduction.

The net effect of being able to derive all of the predictions Pugesek (1990) tested without reference to Trivers' (1974) theory is that Pugesek's (1990) results support *any* theory based on reproductive value, not just Trivers' (1974) theory. Therefore Pugesek's (1990) results, while supportive of Trivers' (1974) theory, are not a decisive test of it. This must be kept in mind when judging how generalizable Trivers' (1974) theory is to matters not predicted by other theories. Thus Pugesek's (1990) results can in no way be considered support for Trivers' (1974) conclusion that offspring victory can be frequent. In Pugesek's (1990) defense, we hasten to add that he neither made nor implied any such claim.

2) Pugesek's (1990) measure of conflict is not fully convincing because it is very indirect. He used feeding latency [i.e., "the number of minutes parents waited to feed chicks after returning from foraging" (Pugesek 1990:213)] as the measure of conflict: the greater the latency, the greater the conflict. A more direct measure of conflict would have been feeding visits by parents or amount of food they brought, i.e., conflict would be said to rise as feeding frequency or amount declined. The fact that feeding latency was greater for younger parents than older parents may mean that the former had more conflict with their offspring than the latter [as Pugesek (1990) interpreted], or it may only mean that younger parents needed more time to decide which chick was the best beggar because they were less experienced parents. Thus Pugesek's (1990) second result is more ambiguous than it initially seems. In Pugesek's (1990) defense, we note that the fact that feeding latency increased throughout the nestling period for both younger and older parents suggests that parental experience was not the only factor, i.e., if experience were the only factor, then both age classes of parent should have decreased their feeding latency as the nestling period progressed. But even this phenological progression does not prove that younger parents had more conflict with their offspring than older parents. Both age groups might have had longer feeding latencies as the time of fledging neared because the ability of chicks to deceive their parents in a best beggar competition might have grown as their physical strength and endurance grew, forcing parents to prolong the length of each bout of best beggar competition in order to determine which chick was truly the best beggar.

We do not state this caveat about Pugesek's (1990) measure of conflict in order to discredit his results, but in order to show that measures of conflict should ideally be unambiguous. That goal can best be served by choosing the most direct measures.

Because Pugesek (1990) did not design his study in order to determine who wins in parent–offspring conflict, his results cannot be used to decide that question. However, the fact that the pattern of parental behavior coincides with that expected from a consideration of parental reproductive value suggests that parents were winning. Of course, this cannot be a firm conclusion because a compromise between parental and offspring interest might also follow the same pattern if the compromise were weighted in the parent's favor.

Graves et al. (1991) studied the termination of feeding conflict in Herring Gulls (*Larus argentatus*) in Scotland. Among the most important of their contributions to the parent–offspring conflict debate is their listing of the evidence necessary to show that a conflict of genetic interests exists between parents and offspring at

the termination of feeding. The evidence must show that (1) parents decrease their investment and that the reduction of food given chicks is not just a reflection of lower food availability; (2) offspring attempt to increase the level of parental investment; (3) the decrease in investment is costly to offspring; and (4) parents would incur a cost if they did not decrease investment.

Graves et al. (1991) found compelling evidence for the first 3 requirements but not the fourth, preventing them from proving that bona fide genetic conflict exists in their population. However, they clearly believe that such conflict occurs. Their lack of good evidence for the fourth requirement is not troubling because annual adult survivorship is normally so high (0.9–0.93) that even large percentage increases in mortality consequent to continual high-level parental investment would be very difficult to measure.

Burger's (1980, 1981) results on Herring Gulls in New Jersey were very different from Graves et al. (1991). She found no evidence of a "weaning" conflict in her population. A possible answer for the different results in the Scottish and New Jersey populations is relative food abundance. The New Jersey population had exactly twice the fledging success of the Scottish population, suggesting greater food availability in New Jersey. If food were sufficiently more abundant in New Jersey, then parents might not have been food stressed, allowing them to accede to offspring demands for a longer period of time without damage to themselves.

This chronological overview shows that while models can be constructed that allow any number of possible outcomes, with few exceptions they cannot specify which will occur in which species or how to recognize them in nature. Models are often useful predecessors for empirical studies but never substitutes for them (Stamps and Metcalf 1980).

Despite the obviousness of this conclusion, there often appears to be an acceptance of the idea that models can decide empirical questions. The literature of the parent–offspring conflict debate sometimes has this flavor, e.g., in an otherwise balanced review, Clutton-Brock (1991:203) claims that the qualitative prediction from the various mathematical models "that solicitation by offspring should cause parents to exceed their optimum level of investment and reduce parental fitness" is upheld in birds and exemplified by the feeding behavior of Budgerigars (Stamps et al. 1985, 1987; reviewed above). In fact, that prediction is not upheld because it has not been shown in Budgerigars or any other species that adults are in anyway hurt or that their feeding behavior is controlled by offspring. We repeat: empirical questions can only be answered by empirical means.

This overview also shows that empirical work on parent–offspring conflict in birds (outside the study of siblicide—see below) is still in its infancy. Too few studies have been performed to allow any generalization beyond the statement that no real evidence of offspring victory has as yet been presented in birds. No robust generalizations will be possible until a generally applicable empirical test is developed and widely adopted that enables determination of who wins in parent–offspring conflict. We will propose such a test below.

THE HONESTY OF BEGGING AS A SIGNAL

As noted in Chapter 1, offspring can potentially win in parent–offspring conflict only by coercing or deceiving their parents into giving them more than is in the parent's best interest to give. In altricial birds coercion during the nestling period

is impossible, leaving only deception as a ploy. That fact brings up the question of the honesty of begging as a signal. Is begging a true signal of offspring need, a deceptive trick, or some combination of both? As noted in Chapter 2, some biologists believe communication is fundamentally deceptive and we accepted this view with reservations. However, we argued in Chapter 3 that when the parent chooses which offspring to feed on the basis of a best beggar competition, it cannot be deceived, at least not over a series of best beggar competitions. If we are right, then honest offspring would be favored over deceptive ones because both would gain the same food reward from the parent, but the latter would pay both a suppression cost from the parent and a potential predation cost. Honesty in this context means begging only when genuinely hungry and stopping begging as soon as fed.

As noted in Chapters 1 and 2, Trivers (1974), Dawkins (1976), and Dawkins and Krebs (1978) all believed that dishonesty could be successful in offspring, and human experience suggests that it may be. More recently, Dawkins and Guilford (1991) considered the meaning of "honesty" and gave five contextual definitions for it. Generally speaking, they believe that honesty will be corrupted, i.e., that some level of cheating will coexist with truth. They call this coexistence, "conventional signalling." Dawkins and Guilford (1991) believe that deception is rife not because lying always has high rewards but because "probing" for the truth by the *receiver* has costs for the receiver. The higher these costs, the greater the opportunity for lying. However, Dawkins and Guilford (1991:870) admit that there can be cases (their context #2) where signals are "necessarily and reliably related to something that is worth predicting." We believe that offspring begging is such a case because the offspring's condition is important to both the parent and the offspring. Begging should be honest by Dawkins and Guilford's (1991) reasoning because the cost of "probing" should be cheap for the parent. In a best beggar competition all the parent has to do is to wait a few extra seconds in order to see which offspring is the best beggar; this should not appreciably raise its costs in terms of "energy, time or risk" (Dawkins and Guilford 1991:865), and therefore the parent has the advantage.

Not all workers in communication believe that signalling is fundamentally dishonest. Zahavi (1977, 1981, 1985, 1991) seems to be the leader of this school. He has argued forcefully for years that a costly signal is inevitably an honest signal. His reason is that parents will be disfavored from responding to communication that is not costly because the offspring will incur no significant punishment for lying under that circumstance. But parents will be favored for responding to communication that is costly for the offspring to make because a high cost to benefit ratio automatically forces offspring to communicate only what they truly need when they truly need it. In a general sense, Zahavi's theory of costly signalling has been upheld by a model of Grafen (1990).

Perhaps the most convincing mathematical analysis of the honesty of begging is found in Godfray (1991). He modelled the case where the parent has only one offspring per year and begging is expensive. The result was a parent-wins outcome with the parent giving the offspring only what it needed and the offspring asking only for that. Godfray (1991) recognized that his result is more in agreement with Alexander (1974) than with Alexander's critics.

If we accept Godfray's (1991) result that begging is honest, we are still confronted

with the problem of how the parent should distribute food among several simultaneously begging offspring. The fact that all were honest (in the sense that none begged unless hungry) would not be particularly helpful because the parent would still have to decide how to allocate the food. Allocation on the basis of *comparative* honesty is clearly not done. If it were, then starling runts would be fed preferentially since their need is greatest, and the largest, most aggressive nestlings would be discriminated against because their need is least. Yet we know that the starling parent feeds on the basis of the best beggar rule (Relevant Result #2). This implies that honesty is important to the parent only to the extent that no begging offspring is without need. Comparative reproductive value appears to be what drives the parent's decision when confronted with a brood of honest beggars even though this often results in the parent not feeding young according to their relative need.

Godfray (1991) discussed the case where brood size was larger than one but did not formally model it. Hence his remarks on that case are necessarily speculative. Our reading of Godfray (1991) is that he thinks the most adaptive parental response when broods have more than one offspring would be to feed young according to need only.

We disagree. If young were fed according to need only and there was insufficient food for all, the parent might wind up feeding equal but insufficient amounts to each of its equally starving young. Under such circumstances the parent would be better off feeding according to the best beggar rule because that would guarantee that the parent invested only in the most competitive young.

We resolve our results with the theoretical literature of begging by postulating a 2-level evolutionary process. On the first level, offspring are favored for begging honestly because parental hesitation to feed and predation pressure make deception costly. On the second level, the parent chooses which of several honestly begging offspring to feed on the basis of their comparative reproductive value rather than their comparative need. The result is that the parent fledges only the offspring most likely to give it grandoffspring although that might frequently come at the expense of offspring (especially runt) mortality. Thus by feeding according to reproductive value instead of need, the parent often trades quantity for quality.

SIBLICIDE AND THE BEST BEGGAR RULE

Siblicide can be thought of as the consequence of the best beggar rule taken to its extreme. Instead of the parent choosing which offspring to feed on the basis of a non-lethal competition, the parent rigs a lethal competition among its offspring by hatching them asynchronously and abides by the result. This "laissez-faire policy" results in parental investment according to the relative reproductive value of offspring (Mock 1987).

Because some young kill others, siblicide initially seems like a form of offspring victory in a dispute between parent and offspring over clutch size (Parker and Mock 1987). However, theoretical analyses from O'Connor (1978) on, all conclude that siblicide in birds is not necessarily the victory of larger offspring against their parents and smaller siblings; it can be to the advantage of all parties, including those that die (Godfray and Harper 1990; Godfray and Parker 1991). This is because the inclusive fitness interests of all parties can be better served by the fledging of a smaller number of highly competitive offspring than by the fledging

of a larger number of weaklings with poor prospects of survival and victory in reproductive competition.

In comparing offspring death in starlings and siblicidal species, we note that the fate of starling runts is both different from and similar to the fate of runts in truly siblicidal species. [These include a variety of relatively large, long-lived, birds with clutches of two or three, e.g., some raptors, bee-eaters, boobies and herons (Mock et al. 1990).] A number of careful studies of these species (Drummond et al. 1986; Drummond 1987, 1988; Mock 1987; Anderson 1990; Bryant and Tatner 1990; Mock et al. 1990) have shown that runts die not from starvation due to poor competitive ability (as do starling runts) but rather from being evicted from their nests or pecked to death. Mock et al. (1990) have summarized the literature of siblicide and reported four elements necessary for siblicide to be a regular feature of nestling life: resource competition, provision of food in small units, weaponry, and spatial confinement. Starling nestlings have no weaponry. Thus it is not surprising that starling runt mortality occurs without overt killing. Nevertheless, the effect is the same though the cause is less dramatic, and the timing is as predicted by O'Connor (1978) for species with regular brood reduction whether or not they are siblicidal, i.e., early in the nestling period (see Fig. 1 in Stouffer and Power 1991).

A Simple Test to Determine Who Wins in Parent–Offspring Conflict

We believe that there is an empirically simple way to determine who wins in parent–offspring conflict. We provide it here and apply it to starlings in the next section.

The winner in parent–offspring conflict can be established by:

1) Discovering the rule(s) by which PI is dispensed;

2) Deciding who wins when the rule(s) is obeyed; and

3) Determining whether the party that loses when the rule(s) is obeyed can break the rule(s) in order to win.

Winning and losing are ideally measured in terms of fitness or at least of the relative reproductive success of the contestants but that will usually be difficult and often impossible. A simpler method is to keep track of resource control. This assumes that the party that controls the resource(s) automatically wins; it is difficult to imagine that controlling resources could result in consistently losing.

Support for the idea that resource control is the key to victory in parent–offspring conflict comes from 2 very different kinds of study. The first is the study of Clark and Ydenberg (1990b) reviewed above. As noted, their results show parental victory. Parents control the critical resource, food, in their study species, the Dovekie. Offspring have little choice but to fledge when their parents stop feeding them after they have attained fledging size.

The second kind of study is the investigation of parent–offspring conflict in social insects. This investigation has tested the genetic relatedness hypothesis formalized by Trivers and Hare (1976) but based on Hamilton (1967). Briefly stated, that hypothesis holds that, in haplodiploid species with effective monogamy and eusocial colony structure (*sensu* Wilson 1971), (1) sterile workers should prefer to invest 3 times more in fertile sisters than in fertile brothers because $r = \frac{3}{4}$ between workers and sisters, but $r = \frac{1}{4}$ between workers and brothers, i.e.,

sisters are 3 times more valuable than brothers in genetic relatedness, but (2) queens should prefer that workers invest equally in their fertile brothers and sisters because queens are as closely related to their sons as to their daughters ($r = \frac{1}{2}$ in both cases). Thus a fundamental genetic conflict exists between queens and their worker daughters. Despite serious deficiencies in Trivers and Hare's (1976) development of the genetic relatedness hypothesis (Alexander and Sherman 1977), a growing body of evidence (reviewed in Oster and Wilson 1978; Nonacs 1986) supports the view that worker investment is heavily weighted in favor of fertile sisters, suggesting at least a worker dominated compromise. Perhaps the most direct support for the hypothesis comes from Mueller's (1991) experimental manipulation of r in the bee *Augochlorella striata*. He manipulated r by removing or not removing foundress queens ($r = 0$ between workers and their dependents in the former case, and $r > 0$ in the latter case), and found that the sex ratio was more female-biased when queens were not removed in keeping with the genetic relatedness hypothesis. This study is particularly important because it gets around one of the fundamental difficulties of the genetic relatedness hypothesis as originally stated. That difficulty is that the asymmetry in worker investment was believed to rely in an exact sense on the asymmetry in r values, and this required that queens be monogamous otherwise the asymmetry in r values would decline. In fact, monogamy is not always a valid assumption in eusocial insects, e.g., Blanchetot (1991) found 11 different patrilines in the brood of a single honeybee (*Apis mellifera*). Mueller's (1991) study gets around the problem of polyandry-depreciated r values by making asymmetry in r an *absolute* matter, i.e., $r = 0$ or $r > 0$ with closer relatedness between workers and fertile sisters than between workers and brothers in the latter case even if the difference in relatedness is <3-fold. Thus what counts is not the exact magnitude of the asymmetry but the simple fact of the asymmetry.

Of critical importance to judging the value of our empirical test for determining who wins is the fact that workers physically control most resources in eusocial insects, not the queens that are totally dependent upon them. Thus the critical assumption of our test, control of resources bestows victory, is supported by both the parent-wins outcome in Dovekies and the offspring-dominated outcome in eusocial insects.

Who Wins in Parent–Offspring Conflict in Starlings?

Application of the simple test to European Starlings leads to the conclusion that parents win in parent–offspring conflict during the nestling period:

1) *The rule by which PI is dispensed:* parent starlings dispense food to the best beggars and hole-blockers.

2) *Who wins when the rule is obeyed:* parents win because distributing food to the best beggars and hole-blockers assures that parents invest only in the most vigorous offspring and hence only in those most likely to reproduce successfully. This always promotes the parent's interests but does not always promote the offspring's interests.

The parent's interests are always promoted because only the best possible investment is made at any given feeding. No long-term bad investment is ever made because successful deceit by unworthy offspring is not sustainable (Relevant Result #2).

The offspring's interests are not always promoted because it is fed only when it complies with the parent's rules even though it would benefit from being fed when it doesn't comply with the rules as long as its chances of fledging were so good that it was not favored for "suicide" (*sensu* O'Connor 1978). That even starling runts are seldom favored for "suicide" is shown by the results of Stouffer and Power (1991) who found that experimentally synchronized broods had significantly higher fledging success than normally asynchronous broods of the same starting size. Synchronized broods require more food because they have no runts and therefore fewer young that die in the first few days of the nestling period and more young that consume food over the entire period.

3) *The loser when the rule is obeyed cannot win by breaking the rule:* offspring cannot force their parents into changing the rules of food dispensation because they do not have the physical means to do so, and deceit does not work.

On an *intrabrood* basis, deceitful offspring (those pretending to be the best investment when they are not) might sometimes be fed when it would be in the parent's best interest to feed other offspring, but it appears impossible that they could successfully sustain their deceit over the entire nestling period (Relevant Result #2). From a parental perspective, the motivation behind begging is irrelevant (i.e., whether the offspring intends to deceive or tell the truth) because the only thing that counts is the investment potential of the offspring. If that potential is revealed as clearly when the offspring lies as when it tells the truth, the parent cannot be deceived, and what a deceitful offspring "intends" as a lie reduces to exaggeration harmless to the parent's interests.

Nor can offspring attempts at deceit result in a compromise between parental and offspring victory on an intrabrood basis. This is simply because the parent's interests are not compromised by attempts at lying by offspring, and the offspring's interests are not promoted since it ultimately tells the truth anyway.

In theory, attempts to break the best beggar rule could result in either offspring victory or a compromise between parental and offspring victory on an *interbrood* basis. This is because the brood as a whole could theoretically deceive their parents into giving them more than they were worth as a collective investment. Such deception would work through the brood appearing to be better beggars than they really were compared to some hypothetical other or future brood.

However, it is difficult to see how this could work in practice. Even if a particular brood were not as good an investment as some other brood might have been or some future brood might be, it is the only brood the parent has to invest in. Therefore the parent's interests are not hurt by investing in the present brood so long as it does not exceed some threshold amount of PI that results in negative interbrood effects. Despite efforts to find such effects in our population, Power et al. (1989) and Stouffer (1989) could not find them (see Relevant Result #1). Therefore we conclude that the parent's interests are not injured at an interbrood level by following the best beggar rule or by (possible) offspring attempts to break that rule.

Nor can offspring achieve a total or compromise victory by attempting to extract more PI from their parents than the latter are willing to give by refusing to fledge on schedule. We experimentally simulated such offspring defection but found that parents appeared to give no more PI than they normally would have given had offspring fledged on schedule (Relevant Result #7).

Thus there appears to be no way by which nestling starlings can successfully break the best beggar rule that generates parental victory, or impose a new rule of their own (delayed fledging) that could potentially allow them to gain at their parent's expense. This leaves parental victory as the most parsimonious explanation of the pattern of parent–offspring conflict seen in starlings during the nestling period.

CHAPTER 7

GENERAL SUMMARY

Parent–offspring conflict has been the subject of controversy and investigation among biologists since the Trivers (1974)–Alexander (1974) debate brought it to the attention of a large audience. This debate focuses on the question of who wins in parent–offspring conflict. Unfortunately, many of these publications are purely theoretical and so provide neither legitimate evidence nor empirical tests with which to decide who wins, how often, under what circumstances, by how much, and with what consequences. These questions can only be answered by empirical, ideally experimental, studies.

This monograph reports the results of a series of experiments on European Starlings nesting on the Livingston College Campus of Rutgers University in Piscataway, N.J. Starlings are suitable study subjects for several reasons, most importantly that there are grounds for genuine parent–offspring conflict in them.

Closed-circuit television and specially constructed viewing boxes were used to monitor events within nests. Experimental subjects were individually marked.

Using the experimental treatments of (a) supplemental feeding and (b) drugging nestlings by means of raisins soaked in alcohol, we show (1) that parental feeding visits (but not fecal sac removals) increase when broods are sober/hungry and decline when broods are drunk/sated, and (2) that individual nestlings are fed more when they are sober/hungry than when they are drunk/sated. Parental feeding is stimulated by nestling begging. Nestling begging (as measured by an ethogram that incorporates alertness, posture, movement, vocalization and relative effort) declines when nestlings (either as broods or individuals) are drunk/sated and rises when they are sober/hungry.

The first result demonstrates communication between parent and brood, and adds starlings to the growing list of species where such communication has been shown. The second demonstrates communication between parent and individual offspring. Individual communication is a prerequisite for offspring victory through deception of parents.

Parents preferentially feed the "best beggar." This is the nestling that chirps the loudest, gapes the widest, stretches its neck the longest, and flaps its wings the most relative to its nestmates at the time of a feeding visit. By feeding the best beggar, parents invest in the most robust offspring, the ones most likely to survive and hence to reproduce, i.e., the ones with the highest reproductive value.

Although individual communication creates the hypothetical opportunity for offspring to use deception in order to get more than is in their parents' best interests to give them, their parents' preference for best beggars makes successful, sustained deception almost impossible. This is because the truly best beggar will be obvious in time while a faker will collapse from exhaustion. Thus offspring inevitably tell their parents the truth about their own investment potential in a best beggar competition. What may start out as offspring deception ends up as mere exaggeration harmless to the parent's interests.

Intense begging by nestlings is usually attributed to nestmate competition. However, our discovery that parents prefer best beggars suggests that begging intensity is more a product of parental selection than offspring competition. If so, then occasional loss of broods to predators attracted to nests by loud, frequent begging

calls is the price parents pay for selecting for best beggars, and it applies counterselection on parental preference for best beggars.

Best beggar competition takes a new form late in the nestling period. At that time, the nestling successfully blocking the entrance and extending its head through the hole is the one that usually gets fed. Feeding the hole-blocker effectively moves the operational decision about whom gets fed from the parent to the offspring. Yet this has the same effect as feeding the best beggar because only the most vigorous offspring can succeed in either tactic.

We looked for evidence of sexual dimorphism in parental feeding behavior but found none. Apparently male and female parents use the same criteria for deciding which young to feed. This eliminates the opportunity for offspring to play one parent against the other by meeting some of the criteria of each parent but not all of both.

Despite the greater needs of runts due to their poor competitive abilities, parents give them no special treatment. Runts also must be the best beggar or hole-blocker at the time of a parental feeding visit in order to get fed. Nevertheless, more than half of all runts in this study fledged, and did so at about the same weight as the lightest of their older nestmates. Runts achieved this by delaying their own fledging until after their older nestmates had fledged, and used the added time in the nest to get extra feedings by playing the role of best beggar (or hole-blocker) without competition. Yet the total time in the nest was no greater for runts than other nestlings, and so there was no reason to believe that runts got more than their fair share of parental resources. Runts persisted only by submitting to their parents' rules for the dispensation of food.

The fact that runts can delay fledging by a few days in order to garner more parental feedings led us to wonder whether offspring could use delayed fledging as a tactic to win in parent–offspring conflict. We simulated such offspring manipulation by experimentally preventing fledging at the usual time by placing restrictors over entrance holes. These allowed parents to feed nestlings but kept young from fledging. Although parents did feed restricted young for an average of an additional 3.52 days beyond the expected cut-off point for nestlings, restricted young lost weight and were fed less frequently than they had been during the normal nestling period. Moreover, parents clearly spent less effort feeding restricted young than normal nestlings, and their period of extended care did not exceed the normal period of post-fledging care for various starling populations in North America and Europe. Thus there is no reason to believe that offspring would gain through delayed fledging. Nor is there any reason to believe that parents would lose unless the delay in fledging precluded their having a successful second brood. Even if parents did lose in this manner, offspring victory would not ensue because offspring would have achieved nothing more than depriving themselves of second brood siblings.

A striking result of the delayed fledging experiment was the variability in the length of extended care (0–20 days). We speculate that the novelty of restriction may have caused parents to choose different responses because there was no pattern of response in their evolutionary past that would have consistently generated higher fitness. Alternatively, different responses may have reflected different cost-benefit schedules for different individuals. Whatever the cause of variability in response, extended care itself is known in several species, suggesting that it

may be fairly common when parents "judge" that specific offspring or broods are worth extra care.

In order to resolve the question of who wins in parent–offspring conflict, we summarize the 7 results we believe to be most relevant (Chapter 6). We then use them in a discussion of the literature of the parent–offspring debate. We find some of this literature to be insightful but far too much of it to be without value in understanding nature. This is because much of it is too abstract to make detailed, testable predictions, e.g., several authors predict a compromise between the parental investment optima of parent and offspring but give no clue as to how to recognize or measure any optimum in nature. Without testable predictions and empirical measures it is not possible to resolve any of the issues about parent–offspring conflict with which we open this summary chapter.

In order to fill the need for an empirical method to determine who wins in parent–offspring conflict, we propose a simple 3-part test:

1) Discover the rules by which parental investment is dispensed.

2) Decide who wins when those rules are obeyed.

3) Determine whether the party that loses when the rules are obeyed can break the rules in order to win.

Application of this simple test to our study population leads to the conclusion that parent starlings win in parent–offspring conflict during the nestling period. This is because:

1) Parents dispense food to best beggars and hole-blockers.

2) Parents win when this rule is followed because it assures that they invest only in the most vigorous offspring and hence those most likely to reproduce successfully. This always promotes the parent's interests but does not always promote the offspring's interest. The parent's interests are always promoted because parents always make the best possible investment at any given feeding. They never make a long-term bad investment because successful deceit by unworthy offspring is not sustainable (see above). The offspring's interests are not always promoted when it obeys the rule because it is not fed when it may profit from being fed but is physically unable to be the best beggar or hole blocker.

3) Offspring cannot win by breaking the rule because they cannot force their parents to change the rule and they cannot long deceive their parents into believing that they are abiding by the rule when they are not. Deception reduces to exaggeration harmless to the parent's interests.

In closing, we find it deeply unfortunate that the parent–offspring conflict debate was trivialized in its early history into a purely theoretical consideration of which of two abstractions, parent or offspring, wins in some all-encompassing sense, and who was right in the most narrow sense, Trivers (1974) or Alexander (1974). Parent–offspring conflict is a far richer and more important topic than that, one with practical as well as theoretical consequences. Fortunately, the current trend is toward empirical studies (e.g., Anderson 1990; Clark and Ydenberg 1990b; this study).

ACKNOWLEDGMENTS

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