Intergenerational Communication and Parental Care

in American White Pelicans (*Pelecanus erythrorhynchos*):

Conflict or Honesty?

by

Steve Daniels

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INTERGENERATIONAL COMMUNICATION AND PARENTAL CARE
IN AMERICAN WHITE PELICANS (PELECANUS ERYTHRORHYNCHOS):
CONFLICT OR HONESTY?

by

STEVE DANIELS

A Thesis/Practicum submitted to the Faculty of Graduate Studies of The University

of Manitoba in partial fulfillment of the requirements of the degree

MASTER of SCIENCE

STEVE DANIELS   1997 (c)

Abstract

Parent-offspring conflict and honest signalling theories provide distinct views of the kinds of communication systems which could evolve between offspring and their parents. Conflict theory operates under the premise that parent and young disagree over achieved levels of care while honest signalling theory assumes that parent and offspring are relatively more cooperative and mediate care provisioning with accurate information provided by young. In both field and laboratory settings I tested the extent to which conflict and honesty have shaped solicitation and care in the American white pelican (*Pelecanus erythrorhynchos*).

Field tests examined heat and food solicitation and provisioning over the first two weeks post hatch in a natural setting. Solicitation and care patterns differed markedly between the two resources. Offspring solicitation for, and parental delivery of heat were consistent with conflict and support the possibility that parent and young can disagree over resource distribution. In contrast, the behavioural patterns associated with the solicitation and delivery of food indicate that young pelicans honestly indicate their nutritional requirements and that parents respond according to these requests. These markedly disparate patterns likely arise because of differences in the expected continuation of care. Offspring are weaned of parental heat at the ages immediately following termination of my study while food deliveries are expected to continue for several weeks.

Laboratory studies explored the energetic cost of solicitation using respirometery techniques. Both conflict and honest signalling theories predict that communication by young will be costly. Solicitation for both resources was found to be energetically inexpensive with the costs for manipulative signals exceeding those for honest communication.

Future research possibilities and a theoretical framework for understanding changes in communication through time are considered.

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Most importantly, to the pelicans, for their nobility, grace, beauty and for the inspiration to follow my heart.

Table of Contents

List of Tables

List of Figures

General Introduction

"The old bird backed up as if she were getting a good footing and slowly opened her mouth to admit the bill of the little pelican. She drew her neck up till the ends of the upper and lower mandibles were braced against the ground and her pouch was distended to the limit. Jonah-like, down the mother's throat went the head and neck of the child till he seemed about to be swallowed had it not been for his fluttering wings. He remained buried in the depths for about two minutes, eating everything he could find. Nor did he withdraw from the family cupboard voluntarily, but when the supply was exhausted or the mother thought he had enough, she began slowly to raise and struggle to regain her upright position. The youngster was loath to come out and flapping his wings, he tried in every way to hold on as she began shaking back and forth. The mother shook around over ten or twelve feet of ground till she literally swung the young bird off his feet and sent him sprawling..."

From, Among the Pelicans
W.L. Finley, 1907

The observations of the above passage not only capture the drama and excitement of observing pelicans but also anticipate one of the most influential theories to arise from studies of parental care – namely parent-offspring conflict (Trivers 1974). Parent-offspring conflict (POC) is a logical consequence of inclusive fitness theory (Hamilton 1964). Such conflict is predicted to arise because of the divergent fitness interests of genetically similar but not identical parent and young. Specifically, parents are equally related to all of their offspring while offspring are only partially related to all of their siblings. Thus, from a genetic standpoint, parents should invest equally in all of their young

while individual offspring should attempt to acquire levels of care which exceed this parental optimum. The result is a genetic conflict of interest over realized levels of parental care.

POC theory is revolutionary because it represents a major shift away from the classical view which posits that offspring are passive recipients of care (Trivers 1974) and that parents alone regulate the distribution of resources. Trivers viewed offspring as actors in the provisioning and partitioning of care among siblings and for the first time presented a theoretical context within which offspring solicitation could be explored. Prior to this it was recognized that most altruistic social activities involved parents caring for their young (Williams and Williams 1957) but the role of offspring in such interactions received limited attention (e.g. Gibb 1950; Perrins 1965; see Trivers 1974). Conflict theory, however, placed offspring solicitation and behaviour in the forefront of understanding how parents ultimately allocate care.

The Rise and Resolution of Conflict

POC theory was born of observations taken primarily from the literature on parental care patterns in mammals although some evidence from avian species was also included (Trivers 1974). Since its inception extensive work in the area has been completed and evidence consistent with the theory comes from observations of many groups of organisms. The strongest evidence comes from achieved investment ratios in male and female offspring of haplodiploid social insects (Trivers and Hare 1976). Circumstantial evidence arises in the

form of parental avoidance of young or aggression directed towards offspring (Finley 1907; Schaller 1964; Gomendio 1991; Redondo *et al.* 1992) while provisioning patterns of several bird species indicate that offspring can acquire greater levels of investment through solicitation (Henderson 1975; Bengtsson and Ryden 1983; Kacelnik *et al.* 1995). With the possible exception of haplo-diploid insects, clear evidence (see Clutton-Brock 1991 for review) that any of the above patterns represent deviations away from the parental optima has yet to be attained (Mock and Forbes 1992).

Though intuitively appealing, and at least superficially supported, the predictions which arise from POC theory have proven difficult to test (Stamps *et al.* 1985; Mock and Forbes 1992). Because of this many of the significant advances in our understanding of parental care and potential conflicts have come from theoretical developments (Parker and Macnair 1978; Stamps *et al.* 1979; Parker 1985; Lazarus and Inglis 1986; Haig 1990; Eshel and Feldman 1991; Yamamura and Higashi 1992). These models are rich in detail and encompass many real biological problems but have greatly outpaced the empirical testing which is required to ensure that the systems in question are properly understood (Mock and Forbes 1992). Further, these models predominantly come to similar conclusions -- an outcome which superficially gives one confidence in their predictions while leaving empirical workers without specific alternate hypotheses to test. Acceptance of the theory (Dawkins 1986) may therefore be premature and careful thought should be given when

assessing our current understanding of parent-offspring interactions (Kilner and Johnstone 1997).

Signalling a Solution

Current explorations of POC concede that genetic differences between generations lead to genetic conflict and focus on how such conflicts will be resolved at a behavioural level (Mock and Forbes 1992). Studies of resolution recognize that due to their smaller size offspring will be unable to physically overpower their parents (Alexander 1974) and will therefore rely on manipulative tactics available to them through communication. Trivers verbally forwarded such a resolution in his 1974 paper in which he portrayed offspring as psychological manipulators. Additional investigations also suggest that offspring could win battles with their parents (victory defined as the party which achieves its own investment optimum) by exaggerating the signals directed to these care givers (Parker and Macnair 1978; Stamps *et al.* 1979; Harper 1986).

Recent developments in the study of animal communication and honest signalling theory may provide an alternate resolution to POC and for the first time establish testable alternate hypotheses. Godfray has shown that both intergenerational (Godfray 1991) and intragenerational (Godfray 1995a) conflicts may be resolved through honest solicitation by young. This solution is particularly interesting because it represents a departure from previous models which pit parent against offspring and suggests a more cooperative solution which involves honest (Godfray 1991) rather than manipulative communication.

Predictions regarding the signalling strategies of honest and conflicting offspring differ considerably though some common ground exists. Changes in solicitation patterns associated with conflict strategies are predicted to be directly proportional to parental future fitness costs (Trivers 1974) while similar changes in honest systems are expected to be inversely related to such costs (Godfray 1991, 1995a). Both resolutions (conflict and honesty) suggest that solicitation will be costly. High costs of conflict stem from the need to exaggerate signals in an attempt to acquire greater resource share (Trivers 1974; Harper 1986) while high costs in honest systems arise to prevent such exaggeration (Zahavi 1975; Godfray 1991).

American white pelicans (*Pelecanus erythrorhynchos*) are an ideal species with which to test predictions about offspring solicitation of parental care. Offspring solicit brooding responses and food using two unique displays, each with an identifiable vocalization (Evans 1988, 1992). The cost to parents of providing these resources likely differs considerably (Evans and Knopf 1993). Further, the altricial young remain in the nest for about two weeks (Evans 1984a) providing the opportunity to examine changes in solicitation as offspring develop.

This thesis explores solicitation patterns and energetic costs of solicitation in the American white pelican in hopes of clarifying the strategic aspects of such communication. The first chapter summarizes a field study in which I examined changes in solicitation for heat and food, and the parental response to such requests during the first two weeks post-hatch. In chapter two

I explore the cost of solicitation in a laboratory setting by measuring the rate of

oxygen consumption during solicitation bouts for each resource. Together these

studies address strategic aspects of solicitation by young pelicans and suggest

new directions for the empirical and theoretical study of POC. The two chapters

are written in manuscript format, each representing a complete study in its own

right.

Chapter 1: Solicitation and Provisioning in American White Pelicans

Introduction

Parents of many avian species appear to rely on the solicitation behaviour of their offspring to determine the appropriate levels of care. Historically this communication was given limited attention or was assumed to benefit the parent receiving the signal (Gibb 1950; Perrins 1965). However, it has been postulated that parent and offspring are in genetic conflict over the distribution of parental care (Trivers 1974) and as such the assumed benefits to parents may be restricted.

Parent-offspring conflicts (Trivers 1974) stem from the genetic differences which necessarily arise in species with sexual reproduction. Because parents are equally related to all of their offspring they are predicted to allocate care equally to all young. However, as all non-identical young have a greater genetic interest in themselves than they do their siblings, each offspring is selected to demand, and where possible acquire, a greater share of available care than parents are selected to provide.

The theory of POC is widely accepted despite a virtual absence of strong empirical tests (Mock and Forbes 1992). One could argue that the theory has been accepted uncritically as only one paper (Alexander 1974) of the several

hundred (Science Citation Index) which cite Trivers' definitive work is recognized

(in the Zoological literature) as being opposed to the initial view (Clutton-Brock

1991, Mock and Forbes 1992). However, several authors (e.g. Blick 1977;

Parker and Macnair 1978, 1979; Macnair and Parker 1978, 1979; Stamps et al.

1979) found that genes acting in offspring, which cause them to acquire greater

levels of care, could be maintained despite deleterious effects on parental

fitness. It therefore seemed clear that at the genetic level POC was possible

and that Trivers' insights were valid.

Given the apparent agreement over the existence of POC (genetic

battleground; Mock and Forbes 1992), the focus of research has turned to

understanding how such conflicts influence the behavioural repertoires of parent

and young. Potential outcomes (resolutions) are usually phrased in terms of

victory for either parent or offspring depending on the levels of care which are

ultimately dispensed (Mock and Forbes 1992). Victory is defined as achieving

ones own optimum while intermediate levels of investment are referred to as pro-

rata compromises (Parker 1985; Godfray 1995b; Mock and Parker 1997).

Models used to predict resolutions to conflict (Parker and Macnair 1978; Parker

1985; Zahavi in Dawkins 1986; Eshel and Feldman 1991; Yamamura and

Higashi 1992) tend to be as complex as the models which define the

battleground and consistent predictions are few. The later characteristic arises

because most resolution models start with different assumptions or exploit

alternate mathematical approaches to understanding evolutionary change

(Godfray 1995b).

Though variable, most of the resolution models involve some form of

manipulative communication by offspring. Hypothesized forms include

psychological means such as withheld appreciation or exaggeration of

solicitation signals (Trivers 1974), blackmail strategies such as signalling to

attract predators (Zahavi in Dawkins 1986; Eshel and Feldman 1991) and a

combination of the two in which signals are escalated to manipulate parents into

providing additional care while simultaneously driving up costs such that parents

are selected to respond (Parker and Macnair 1978, 1979; Macnair and Parker

1978, 1979) to limit further expensive increases. Recently, however, Godfray

(1991, 1995a) has applied advances in honest signalling theory (Grafen 1990) to

offspring-parent communication and has shown that honest, rather than

manipulative (conflicting) signals can also be evolutionarily stable (i.e. an

evolutionary stable strategy [ESS]). Honest signals reflect the true state of a

character in question (Guilford and Dawkins 1991); thus the communication

system modeled by Godfray (1991, 1995a) is distinct from all previous attempts

to understand solicitation by offspring.

Trivers (and analogous models that also depend on conflict manifesting

itself as manipulation) and Godfray both present resolutions to the predicted

conflicts between parent and young but only manipulative solutions demand that

offspring attempt to acquire excessive care as suggested by POC theory (Trivers

1974). Offspring which honestly signal their needs accept levels of care that correspond to their parents optimum (Godfray 1991, 1995a). Thus, Godfray's models provide, for the first time, an alternate frame work for constructing testable hypotheses regarding offspring solicitation. Without such a frame work an explicit understanding of the optimal investment levels for parent and young is needed to test predictions about POC (Stamps *et al.* 1985). Although such measures would make definitive statements about POC possible they are rarely (if ever) attainable (Walsberg 1983; Mock and Forbes 1992; Ydenberg 1994, but see Evans *et al.* 1995).

Given that definitive measures of either parties optima are virtually impossible to obtain, it is necessary to consider predictions which extend beyond achieved investment levels at any single instant in time. Manipulative and honest signals are often contrasted in signalling literature (Dawkins and Krebs 1978; Krebs and Dawkins 1984; Guilford and Dawkins 1995) and their distinctions hold the key to constructing testable predictions regarding parent and offspring behaviour.

In this study I attempt to understand the extent of conflict between parent and young by examining behavioural changes through time. Within this context it is not necessary to predict investment levels at any specific instant. However, it is necessary to understand how predictions derived from both theories (conflict and honesty) are expected to change through time. To establish a consistent framework for making behavioural predictions using conflict and honest

signalling models I assume that the benefit to cost ratio (B/C) of providing care declines through time (Trivers 1974).

Trivers' model of POC predicts that the degree to which conflict is manifest at any point in time depends on the magnitude of lost reproductive success (in the case of parents) or reduced inclusive fitness (in the case of offspring) which is associated with failing to achieve ones own optimum. Conflict, therefore, depends on the distance between the benefit and cost curves of Trivers' model (Fig. 1a). As the benefit and cost curves approach one another conflict increases, and as the curves become increasingly distant, conflict declines. Given a declining B/C, either due to decreasing benefits or increasing costs (Fig. 1b) conflict is predicted to increase through time (conflict would decrease if benefits increased or costs declined — i.e. if B/C increased). Trivers' (1974) model predicts that increased conflict will result in increased signalling effort by offspring and increased resistance to providing further care on the part of parents.

Godfray's models are game theoretic and therefore search for ESS's rather than simple optima (Parker 1984). At the ESS the incremental benefits and costs of solicitation are equal (Clutton-Brock and Godfray 1991). Thus arbitrary increases to one component lead to similar increases in the other. More complex changes can arise when offspring costs are partitioned into direct (self) and indirect (kin — parent) components. For fixed benefits, increases in parental reproductive costs are predicted to lead to declines in offspring solicitation (Godfray 1995a). Alternately, if parental costs are fixed, a direct

Figure 1. The benefits (B) and costs (C) of parental acts with (a) low costs and
(b) high costs. The difference between parental reproductive success (RS) at P
and O is smaller for (a) than it is for (b). The same is true for offspring (young)
inclusive fitness (IF). Correspondingly, conflict is predicted to be less intense in
(a). For (a) and (b) benefits (B) are indicated by the dashed line. Costs to
parent (C) and offspring (0.5C) are indicated by solid lines (after Trivers 1974).

a

parent's
RS at O

parent's
max RS

young's
IF at P

young's
max IF

B

C

0.5 C

P   O

Benefit or Cost

b

C

parent's
RS at O

parent's
max RS

young's
max IF

young's
IF at P

B

0.5 C

P   O
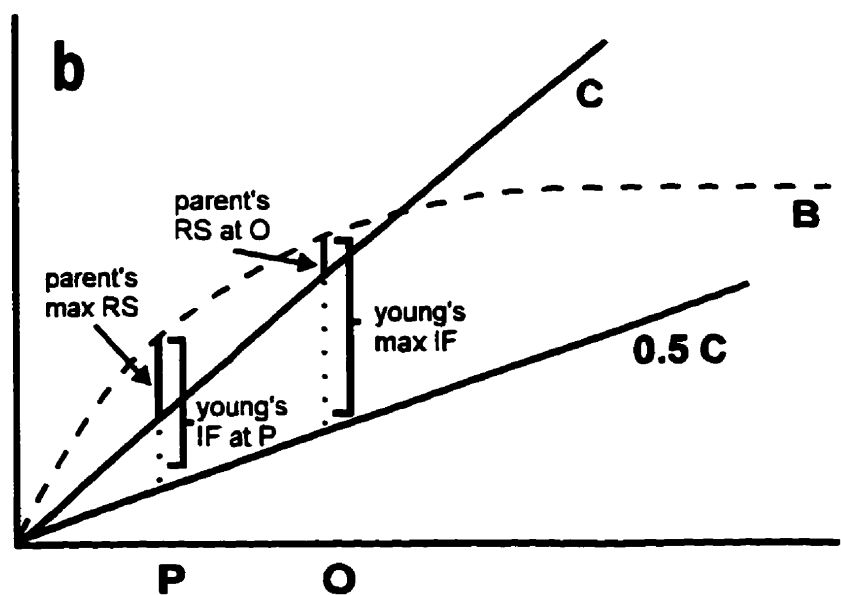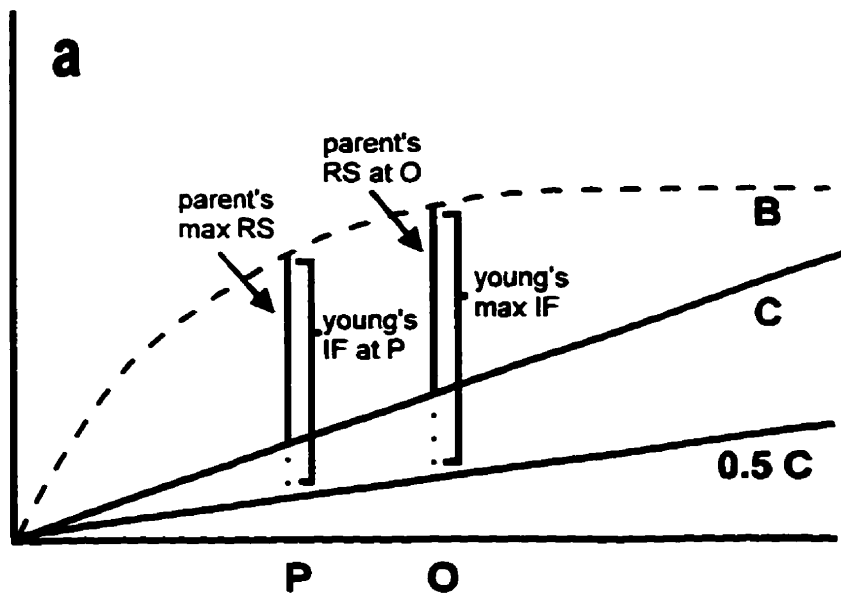
Parental Investment

relationship between solicitation costs and benefits is expected. Thus, reduced

benefits lead to reduced solicitation (Godfray 1991, 1995a). Again, opposite

predictions arise when parameters are varied in the opposite direction (e.g. fixed

benefits and decreased parental costs predicts increased offspring solicitation).

Unlike offspring behaviours, parental behaviour is not directly predicted by the

mathematical relationships of Godfray's models. Rather, within the context of

honest signalling systems parents are predicted to respond proportionally to

offspring solicitation. Thus when decreased solicitation by young is anticipated,

reduced care is predicted, and vice versa.

I applied the above logic, for each model, over a portion of the period of

parental care in American white pelicans to determine what kinds of changes

might be expected as offspring develop and approach independence. The

resulting predictions were then tested to determine whether offspring honestly

signal their needs, or conflict with their parents by attempting to manipulate them

into providing detrimentally high (for the parent) levels of care.

The American white pelican is an ideal species for testing the predictions

of Trivers (1974) and Godfray (1991) and for potentially distinguishing between

the two models. Immediately upon hatching the offspring give two distinct

solicitation calls; one, a squawk, which solicits thermal adjustment (brooding

changes which may lead to heat acquisition or dissipation), the other, a beg,

which solicits food (Evans 1992). Parents respond to these calls in such a way

as to address the homeostatic needs of their young (Evans 1988, 1992).

Further, the limited predation which occurs in this species is not related to the solicitation effort of chicks (Evans and Knopf 1993). Thus the direct costs incurred by signalling offspring are likely energetic.

As the period of parental care proceeds, one can anticipate that changes in the costs and benefits will differ for the two types of care. White pelican chicks are altricial and at hatch are unable to maintain a stable body temperature without parental brooding (Evans and Knopf 1993). However, chicks grow rapidly and are functionally endothermic by 15-18 d of age (Evans 1984a). Thus offspring should be able to provide at least part of the heat they require and it can be assumed that their overall need of parental brooding will correspondingly decline. As benefits are directly proportional to amelioration of needs (Trivers 1974; Godfray 1991) it can be assumed that the benefits associated with brooding will decline as chicks become functionally endothermic. Costs associated with providing the heat that chicks require are likely to remain relatively more constant (compared to changes in benefits) during this time. Most studies dealing with the energetics of providing care to offspring tend to only consider the costs of food provisioning once chicks have hatched (Utter and LeFebvre 1973; Hails and Bryant 1979; Bryant 1988). However, results of those studies which consider incubation indicate that energy costs of providing heat are low (Walsberg 1983 for review). It seems likely then that declines in the cost of brooding, if they occur, will be very small, with overall parental energetic

expenses remaining approximately constant. Thus the B/C of providing heat is expected to decline during the study period.

Changes in costs and benefits of providing food are expected to be very different than those of providing additional heat. Young pelicans cannot acquire food for themselves until nearly the end of the parental care period when they depart the natal colony (approx. 90 d). Nestling offspring cannot supplement their own food supply, nor alter their requirements for optimal growth (needs) or, therefore, the benefits of receiving such care (Trivers 1974). Thus it is likely that the benefits of feeding young chicks are relatively constant. The cost of providing food, in contrast, seems likely to increase as chicks develop (Trivers 1974). The food requirements of a young pelican increases dramatically as chicks grow (food demands: 227g at 10 d, 908g at 30 d up to 1,816g by 55 d; Hall 1925) and the costs to parents can be expected to increase in concert with these demands. Again then the B/C is expected to decline.

In light of the relationships between costs and benefits for Trivers' and Godfray's models and the specific aspects of white pelican biology outlined above, the following specific predictions emerged (Table 1), and were tested. Predictions regarding parent and offspring behaviour independently, and then total offspring effort to acquire resources (a measure which is directly proportional to the combined behaviours of parent and young) were developed. Because the B/C of both resources is expected to decline through time the predictions for both resources within each model are similar. However, for clarity, I will review all predictions below.

Table 1: Predicted changes in solicitation and care providing behaviours of offspring and parent American white pelicans. Predictions are derived from Trivers' (1974) conflict and Godfray's (1991, 1995a) honest signalling models combined with white pelican biology. The B/C of providing heat and food decline with time.

Changes in			Predicted Behavioural Changes Though Time	
Resource	B and C	Behaviour	Conflict	Honest Signalling
Heat	Benefits Decline Costs Constant	Offspring	increasing solicitation	decreasing solicitation
		Parent	increasing resistance	stable resistance
		Offspring Effort	increasing effort	decreasing effort
Food	Benefits Constant Costs Increase	Offspring	increasing solicitation	decreasing solicitation
		Parent	increasing resistance	decreasing resistance
		Offspring Effort	increasing effort	decreasing effort

Under Trivers' conflict resolution the declining benefit of continued brooding combined with relatively stable costs of providing such care leads to the prediction of increased conflict over heat provisioning. Hence older chicks are predicted to solicit more for heat while parents are predicted to become less willing to provide further care. The total effort to obtain a parental response is therefore expected to increase with chick age as offspring are increasing solicitation while parents are reducing care. Similarly, increasing costs and fixed benefits of providing food to older chicks will also lead to greater levels of conflict. I therefore predict that, under Trivers' manipulation resolution, offspring solicitation for food will also increase as chicks grow older and that parents will become less responsive to requests for additional food. In these fully-dependent, developing young, offspring effort per parental response is expected to increase.

Alternately, under Godfray's honest signalling resolution model, the declining marginal benefits of continued brooding require a decline in total (direct and indirect) costs at the ESS. As parental costs of providing heat appear relatively stable, reductions in overall solicitation for additional brooding are predicted. In the absence of other constraints on parental care, the responsiveness of parents to honest offspring solicitation is expected to remain stable as chicks develop. The level of brooding care by parents is therefore expected to decline in proportion to reductions in offspring solicitation. In an analogous way the increasing parental costs and fixed benefits of providing full

food care also select for lower offspring solicitation for this resource at the ESS.

As for heat, offspring solicitation for food is predicted to be lower in older chicks.

Parents are again expected to respond proportionally to honest offspring

solicitation, but the total amount of care provided is assumed not to decrease,

given the continuing need for full care in these dependent young. It follows that

parents are predicted to become more responsive to signals of food need in

older chicks, and chick effort per parental response will decline.

It is critical to note that Godfray's model predicts different age trends in

parental care for the two resources for different reasons. Reduced care is

predicted for heat in response to decreasing offspring needs and demands,

while food delivery within the constrained honest signalling system is predicted

to be maintained despite reduced solicitation as a result of an increase in

parental responsiveness.

Methods

The behaviours of adult and young American white pelicans were studied at a breeding colony located on a small island in East Shoal Lake Manitoba (see O'Malley and Evans 1980 for description of study site). Observations were completed between May 23 and June 17 of 1994. Average ambient temperature ranged from 19 °C to 33 °C during the study (Appendix). Hatch date was approximated through observation of courtship flights (Evans and Cash 1985) thus minimizing the need to visit the colony prior to initiation of this study.

A plywood blind with an elevated viewing platform (approx. 1.3m above ground) was erected on the shoreline of the island near one sub-colony where eggs were on the threshold of hatching. The blind provided an excellent view of active nests.

Nest Selection

To ensure equality of age for all study hatchlings the colony was visited in the evening (after 4:00 PM) to identify potential study nests. Nests which had at least one egg in the late-pip stage and were clearly visible from the blind were identified with individually marked wooden stakes. Where possible, nests with the modal clutch size of two eggs (Evans and Knopf 1993) were chosen. To complete the target sample size, two nests with single egg clutches were staked and ultimately incorporated into the study. Marked nests were surveyed the following morning at

approximately 6:30 AM to determine if young had hatched. Individuals were defined as 0 (zero) day (d) old chicks on their day of hatch.

Twelve experimental nests, used for tape recording chick vocalizations, were initiated over a period of twelve days. One experimental chick died at 4 d and was removed from analysis. The remaining eleven experimental nests were observed for the duration of the study. Of these, the data from an additional nest was removed from analysis as adults frequently removed study microphones and consequently recordings of chick vocalizations were rarely obtained. Experimental chicks were wing tagged when 4 d old to ensure proper identification as they grew increasingly mobile. Twenty-two control nests, used only for visual observation, were also established. Two of these nests were removed from the study as they suffered chick mortality which may have been directly attributed to my disturbance. Observations were made on the remaining 20 control nests. Of these, ten nests which had at least one surviving chick at 14 d were randomly selected for analysis.

The models of Trivers (1974) and Godfray (1991) were developed specifically for situations in which a single offspring is being reared. White pelicans are obligate brood reducers (Cash and Evans 1986) -- thus only one offspring per nest is expected to survive to the fledgling stage. At those experimental nests which initially had two eggs, the last-hatched (b-) egg was removed on the day the a-chick hatched and fostered to nests not used in the study. Brood reduction was permitted to occur naturally at control nests. Removal of the b-egg at experimental nests simplified assessment of parent-offspring interactions, while creating a context

appropriate for testing the predictions of Trivers (1974) and Godfray (1991).

Fostering also removed the potentially confounding influence of competitive

interactions between offspring in a single nest (Harper 1986, Smith and

Montgomerie 1991).

The vocalizations of young pelicans at experimental nests were recorded by

placing a miniature microphone (Realistic 33-1052) in the bottom of each

experimental nest. Microphones were covered with a layer of thin plastic and

parafilm. This permitted good sound transmission while ensuring protection from the

elements. The microphone lead was buried in the nest floor and led out under the

nest rim. The lead was then secured with a 20 cm. spike near the nest edge and led

on the surface of the ground to the blind. Adults returned to nests quickly following

the insertion of microphones and appeared to behave normally following my return

to the blind.

In the blind, microphone extensions were plugged into an 8-channel switch

box connected to one channel of a portable stereo cassette recorder (Realistic SCR-

51). This arrangement facilitated switching between experimental nests during vocal

recording sessions. An additional microphone within the blind, used for recording

behavioural observations, was fed directly to the second channel of the recorder. It

was therefore possible to record chick vocalizations while simultaneously describing

the behaviours of parent and young. All recording sessions were monitored using a

pair of portable head phones connected to the recorder.

On any given day, vocal recordings were collected at a maximum of six nests (see sampling details below). Two groups of experimental nests (maximum 6 nests per group) were identified as hatching proceeded. Vocalizations of all experimental chicks were collected starting on the day of hatch (0 d chicks) and continued every second day until chicks were 14 d old. Thus vocalizations were collected for experimental nests at eight different age classes. Beyond 14 d of age chicks become highly mobile (Evans and Knopf 1993) and collecting unambiguous vocal recordings at the nest is no longer possible (pers. obs.).

Daily Sampling Procedure

Behavioural Sampling

On days when new nests were being selected I exited the colony and returned to my blind by 7:15 AM. Once nests were established I arrived on the island no later than 7:30 AM and directly entered the blind. These times permitted nest stage assessment and selection of experimental and control nests while still providing enough time for disturbed adults to calm down before I initiated behavioural observations.

Sampling began at 8:00 AM and continued until 4:00 PM each day. Each 8 h sampling day was divided into four 2 h blocks. Each block was further divided into six 20 min sampling periods. Finally each sample period was divided into a 5 min scanning and a 15 min focal component (Fig. 2). Each experimental nest was

Figure 2. Daily sampling procedure. The sampling day was broken into four, 2 h blocks. Each block was divided into six 20 min sampling periods. Each period was then divided into 5 min scanning and 15 min sampling components. See text for sampling details within each sampling component.

8:00

10:00

12:00

2:00

4:00

Block

20 min

Sample
Period

Scanning   5 min

Focal
Nest   15 min

24
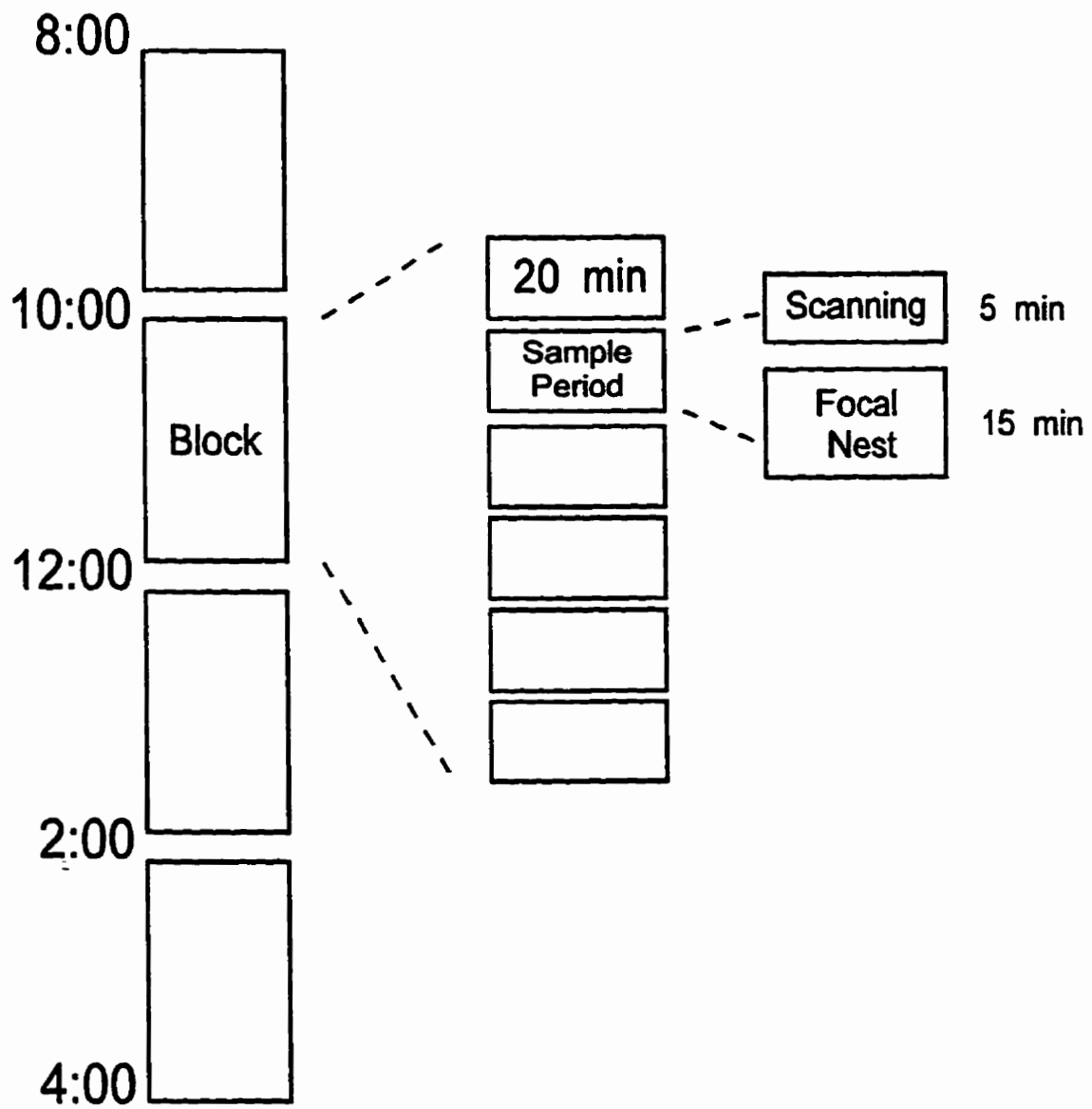
randomly assigned to one of the six sample periods for each of the four main blocks. Thus experimental nests were treated as focal nests four times on each sampling day.

During the 5 min scanning component of each sample period all experimental and control nests of all ages were scanned and observations of ongoing behaviours were dictated onto the continuously running tape recorder. Where possible, the gender of the attending adult at each nest was determined. This identification was usually made by comparing the relative bill length (males longer, Evans and Knopf 1993) of adults during nest reliefs when both adults were at the nest.

During the 15 min focal component the randomly chosen focal nest was continuously observed. All vocalizations of the offspring were recorded, and all visible chick behaviours and parental responses to solicitation were simultaneously dictated onto the recorder. Observations at focal nests were occasionally continued beyond the 15-min sampling component to permit ongoing behavioural sequences which extended beyond the planned sampling period to be observed to completion.

Parental activities were divided into behaviours associated with brooding and feeding. Brooding and associated behaviours were categorized as follows: (1) brooding -- nest contents well covered; (2) shuffle -- nest contents remain covered as in brooding but parent visibly shifts back and forth; (3) raised -- legs and foot-webs visible, (see Evans 1992) and (4) standing. Three feeding behaviours were identified: (1) feeding posture -- head held high and turned back, bill tip down towards foot web or chick; (2) feeding attempt -- as in feeding posture but head

shaking and/or head lowered, sometimes with bill nearly parallel to the ground; and (3) feeding -- food visible on the ground, on foot webs, or in the adults gular pouch. Whether offspring were covered (not visible due to parental brooding) or exposed (at least partially visible) at the beginning and end of a solicitation bout was also recorded. Additional parental activities such as preening of self and offspring, adjusting chick position with bill (bill chick), nest cup adjustments, and interactions with neighbours were also noted.

When feedings were observed, it was noted whether food was received on the ground, on the foot web, or within the parents gular pouch. Food transfer was noted when seen. However, as young pelicans are able to feed from within the parents gular pouch within a few days (Evans and Knopf 1993) food transfer often cannot be seen, especially with older chicks. The occurrence of hidden feeding and extent of all feedings was estimated by the presence of food on the chicks bill and distension of the chicks throat following parental regurgitation attempts.

Chick Mass and Development

Growth and development will influence the strategic aspects of solicitation by an offspring. Heat and food requirements are likely to be influenced by both the size of a chick and its external insulation (Ricklefs 1968). Thus, the mass of experimental chicks was obtained (in g, $\pm$ 2% for 0 - 10 d, $\pm$ 2.5% for 12 and 14 d) on the morning of hatch and at the end of all focal sampling days using Pesola spring scales. Plumage development was estimated at the end of each focal

sampling day by measuring length of down feathers (nearest mm) at a standardized spot on the right flank of each experimental chick.

Analysis of Recordings

Comparison of Experimental and Control Broods

Colony scan data were used to determine differences in feeding behaviour frequency between control nests and experimental focal nests. I tallied the number of feeding postures, feeding attempts and actual feedings observed for each group (experimental and control) for all of the scan periods at each age. Thus a maximum of 240 feeding related behaviours per age could be observed per group (24 scans per nest per day, 10 nests per group) if all nests were feeding during every scan.

Prior to the initiation of daily sampling all control nests were surveyed from the blind to determine progress of hatching of b-chicks and brood reduction. The b-chicks at control nests were defined as 0 d old on the first day they were observed during these early morning surveys. Brood reduction was said to have occurred on the first day that only a single chick was observed in a control nest by 8:00 AM. I could not be certain which chick was eliminated, as control chicks were not individually marked.

Focal Observations

Analysis of focal nest observations was facilitated by transcribing observations in real time to an event recorder (Esterline Angus). Parent and offspring behaviours were hand written directly on the recorder paper; heat and food

calls were keyed with a contact switch onto separate channels of the recorder. Total play-back time for each focal period was measured with a stop watch and noted on the recorder chart.

A heat calling bout was defined as any group of squawk calls which was preceded and followed by at least 10 s of silence. Food calling bouts were defined as any group of food begs which was preceded and followed by 20 s of silence. Ten and 20 s of silence were selected respectively as these intervals were found to be approximately 10 times the interval between successive calls of each type when offspring are calling strongly. Mixed bouts (bouts in which squawks and begs were given without significant silent periods separating them) occurred occasionally (<3%). Such bouts were usually dominated by one call type with single calls of the other kind occurring irregularly. In such cases bouts were identified by the call type which predominated (minimum proportion of dominant call 85%). Older chicks (12-14 d) occasionally (about 10% of bouts in 12 and 14 d chicks, none at earlier ages) mixed numerous calls of each type. In these cases calls of each type were identified as solicitation bouts for their respective resources. For both heat and food solicitation single calls which were preceded or followed by the appropriate silent periods were considered bouts of 1 call. As not all focal sampling periods were of identical length (range 15 to 21 min), bouts were standardized to the number observed per 15 min and then combined to a one hour measure.

Defining and Quantifying Offspring Solicitation

Four parameters of call bout structure were considered for both call types; (1) the number of calling bouts per hour (hereafter referred to as bout frequency), (2) the number of calls per bout, (3) the duration of calling bouts and (4) the calling rate (calls / s within calling bouts exclusive of bouts of one call). Due to the relative rarity of food solicitation, the four sampling periods for each day were pooled for each call type and averages for one hour of observation for each parameter were calculated.

Defining and Quantifying Parental Response

Parental responses to offspring solicitation were considered on two levels: responsiveness and complete responses. Parental responsiveness was defined as any brooding response in the case of heat solicitation and any feeding behaviour in the case of food solicitation. Responsiveness was standardized by dividing the number of responses by the total number of bouts given for each resource. The second level, complete response, was defined as a change in coverage (exposing a covered chick or covering an exposed chick) for heat solicitation, and a feeding in the case of food solicitation. As responsiveness and complete responses are not mutually exclusive, all parents which completely responded were also included in the responsiveness data.

Evans (1992) found that parents responded differentially to bouts of various lengths. To examine this possibility I further classified all bouts for each resource as either short or long depending on whether they exceeded the overall median

number of calls per bout. Bouts exceeding 3 calls and 8.5 calls for heat and food respectively were defined as long bouts.

The latency to the first response (when responses were given) for heat and food solicitation and for long and short bouts was defined as the time (s) from the first offspring vocalization to the first behavioural change by the parent. Response latency for complete responses to heat or food solicitation were defined, respectively, as the amount of time (s) from the first call to the first change in cover or feeding. For both the occurrence of parental responses and response latencies only those postural changes which occurred within the bout itself, or within 10 s of the last call in the case of heat bouts, and 20 s of the last call in the case of food soliciting bouts were included. This protocol ensured that parental responses to bouts were considered on time scales equivalent to those used to define the bouts themselves.

Estimating Offspring Effort

Offspring effort per parental response (s) was estimated as the inverse of the proportion of bouts to which parents responded, multiplied by the mean bout duration. Estimates of effort were made for both parental responsiveness and complete responses for both resources. Long and short bouts were pooled for these measures.

Statistical Analysis

I performed profile analysis (von Ende, 1993) to test statistically for differences between long and short bouts and for changes through time. A separate analysis for each behaviour of chick and adult was completed. Profile analysis is analogous to analysis of variance (ANOVA) on repeated measures data. I first calculated a least-squares regression line for each nest across all ages. The slope and intercept of each fitted line provided independent data points for each nest. These were then used to test for differences between the two resources for each parameter by two-sample t-tests. Single sample t-tests were used to determine whether slopes differed significantly from zero. Additional comparisons were done to assess differences and trends between short and long bouts within each resource and response level. All statistical tests were conducted at $\alpha = 0.05$, using Statistix analytical software.

Results

Chick Mass and Development

Young pelican chicks grow quickly during the first two weeks post-hatch. Chick mass increased exponentially from a mean of 110 g at hatch (experimentals, n = 10) to nearly 2000 g, on average, at 14 d (Fig. 3). Plumage emerged by the sixth day in all cases. Plumage growth was rapid with more than one cm of down present on most 14 d chicks (Fig. 3).

Comparison of Experimental and Control Broods

Feeding related behaviours were rare for both experimental and control groups with the lowest frequency occurring on the day of hatch. Experimental nests showed a dramatic increase to relatively stable feeding levels by 2 d. Control nests on the other hand were rarely observed to feed through 2 d, when some b-eggs were still unhatched. Feeding behaviours at these nests increased in frequency to levels similar to experimental nests by the time a-chicks reached 4 d old. Control feedings were then much like at experimental nests and were unaffected by ensuing brood reduction (Fig. 4).

Figure 3. Changes in mass and development of plumage in 10 young pelican chicks (mean ± s.e.).

Chick Mass

Flank Plumage
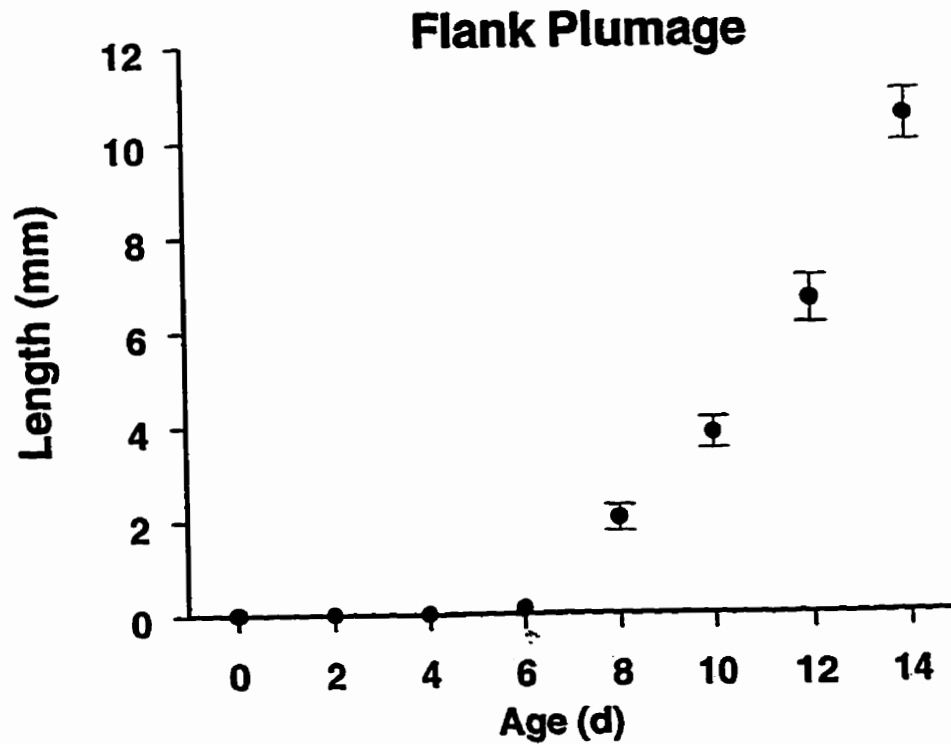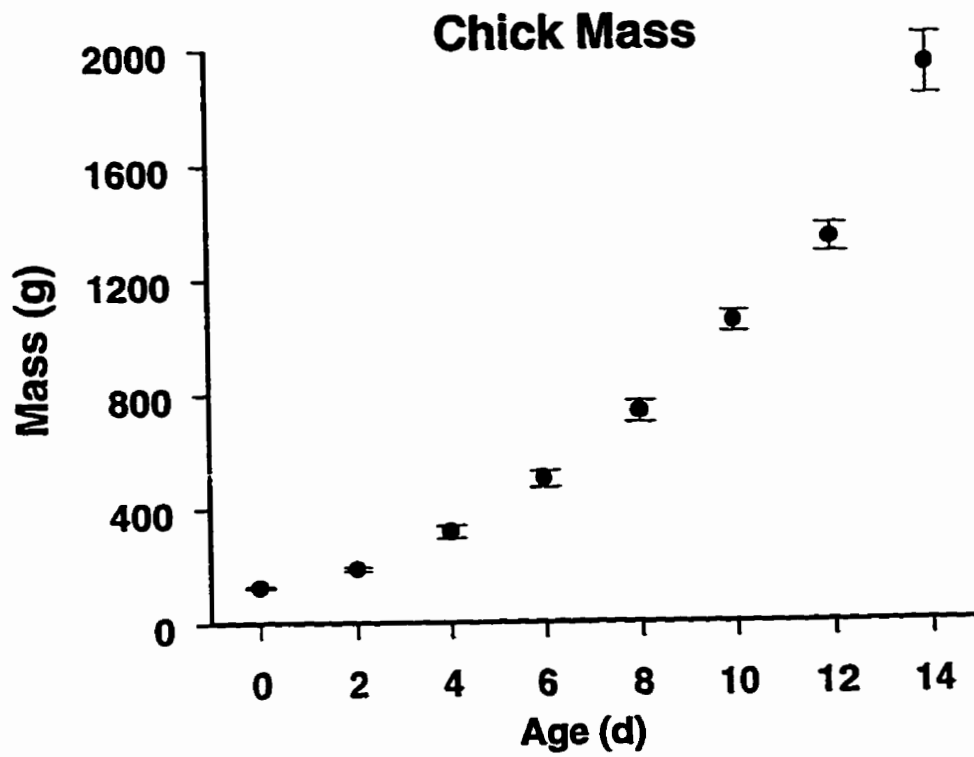
Figure 4. Frequency of feeding related behaviours (experimental, open bars; control, solid bars) and mean number of offspring per control nest (solid line. Experimental nests had one chick in the nest at all ages). Frequencies are the number of nest scans (from a total of 240 per age) in which feeding related behaviours occurred at least once. At control nests all ten b-eggs were present at 0 d, six eggs were present at 2 d and all had hatched by 4 d. Brood reduction at control nests was first detect at 4 d. One control nest still had two chicks at the end of the study.
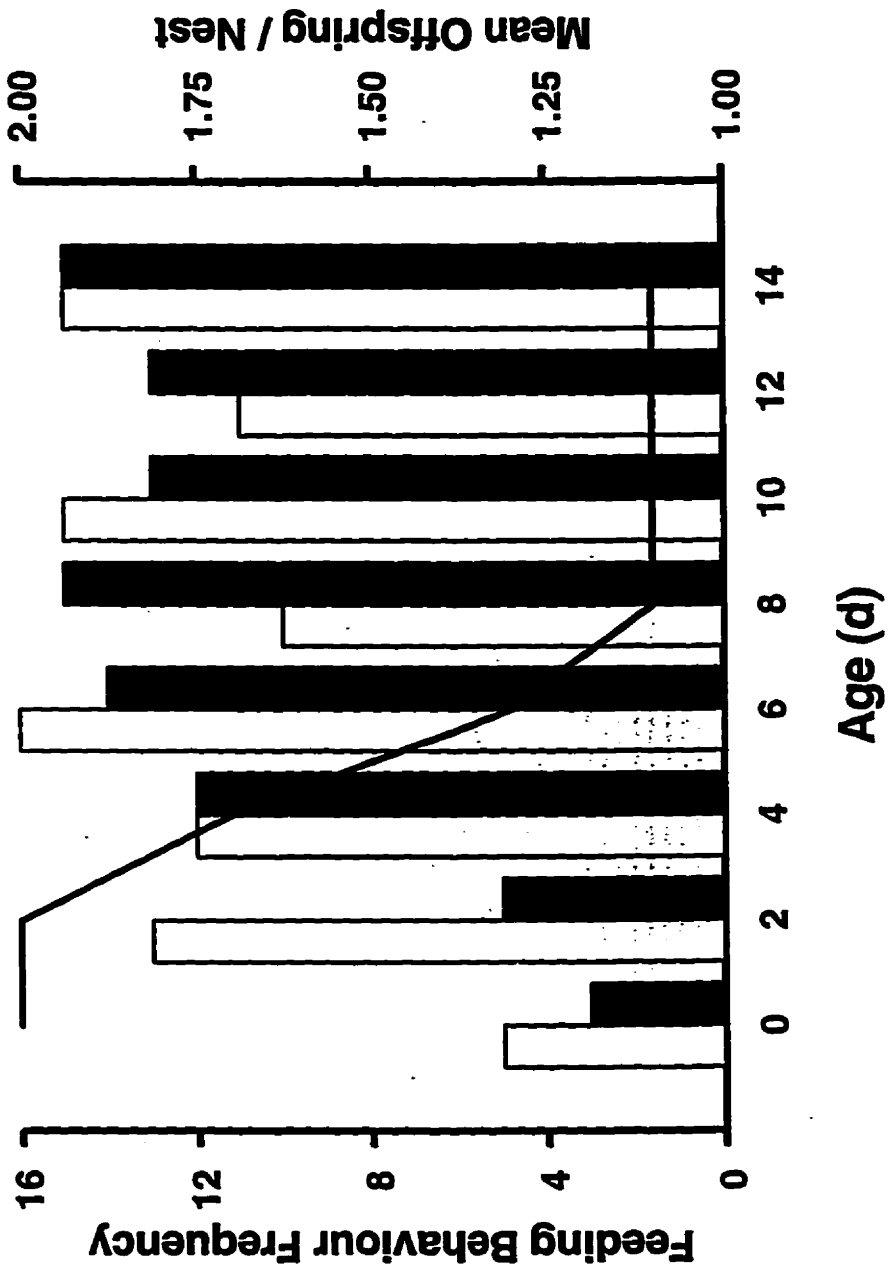
Solicitation of Heat and Food

The number of solicitation bouts for each resource increased significantly over the ages studied (Fig. 5A, Table 2). The changes were not equal across resources (comparison of slopes, t_9=2.59, p = 0.03) with increases in heat solicitation exceeding those of food solicitation (Fig. 5A). The increases in food solicitation appear nearly step wise with an increase (nearly a doubling) between 4 and 6 d preceded and followed by relatively more gradual changes. Increased frequency of heat bout solicitation was more or less gradual throughout. Within bout call rates for both resources, on the other hand, increased similarly as chicks developed (comparison of slopes, t_9=0.84, p = 0.4; Fig. 5B). Both upward trends in call rate were statistically significant (Table 2).

Heat bout durations (s) were approximately stable through time (Fig. 5C). Small fluctuations around 10 s in duration were observed, but were not significant (Table 2). The duration (s) of food bouts, in contrast, decreased significantly as chicks grew older (Table 2). Food solicitation bouts of recently hatched chicks were on average 88 s in duration decreasing to 42 s by two weeks. Changes with age in the number of calls per solicitation bout (Fig. 5D) were similar to changes in duration measured by time. As above, the number of calls per heat bout remained approximately stable while the calls per food bout declined significantly (Table 2). For both measures of duration the declines in food solicitation were not smooth but rather erratic with shortest average durations observed for 6 and 8 d chicks.

Figure 5. Solicitation of resources by young pelicans. Mean values ($\pm$ s. e.) for heat ($\bullet$) and food ($\circ$) solicitation plotted in all cases. Bout Frequency: The mean number of heat and food solicitation bouts per hour given by chicks during their first two weeks of age ($n=10$ for both resources at all ages). Call Rate: Mean within bout call rate for heat and food solicitation calls given by chicks during their first two weeks of age (heat; $n=10$ at all ages: food; $n=8$ for 0 - 2d, $n=9$ for 4-10d, $n=10$ for 12d and $n=7$ for 14d). Bout Duration: The mean ($\pm$ s.e.) duration of heat and food solicitation bouts as measured in time (seconds). Calls per Bout: The mean ($\pm$ s.e.) number of calls per bout of heat and food solicitation (sample sizes for bout duration and calls/bout are the same: heat; $n=10$ for all data points: food; $n=9$ for 0 - 10d, $n=10$ for 12 - 14d). Bout duration and calls per bout are not independent. Differences in bout duration are largely reflected in calls per bout, with longer bouts tending to have more calls.

A: Bout Frequency

B: Call Rate

C: Bout Duration

D: Calls / Bout
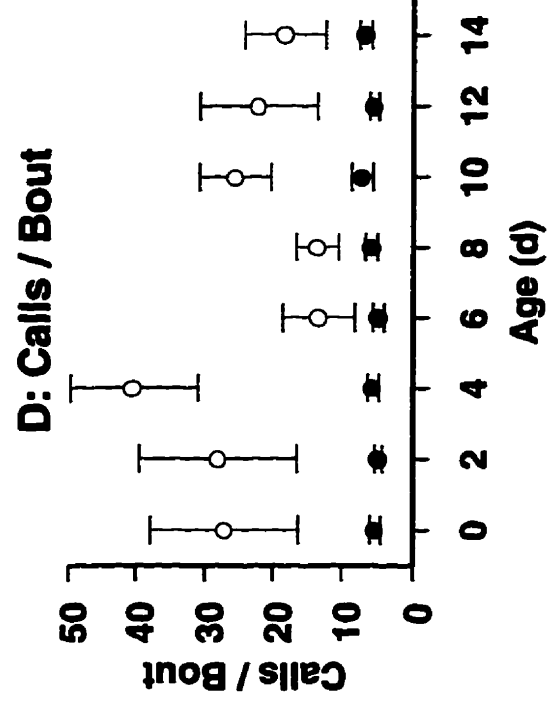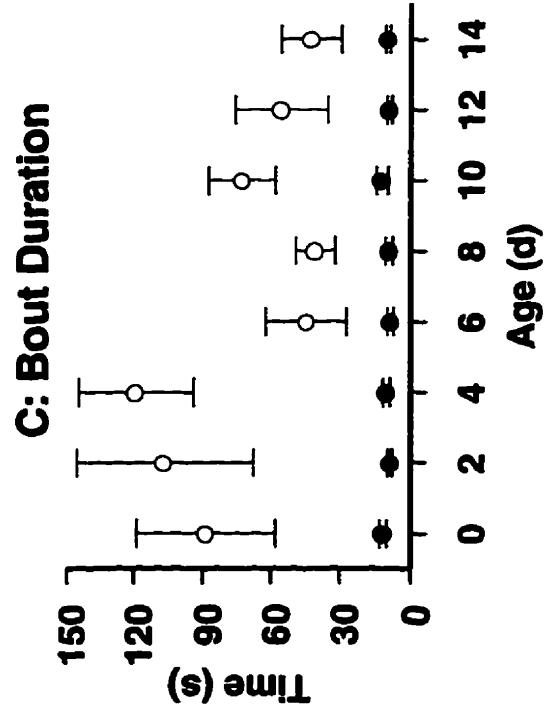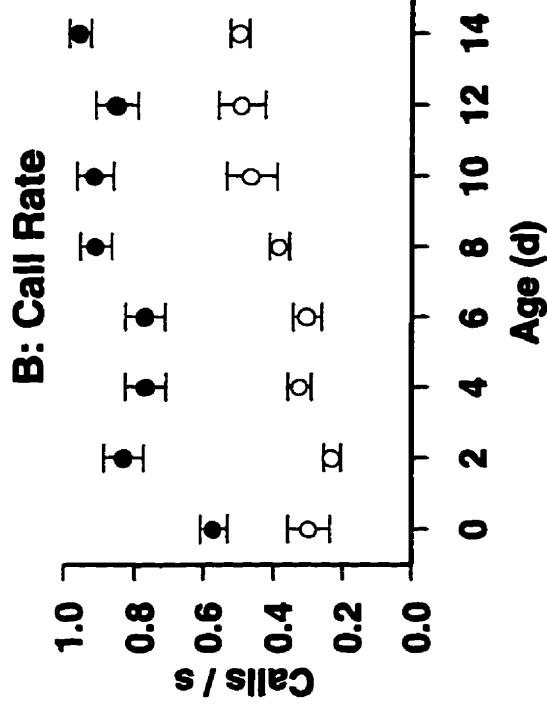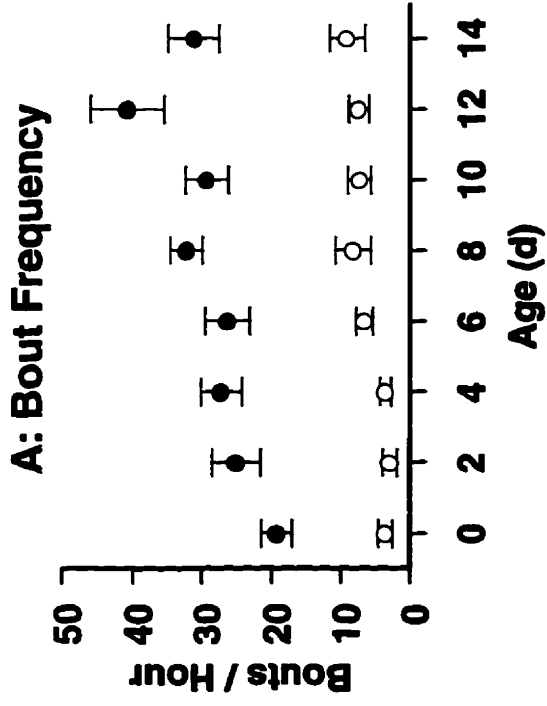
Table 2: Statistical summary of changes through time of care soliciting behaviour of American white pelican chicks during the first two weeks post-hatch.

Parameter	Heat		Food	
Bout Frequency	$t_9 = 3.02$	$p < 0.020$	$t_9 = 2.42$	$p < 0.040$
Call Rate	$t_9 = 7.11$	$p < 0.001$	$t_9 = 4.45$	$p < 0.002$
Bout Duration in:				
Seconds	$t_9 = 0.42$	$p = 0.685$	$t_9 = 3.92^*$	$p < 0.004$
Calls/Bout	$t_9 = 1.88$	$p = 0.093$	$t_9 = 2.36^*$	$p < 0.040$

*Indicates downward trend, all other significant trends are increasing.

Parental Response to Solicitation

Parents responded more frequently to long bouts than they did short bouts for both response levels and both resources (Table 3, Fig. 6). However, for both resources, short bouts were sufficient to initiate some responses. Short heat solicitation bouts were partially effective in eliciting changes in cover but short food solicitation bouts rarely led to feedings (compare Fig. 6B and 6D).

Parents became less responsive to all heat solicitation bouts as young approached 14 d (Table 4, Fig. 6A, B). Overall (short and long bouts combined) parents responded to between one third and one half of all heat solicitation bouts given by young (0 d and 2 d) chicks while such solicitation by older chicks (12 - 14 d) went nearly unheeded (Fig. 6A, B). Similar declines in the frequency of complete responses to heat solicitation were also observed. Changes in cover occurred in response to heat solicitation by young chicks but were usually absent by the time chicks reached 12 - 14 d.

Responsiveness to short and long food solicitation bouts increased, but not significantly (Table 3). Responsiveness to long bouts by 0 d chicks was low but increased to nearly three quarters of all long bouts by 4 d and remained at about that level for the duration of the study (Fig. 6C). Feedings in response to short bouts were rare with the only observations occurring in the second week of study. Feedings in response to long solicitation bouts increased between 0 and 2 d, then declined slightly (Fig. 6D). This decline was not significant over all ages combined (Table 4).

Table 3: Parental response to offspring solicitation. Comparisons of short versus long bouts are summarized within each response level for both resources. Long bouts were responded to more frequently than were short bouts in all cases (n = 10 for all tests).

| | **Response Level** | |
	Responsiveness	**Complete Response**
Heat	$t_9 = 2.96$, $p < 0.02$	$t_9 = 4.97$, $p < 0.001$
Food	$t_9 = 6.06$, $p < 0.001$	$t_9 = 4.45$, $p < 0.002$

Figure 6. The proportion of parental responses to short (•) and long (○) solicitation bouts (means ± s.e. plotted in all cases, dashed line set at 0.5 arbitrarily). Heat Responsiveness: Proportion of heat solicitation bouts to which parents responded with any brood response. Complete Heat Response: Proportion of heat solicitation bouts to which parents responded by exposing covered chicks or covering exposed chicks (n = 10 for all heat data points). Food responsiveness: Proportion of food solicitation bouts to which parents responded with feeding behaviours. Complete Food Response: Proportion of food solicitation bouts which resulted in chicks being fed (Food data points. Short bouts; n = 6 for 0, 4 d; n = 7 for 2 d; n = 9 for 6 - 14 d. Long bouts; n = 6 for 2, 8 d; n = 7 for 0, 6 d; n = 8 for 4, 10 d; n = 9 for 12 d).

A: Heat Responsiveness
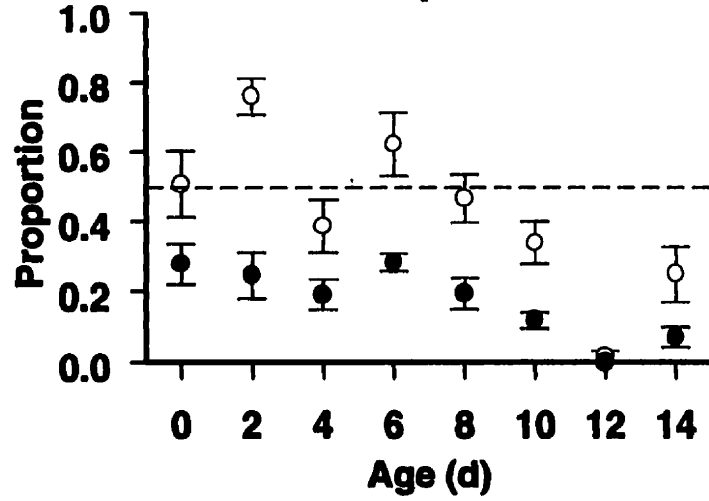
B: Complete Heat Response
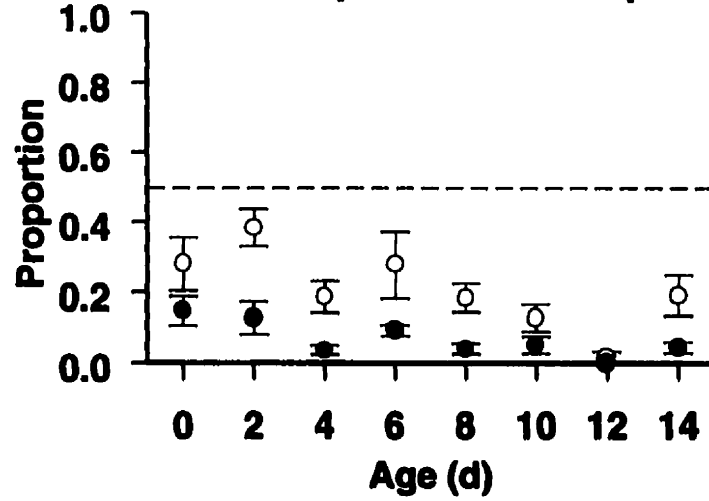
C: Food Responsiveness
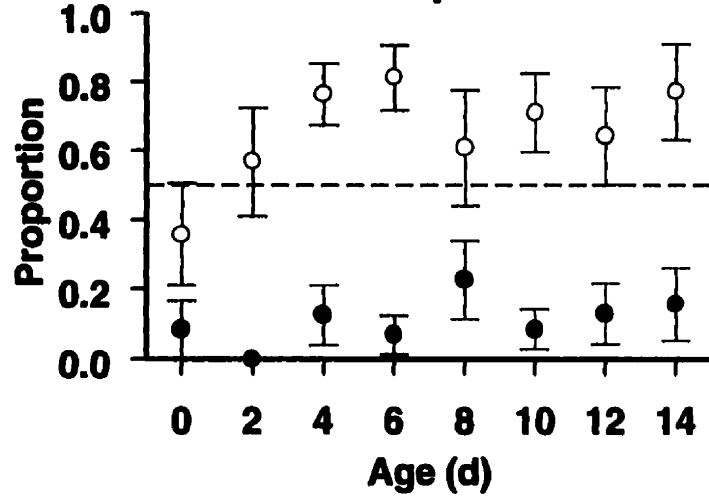
D: Complete Food Response

Table 4: Changes in parental response with increasing chick age. Overall changes for each resource, at each response level, were considered by combining short and long bouts (n = 10 for all tests).

	Response Level	
	Responsiveness	**Complete Response**
Heat Solicitation		
Short	$t_9 = 2.96$, $p < 0.02$	$t_9 = 3.26$, $p < 0.01$
Long	$t_9 = 9.12$, $p < 0.001$	$t_9 = 3.55$, $p < 0.01$
Combined	$t_9 = 4.56$, $p < 0.002$	$t_9 = 6.07$, $p < 0.001$
Food Solicitation		
Short	$t_9 = 1.42^*$, $p = 0.18$	$t_9 = 1.77^*$, $p = 0.11$
Long	$t_9 = 1.42^*$, $p = 0.18$	$t_9 = 0.30$, $p = 0.77$
Combined	$t_9 = 1.59^*$, $p = 0.15$	$t_9 = 0.81$, $p = 0.43$

* indicates upward trends, all others declining

Parental Response Latency

To test whether long bouts arise due to behaviours of offspring or parents I considered response latencies for short and long bouts. If parental reticence is primarily responsible for long bouts, then latencies for such bouts should be greater than for short bouts. But this relationship would not necessarily occur if long bouts arise because offspring attempt to obtain continued investment once parents begin to respond. In all testable cases parental latencies were significantly greater for longer bouts (Table 5, Fig. 7).

Parental response latencies to first and complete responses for heat solicitation tend to decline (Fig. 7A, B) though none of these individual trends were significant (Table 6). Similarly, the overall trends arising from combining short and long bouts for first and complete responses were also not significant (Table 6). Observed changes in parental response latency to food solicitation differed considerably from changes in latency to heat solicitation. Response latencies for short food solicitation bouts could not be statistically tested as such responses were rare. However, response latencies for long bouts were tested, and observed declines proved significant (Table 6) for first and complete responses (Fig. 7C, D). When the few latencies from short bouts were pooled with latencies from long bouts the resulting overall decline in latency remained significant for both levels of response (Table 6).

Table 5: Latency of parental response to offspring solicitation. Comparisons of latencies for short versus long bouts are summarized within each response level for both resources. In all cases short bouts had smaller parental response latencies than long bouts (n = 10 for all tests).

	Response Level	
	Responsiveness	Complete Response
Heat	$t_9 = 5.22$, p < 0.001	$t_9 = 5.96$, p < 0.001
Food	$t_9 = 3.85$, p < 0.005	N/A*

* Sample sizes for short bouts too small for meaningful statistical comparison.

Figure 7. Latencies of first and complete parental responses (when they occur) to short (●) and long (○) solicitation

bouts (means ± s.e. plotted in all cases, dashed line arbitrarily set at 15s for comparison). First Heat Response: Latency

from first squawk to first brooding response of parent. Complete Heat Response: Latency from first squawk to the first

complete change in cover of offspring (Sample sizes for heat responses. Short bouts; n ≥ 9 for 0 - 10d; n= 0 for 12d and

n= 6 for 14d; Long bouts; n ≥ 8 for all ages except 12d when n=1). First Food Response: Latency from first beg to first

feeding behaviour of parent. Complete Food Response: Latency from first beg to the delivery of food by parent. Note

that ordinate scales differ on the lower panes (all short bouts; n ≤ 3; long; n ≤ 5 for 0 and 2d in first and complete

responses and 8d in complete response, all others ≥ 6 [max. = 9]).

A: First Heat Response

B: Complete Heat Response

C: First Food Response

D: Complete Food Response

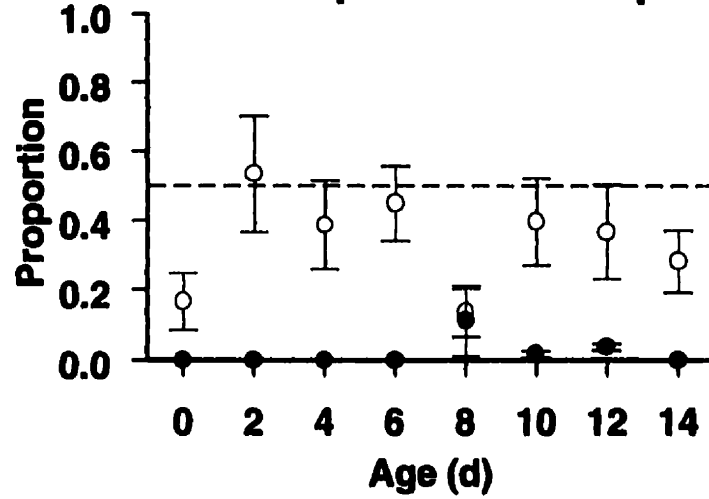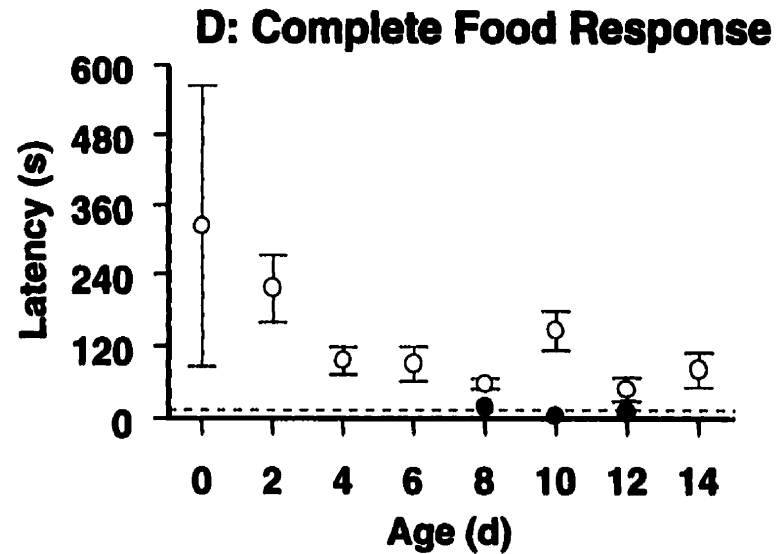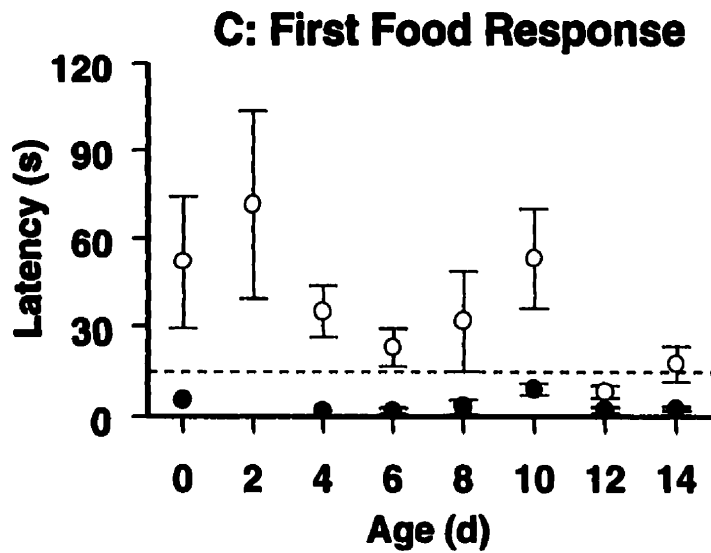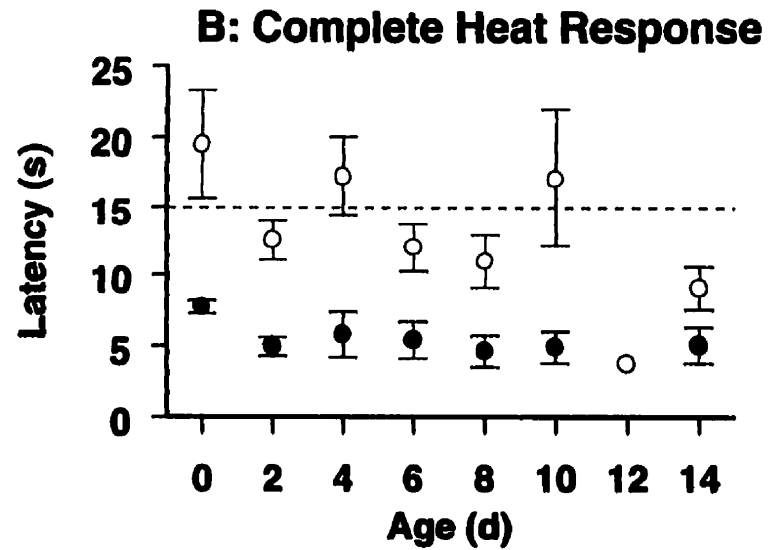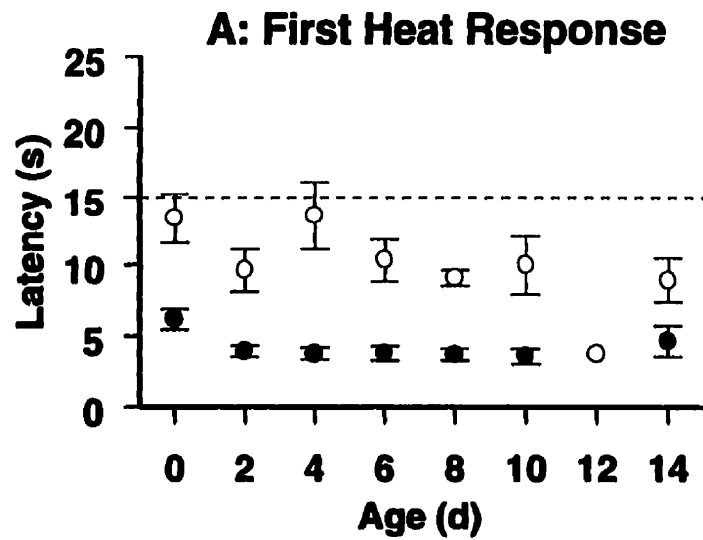Table 6: Changes in parental response latency (when parents respond) as chicks increase in age. Overall changes for each resource, at each response level, were considered by combining short and long bouts. All testable trends are declining (n = 10 for all tests).

	Response Type	
	Responsiveness	**Complete Response**
Heat Solicitation		
Short	$t_9 = 1.92$, $p = 0.09$	$t_9 = 0.69$, $p = 0.51$
Long	$t_9 = 1.56$, $p = 0.15$	$t_9 = 2.07$, $p = 0.07$
Combined	$t_9 = 1.19$, $p = 0.26$	$t_9 = 0.87$, $p = 0.41$
Food Solicitation		
Short	N/A*	N/A*
Long	$t_9 = 2.6$, $p < 0.03$	$t_9 = 3.29$, $p < 0.01$
Combined	$t_9 = 2.4$, $p < 0.04$	$t_9 = 3.08$, $p < 0.02$

* Sample sizes for short food bouts too small for individual statistical tests.

Offspring Effort

Less offspring effort was required to initiate changes in parental brooding than was required to induce feeding responses (t_9 = 5.51, p < 0.001). Initially these differences were substantial but by 14 d effort for each resource was nearly equivalent (Fig. 8). Similarly, less effort was required to obtain complete brooding responses than was required to obtain feedings (t_9 = 5.38, p < 0.001). Again differences were initially substantial but became less so at chicks approached 14 d.

Effort required to initiate changes in brooding increased approximately four-fold between 0 and 14 d, reaching nearly two minutes by the end of this study. Similar increases in effort required to induce complete brooding responses were also observed (Fig. 8). Both of these trends were statistically significant (Table 7). In contrast, effort required to induce a feeding response declined rapidly from nearly 10 minutes at 0 d down to approximately 2 minutes at 14 d. During the same time, the effort required to obtain feedings declined slightly from about 10 to 6 minutes. Only the former of these two trends was significant (Table 7, Fig. 8).

Figure 8. Offspring effort required to initiate responses and to acquire complete responses to heat (•) and food (o) solicitation (mean ± s.e. plotted). Effort = 1/ probability of response multiplied by mean bout duration. Sample sizes for first responses, heat: n = 10 for 0-10d; 1 for 12d and 9 for 14d, for food: n ≤ 5 for 0 and 2 d, n ≥ 6 for 4 to 14 days. Sample sizes for complete responses, heat: n = 10 for 0, 2, 6, 8d; 9 for 4, 10, 14 d and 1 for 12 d, food n ≤ 5 for 0, 2, 4, 8, 14 d; n = 7 for remainder.

First Response
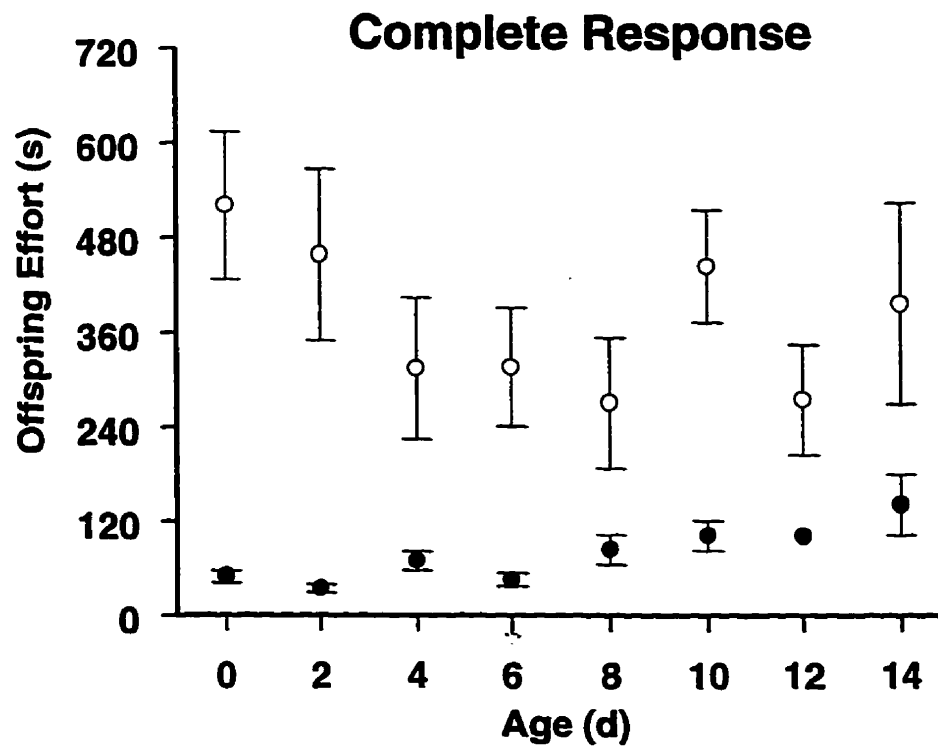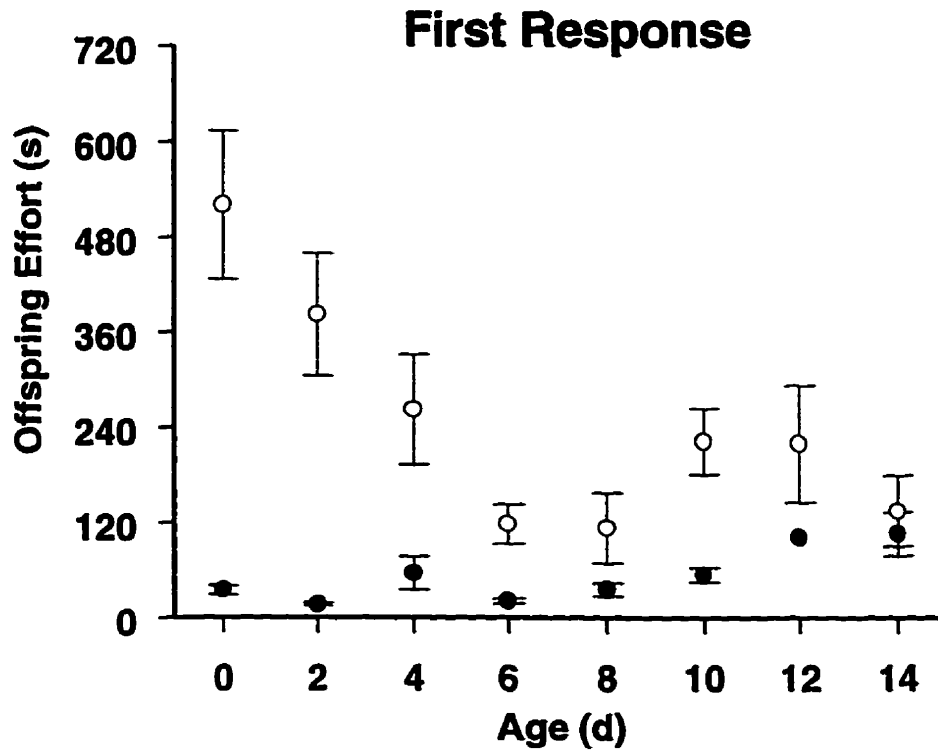
Complete Response

Table 7: Offspring effort per parental response. Statistical comparisons of changes through time of effort required to obtain first and complete responses for heat and food are summarized. Effort is defined as the inverse of parental responsiveness multiplied by the mean duration of solicitation bouts. Heat trends are increasing, food trends declining (n = 10 for all tests).

	Response Level	
	First Response	**Complete Response**
Heat	$t_9 = 3.24$, $p < 0.01$	$t_9 = 3.07$, $p < 0.02$
Food	$t_9 = 2.87$, $p < 0.02$	$t_9 = 0.32$, $p = 0.75$

Discussion

Comparison of Experimental and Control Broods

The similar frequency of feeding behaviours for experimental (a-chick only) and control (unmanipulated) nests (Fig. 4) between 4 and 14 d suggests that the treatment of early removal of the b-egg did not greatly alter the normal pattern of food provisioning. This treatment did have the effect of ensuring that all food was directed solely toward the single remaining chick. However, in natural nests, food is rarely delivered to the b-chick (Cash and Evans 1986; Evans and McMahon 1987) so any increase in food delivery to experimental chicks because of b-egg removal was probably small. Overall, the behavioural patterns observed at experimental nests appeared to be representative of those found at natural nests.

Of considerable interest is the difference in feeding behaviour at experimental and control nests which occurred when a-chicks were 2 d old (Fig. 4). At this age, feedings at experimental nests were rare, but considerably more frequent than they were at control nests. At least two possibilities explain this difference. First, food availability was limiting, and second, the presence of eggs in a nest reduced parental willingness to feed. It is unlikely that low feeding rates at control nests were due to food limitation as experimental nests were feeding more frequently on the same days. Also, the observed rate and pattern of brood reduction was similar to previous studies (Evans 1996), suggesting that

food availability or magnitude of hatching asynchrony were not exceptional during this study. Adults at several control nests were, however, incubating b-eggs at this time. Incubation duties may limit parental willingness or ability to feed first hatched young. If reduced feeding frequency during the modal 2 days prior to b-chick hatch is common across years then chick size asymmetries and competitive dynamics between sibs, which arise due to hatch asynchrony, will possibly be influenced. Low feeding rates prior to hatching of the b-chick could limit sibling size disparities or could act as a cue to older sibs to initiate aggression towards their younger counter-parts. Further work is needed to fully understand the significance of this newly described initial low feeding rate at natural nests.

Honesty or Conflict? Distinguishing between models

Offspring Solicitation

The relative stability of heat solicitation bout durations combined with the increases in bout frequency and call rate (Fig. 5) indicate that greater time and energy was spent by older chicks soliciting this resource. These patterns are all consistent with predictions of Trivers' (1974) conflict model of parent-offspring interactions and are contrary to predictions of Godfray's (1991) honest signalling model (see Table 1). Older chicks also solicited food more frequently and did so with greater within bout call rates (Fig. 5). These changes also favour a conflict resolution to the distribution of food. However, the significant declines in

duration of food bout solicitation were consistent with honest signalling

predictions (Godfray 1991) and counter to the predictions arising from Trivers'

conflict model. Thus, by themselves, heat solicitation results appear in

agreement with conflict resolutions whereas food solicitation results are

equivocal. Investigations which identify those aspects of solicitation to which

parents most strongly respond would increase our understanding of the changes

observed for food solicitation.

Parental Responses and Bout Duration

For both resources parents responded more frequently to long relative to

short solicitation bouts (Table 2). This effect of bout length is consistent with

successful manipulation as a form of conflict resolution (Trivers 1974) by

offspring. Escalated solicitation by young is known to lead to a parental

response in a range of species (zebra finches, Muller and Smith 1978; great tits,

Bengsston and Ryden 1983; robins, Whittingham and Robertson 1993).

Through their responses parents can terminate potentially expensive calling and

may therefore have been manipulated into providing the observed care levels.

However, increased responsiveness and greater frequency of complete care

associated with long bouts is also in agreement with honest signalling by young.

According to Godfray's (1991) model, offspring with greater need will signal at

greater levels and parents are predicted to respond proportionally. If increased

bout duration is in part reflective of greater offspring need, then greater parental

response to long bouts is expected.

Overall, parental response latency was closely related to solicitation bout

duration for both resources. Parental response latencies to heat solicitation did

not change significantly with chick age while heat solicitation bouts remained

approximately constant over the two weeks studied. In contrast, significant

declines in parental latency to food solicitation and in duration of food solicitation

bouts were observed. Together these relationships suggest a strong influence

of parental response latency on the duration of offspring solicitation.

Further evidence that parental response latency influences the duration of

offspring solicitation bouts comes from comparisons of latency to short and long

bouts. Bouts of greater duration appear to have arisen because parents were

unwilling to respond quickly to offspring requests (Table 5). Such delays could

have arisen if parents initially attempted to resist manipulative conflicting young

but eventually conceded (Trivers 1974) or if parents temporarily withheld care to

fully assess offspring signals (Godfray 1991). Differences in response to short

and long bouts thus provided little scope for distinguishing between conflict and

honest signalling models.

Parental Responses and Offspring Effort

Heat

The benefits of providing additional heat to offspring are expected to

decline with developing endothermic abilities of offspring. More intense conflict

over brooding in older chicks is therefore predicted by conflict models, with

reduced heat investment by parents (Trivers 1974). In the absence of other constraints, honesty models (Godfray 1991, 1995a), in contrast, predict that care should be directly proportional to solicitation. In pelicans, offspring solicitation for heat increased significantly with age while parental responsiveness and complete responses showed significant declines (Table 4). Taken together these patterns support the interpretation (Trivers 1974) that parent and offspring are in conflict over additional brooding. Also consistent with the predictions of the conflict model were significant increases with age in effort by offspring required to initiate or obtain complete brooding responses. All significant trends in offspring and parent behaviour are consistent with Trivers' (1974) conflict model and are contrary to Godfray's (1991) honest signalling model (Table 8).

Declining parental responsiveness despite increasing solicitation suggests parents were attempting to restrict levels of care. This could be achieved in two ways: they could either have responded less frequently to solicitation, or maintained response frequency and increased response latency (or some combination of the two). The decline in frequency of brooding responses to heat solicitation as chicks grew older (Fig. 6, Table 4) combined with nearly constant response time for those that did occur (Fig. 7, Table 6) suggest that pelican parents limited brooding effort through a decrease in overall responsiveness rather than by increasing latency (and therefore bout duration). This strategy has the advantage of restricting overall investment while maintaining quick delivery of resources when parents do respond to offspring solicitation. This strategy may also explain the two non-significant trends

Table 8: Summary of offspring and parent behaviours associated with the solicitation and provisioning of additional warmth. Predicted changes for each of these behaviours are summarized in Table 1 (p. 16).

Behaviour	Observation	Supports[1]	Source[2]
Offspring	Significant increases in bout frequency and call rate.	C	F5, T2
	No significant changes in bout duration.	N	F5, T2
Parent	Significant decline in responsiveness and complete responses.	C	F6, T4
	No significant change in latency for first and complete responses	N	F7, T6
Effort	Significant increase to first response.	C	F8, T7
	Significant increase to complete response.	C	F8, T7

[1] C= conflict model, N = neither conflict nor honest signalling models supported.

[2] Figures (F) and Tables (T) from this chapter.

through time observed for offspring heat solicitation and parental behaviour, namely bout duration and response latency (Table 8).

The functional aspects of parental care cannot be examined in isolation from offspring development. Declines in parental responsiveness to heat solicitation were most apparent after chicks reached 6 d old (Fig. 6, Heat Responsiveness). Corresponding with these declines was the emergence and development of downy plumage and a rapid increase in mass (Fig. 3). Both of these changes are presumably apparent to adults and could be cues indicating reduced offspring need for heat. Cues beyond the vocalizations of young are used in several other bird species (e.g. Great tits, Bengtsson and Ryden 1983; budgies, Stamps *et al.* 1985; starlings, Litovich and Power 1992; canaries, Kilner 1995). If these cues are important indicators, then vocal solicitation of heat by older chicks (>8 d) may become a less effective care soliciting signal because alternate unfakable (Maynard Smith and Harper 1988) cues indicate that greater care is not needed.

Food

Unlike heat, the benefits of providing food to fully dependent young are expected to remain fairly constant, while the costs of bringing the required food are expected to increase with chick size and requirement. As for heat, increasing solicitation and reduced willingness to feed older offspring is again predicted by Trivers' (1974) conflict model. Alternately, if food soliciting signals from young are honest indications of nutritional needs, then parents should

respond in proportion to these requests. Young pelicans solicited additional food more frequently, though with shorter bouts when they were older (Table 2). Adult responsiveness (percent of bouts to which parents responded) to these requests remained approximately constant through time (Table 4) but were given significantly sooner to older chicks (Table 6). Combined, these changes suggest that food is given more willingly, an outcome which is consistent with Godfray's model when parents are constrained to provide full care. The significant declines in offspring effort required to initiate feedings, and the slight, though not significant, declines in effort required to obtain food are both supportive of honest signalling rather than conflict resolutions (Table 9).

Evidence that solicitation for food is honest may come from the similar directional changes in solicitation and food delivery. Corresponding with increases in offspring solicitation was a reduction in parental resistance which led to increased food provisioning. While the increase in solicitation supports conflict, the reduced resistance and increased care for less effort all support a constrained honest signalling model in which parents provide full care. If solicitation for food was a manipulative conflicting strategy then increased solicitation would have led to reduced care and greater effort.

The observed parental responses to food solicitation strongly support a constrained honest signalling system which demands complete care to fully dependent young. However, this constraint does not account for the observed increase in offspring solicitation. The prediction that honest offspring would

Table 9: Summary of offspring and parent behaviours associated with the solicitation and provisioning of food. Predicted changes for each of these behaviours are summarized in Table 1 (p. 16).

Behaviour	Observation	Supports[1]	Source[2]
Offspring	Significant increase in bout frequency and call rate.	C	F5, T2
	Significant decrease in bout duration .	H	F5, T2
Parent	No significant change in responsiveness or complete responses.	N	F6, T4
	Significant decrease in response latency (care provided faster).	H	F7, T6
Effort	Significant decrease to first response.	H	F8, T7
	Slight decline to complete response.	H	F8, T7

[1] C = conflict model, H = honest signalling model, N = neither model supported

[2] Figures (F) and Tables (T) from this chapter.

decrease solicitation for food through time stems from the initial assumption that the B/C declines with increasing offspring age. If the B/C actually increased, as it could if the reproductive value of an older chick is higher than the reproductive value of a younger chick, then offspring solicitation would be predicted to increase. Given an increase in B/C and solicitation, honest signalling predicts increased care (Godfray 1991), as observed. It is possible that both constraints of full care and increasing B/C are influencing the food solicitation / parental response cycle.

Similar to the analysis of heat solicitation above, it is necessary to interpret the observed behavioural patterns associated with providing food within the context of offspring development. Over the course of this study, the frequency of complete feedings declined slightly. This decline was small and not statistically significant, but deserves consideration as it appears to be consistent across years and could suggest that parents are reducing care. Schaller (1964) and Cash and Evans (1987) have reported declines from as many as four (4) feedings per day in 0 d chicks to as few as 1.2 feedings per day by the time chicks are crèche-age at 18 - 21 d. While these decreases are consistent with the expected behaviour of a reticent parent faced with caring for conflicting young, it is likely that these changes reflect constraints on parental food delivery patterns, rather than strategic variation arising from conflict. The pattern of food delivery changes considerably during the first three weeks of care. In the first week after hatch, at least one parent is always in attendance at the nest and

chicks receive several small meals throughout the day. As chicks grow, food requirements increase greatly and parents meet these demands with fewer large meals, eventually restricting feeds to one large meal conveyed during once-dailyparental visits to the breeding colony (Cash and Evans 1987). Declines in feeding frequency over the first 14 d of chick life may consequently be a reflection of a growth-dependent transition from the delivery of frequent small meals to the delivery of larger individual meals rather than evidence of reduced parental care. Additional studies, quantifying meal size, are required to further understand the relevance, if any, of meal frequency on conflict versus honest signalling models.

Understanding Behavioural Differences Between Heat and Food

The trends in offspring effort to acquire resources, and parental response, differed strongly between heat and food. I suggest that these disparities can in large part be explained by comparing the timing of this study in relation to differences in the overall care-providing cycle for each resource (Fig. 9). After about 16 -18 days heat is no longer solicited by chicks or provided by parents, who are absent from the colony. Thus, it is very likely that during the 14 days of this study, young pelican chicks were being weaned from this form of care. Concurrently, the age-related changes in behaviour of both offspring and parents were consistent with predictions of weaning conflict which rests on the assumption that care cease when B/C declines to a value below one (Trivers

Figure 9. Comparison of changes in B/C of providing heat and food to young pelican chicks in relation to "weaning" during a single reproductive season. For both heat and food panels, the beginning and ending of this study are indicated by the outermost vertical dotted lines. The development of plumage is indicated by the middle dotted line. The time-axis is broken between the termination of this study and departure of young from the colony; prior to the break time is measured in days while following the break it is measured in weeks. The solid (horizontal) line represents regions where B/C is relatively stable, dashed lines indicate marked changes in B/C associated with weaning, based on observed behavioural trends. For heat, the declines in B/C (due mainly to decreasing B) may begin approximately at hatch or, more likely, when plumage and endothermy develop. Less is known about declines in B/C during weaning for food provisioning as this form of care has yet to be fully explored over the entire period of care in pelicans. It is noteworthy that manifestations of conflict are most evident when B/C is declining rapidly, as the time of weaning approaches while honest signals are more evident in pre-weaning stages when B/C is relatively more stable.

B/C

Food   Heat

Lay (-30 d)

Hatch (0 d)

Plumage (7d)

End Study (14 d)

Depart (12 wks.)

Time

Honesty

"Weaning" Conflict

Convulsions Weaning Conflict ?

?
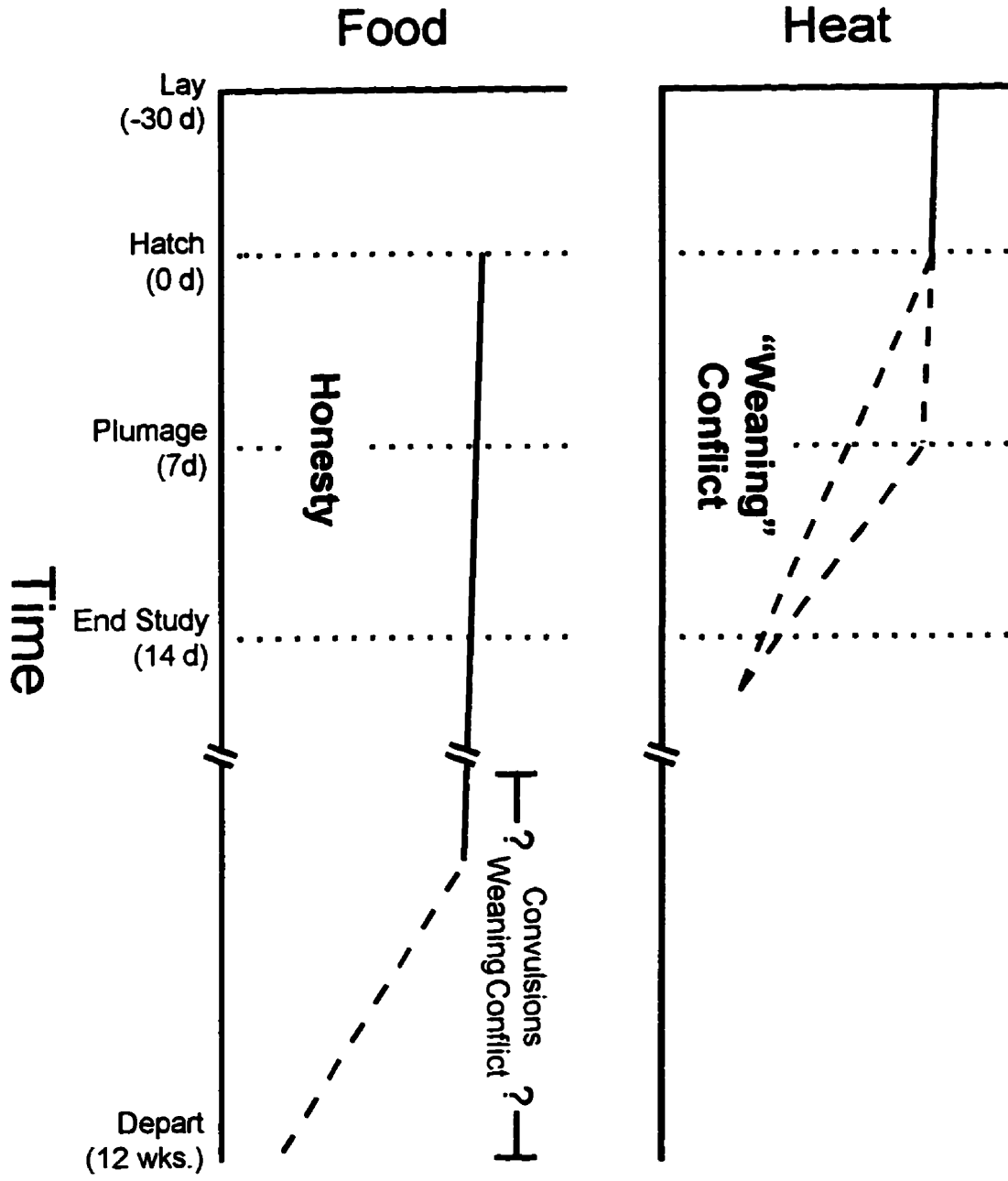
1974). In contrast, food provisioning of fully dependent nestlings continues for several weeks beyond this study. Offspring were not yet being weaned of food. In fact, total food delivery was necessarily increasing during this time (Hall 1925). In the absence of weaning conflict, the alternate resolution, namely honest signalling of need, was manifest.

The apparent absence of overt behavioural conflict over food well before weaning calls into question Trivers (1974) assertion that POC is expected at any instant in time. The observed behavioural patterns in white pelicans suggest that taking offspring development into account can be critical to fully understanding the potential and realized manifestations of disagreement. Perhaps the greatest developmental distinction influencing resource requirements of chicks during this study was the ability of offspring to provide heat for themselves, but not food. Young pelicans begin to develop endothermic capabilities by at least 3 - 5 days (Evans 1984a) and are nearly fully endothermic by 14 d. Thus, as this study progressed, offspring were capable of contributing an increasing share of their own heat requirements. In contrast, pelican chicks remain fully dependent on parental deliveries of food for several months. After leaving the colony they receive few, if any, additional meals (Hall 1925). As a result, young pelicans may rarely if ever be simultaneously self-feeding and fed by their parents. Given these biological differences, it is perhaps not surprising that conflict over feeding does not manifest itself in the

same way as it does for heat.

In older, crèche aged pelicans (>17 d, Evans 1984b), feedings are reduced to as few as one per day. Most food is delivered after the chick begs briefly. Parents regurgitate these meals with little evidence of conflict. However, in the event of small meal delivery (as estimated by pouch distention) offspring respond with a bazaar convulsion-like behaviour, often biting their own wings and thrashing about on the ground (Cash and Evans 1987). These displays are consistent with conflict (Cash and Evans 1987) but the possibility that convulsions are an honest signal of need has yet to be ruled out. Convulsions predominantly follow small feedings and may therefore reflect requirements rather than conflict. It would be profitable to re-examine the significance of convulsions in light of recently developed (Godfray 1991) honest signalling models.

Chapter 2: Energetics of Solicitation

Introduction

Solicitation behaviours of young birds are commonly believed to be unnecessarily costly (Bengtsson and Ryden 1983; Smith and Montgomerie 1991; Harper 1986). These costs may accrue because of increased predation rate due to loud and/or locatable vocalizations (Redondo and De Reyna 1988; Redondo and Castro 1992) or through the energy expenditure associated with begging (Clutton-Brock 1991). When one of these costs is absent it is possible that the other will be the only limiting factor on the magnitude of solicitation (Harper 1986). Various models which explore solicitation by offspring suggest that cost structures will reflect evolutionary tactics of the young (Mock and Parker 1997). Therefore understanding how such costs influence the displays of young birds is important to understanding energy budgets of young and may shed light on strategic aspects of such solicitation (Vehrencamp et al. 1989).

Parent-offspring conflict (Trivers 1974) theory predicts that, among other things, offspring solicitation for additional parental care should be costly. These costs are predicted to arise because offspring vocalizations and displays are seen as manipulative tactics which evolved to induce parents to provide detrimental (to the parents) levels of care. Resolution models which invoke manipulative solicitation suggest that offspring displays could be exaggerated

indefinitely if it were not for the costs indicated above (Mock and Forbes 1992).

An alternate view has been forwarded by Godfray (1991, 1995a). Rather than

assuming that offspring are manipulative, he modeled the possibility that

offspring honestly communicate their needs to parents. Godfray found that

honest signals of need by offspring could evolve, provided such signals were

costly to produce. This finding agrees with previous investigations of honest

signalling (Zahavi 1975; Grafen 1990) and provides an alternate explanation for

the observed solicitation patterns of dependent young (Godfray 1991).

Whether manipulative (Trivers 1974) or honest (Godfray 1991) it appears

that offspring solicitation should be costly. Thus it is unlikely that determining

costs will differentiate between the two models, but both are open to tests of

their prediction that signalling must be costly.

Our current understanding of signal cost is in its infancy and overall

results across groups are variable. The singing behaviour of some insects and

the vocalizations given by frogs are known to be very expensive (factorial scope:

active metabolism / resting metabolism, for insects is up to 29.7, for frogs up to

21.2; values from Ryan 1988, see also Stevens and Josephson 1977; Butcher *et

al.* 1982, Wells and Taigen 1989). Display costs for avian species have

received attention only recently and though some studies indicate large costs

others suggest that signalling can be energetically inexpensive. Work with free

living sage grouse (*Centrocerus urophasianus*) indicate that metabolism for

active displaying may reach as much as 13.9 to 17.4 times basal metabolic rates

(Vehrencamp *et al.* 1989). Studies which explore oxygen consumption using captive animals, however, suggest that vocal display costs are considerably lower. Eberhardt (1994) presented the first values for vocal displays of avian species. She found that singing in Carolina wrens (*Thryothorus ludovicianus*) was from 2.74 to 8.66 times basal rates of oxygen consumption. More recent studies considered vocal displays by red junglefowl (*Gallus gallus*; Chappell *et al.* 1995) and roosters (*Gallus gallus domesticus*; Horn *et al.* 1995). Both found that the energy costs of vocalizing were virtually absent.

McCarty (1996) has presented the first data on energy cost of solicitation in young birds (previously cited studies measured costs in adults). He considered energy expenditure in several passerine species and found that oxygen consumption was low. Surprisingly, some individuals appeared to save energy while displaying. This finding may reflect measurement errors (McCarty 1996) but when taken in combination with the findings of Chappell *et al.* (1995) and Horn *et al.* (1995) it suggests that solicitation can be energetically cheap. This led McCarty (1996) to call into question the prediction that solicitation by offspring must be costly.

White pelicans are an intriguing species in which to consider the costs of solicitation. The altricial young have two unique displays which are used to solicit additional brooding and food (Evans 1992). Parents respond to these vocalizations in a way which appears to address the homeostatic requirements of their dependent young (Evans 1988, 1992). The costs and benefits to parents of providing these resources likely differ considerably and as such the

profitability of responding to such solicitation may differ (previous chapter).

Given these distinctions, strategic differences in solicitation costs can be

compared within individuals. Further, predation of young is rare and

independent of solicitation effort (Evans and Knopf 1993). Most vulnerable

pelican chicks taken by predators in undisturbed colonies are those driven from

the nest (usually the smaller second hatching young) as a part of natural sibling

aggression and brood reduction (Evans and McMahon 1987). In light of the

limited solicitation-dependent predation pressure in this system, the conceptual

framework of both Trivers (1974) and Godfray (1991, 1995a) predict that

energetic expenditure should be large and will limit the solicitation behaviour of

young chicks (Harper 1986). I explored this possibility in a laboratory setting by

measuring the oxygen consumption of resting and soliciting young pelicans.

Methods

The oxygen consumption and call loudness of heat and food solicitation were determined for twelve each of 1 d and 5 d old American white pelican chicks during May and June of 1995. Chicks were collected from the previously used (Chapter 1) colony at East Shoal Lake, Manitoba. Hatch date was estimated through observation of courtship flights (Evans and Cash 1985), minimizing the need to visit the colony prior to initiation of this study. Nests with late-pipped (external pip hole evident) eggs were marked with uniquely numbered stakes and nest contents were checked daily. Hatch dates were determined to the nearest day. Offspring were designated 0 d old on the day of hatch.

Oxygen Analysis

Metabolic Chamber

Metabolic measures were made using a temperature-controlled respirometry chamber and a single-channel, open-flow respirometry system. The metabolic chamber was constructed of plexiglass, insulated on all sides and on the bottom. The top was not insulated to facilitate direct viewing of the chick. Openings in the lid accommodated temperature probes, a microphone to record calls, and incurrent and excurrent air ports. A coil of copper tubing with vertical sides, large enough to surround the test chick, was placed in the chamber.

Temperature-controlled water was pumped through the coil to control chamber temperature (Evans 1990).

The respirometry system was designed following Stack and Rossi (1988). The flow meter (AMETEK R-1 flow control) and pump were placed downstream of the test chamber (Fig. 10). To simplify calculations the excurrent air was scrubbed of water (with drierite), CO_2 (soda lime) and again water (drierite; to eliminate water generated during CO_2 removal) before introduction to the flow meter and analyser (Stack and Rossi 1988). Mixing of air was facilitated by placing the incurrent and excurrent ports (each with multiple openings) at opposite ends of the test chamber. Additionally a small electric fan was placed in an alternate corner.

The rate of O_2 consumption (mass-specific $\dot{V}_{O_2}$ in ml $\bullet$ g^{-1} $\bullet$ h^{-1}) was determined by comparing incurrent and excurrent O_2 content, the latter measured continuously with an AMETEK S-3A oxygen analyser and recorded every 3 s to the nearest 0.01% with a data logger (Grant Instruments, Cambridge). The oxygen concentration of room incurrent air was taken as 20.95% (Stack and Rossi 1988). For analysis, data were imported into Sable Systems analytical software (DATACAN V), and smoothed across three sampling units (three point floating average) to eliminate residual electrical noise that could not be reduced at time of data collection. Percent oxygen values were converted with the software to instantaneous measures for each 3 s interval

Figure 10. Block diagram of the respirometry apparatus used in this study. Temperature coil is not included. Solid arrows represent direction of air flow. Dotted lines represent connections between system components and recording devices.

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                    ┌─────────────┐
                    │  Room Air   │
                    └──────┬──────┘
                           │
                           ▼
    ┌──────────────┐      Thermocouples, From Coil and Chick
    │   Animal     │ ─ ─ ─ ─ ─ ─ ─ ─ ─ ─ ─ ─ ─ ─ ─ ─ ─ ─ ─ ─ ┐
    │   Chamber    │                                           │
    └──────┬───────┘                                           │
           │                                                   │
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    │ CO₂ and H₂O  │                                           │
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    │ Chamber Flow Meter │                                     │
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    │   Pump   │────────▶│ Analyzer Flow│                      │
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         │               └──────┬───────┘                      │
         ▼                      │                              │
    ┌────────┐                  ▼                              │
    │ Bleed  │           ┌──────────────┐                      │
    │ Valve  │           │   Oxygen     │                      │
    └────┬───┘           │  Analyzer    │                      │
         │               └──────┬───────┘                      │
         ▼                      ┊                              │
   ┌─────────────┐       ┌──────────────┐                      │
   │ Atmosphere  │       │Chart Recorder│──────────────────────┘
   └─────────────┘       │or Data Logger│
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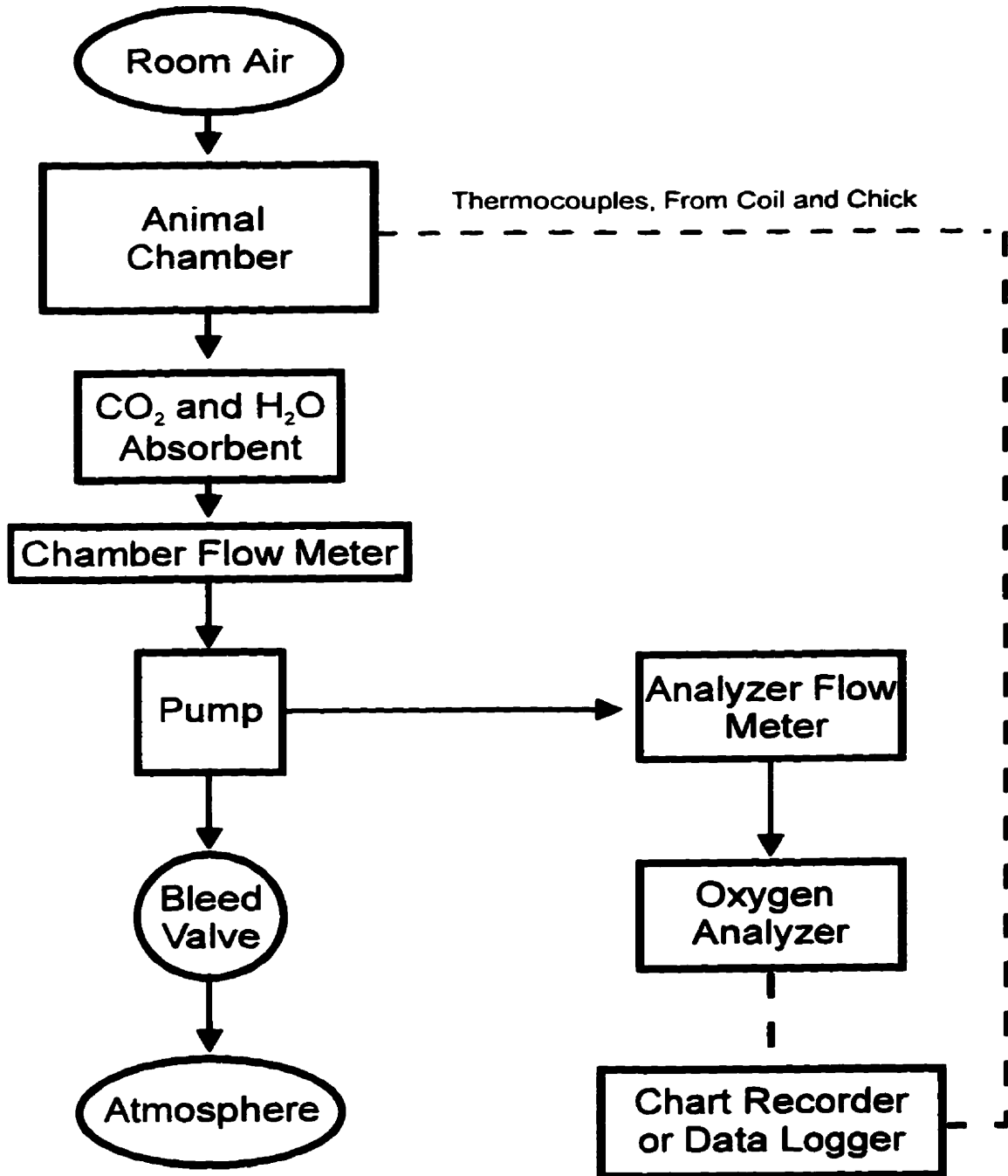
Bartholomew *et al.* 1981), before calculating $\dot{V}_{O_2}$ (Hill 1972; Withers 1977).

Flow rates were confirmed usingthe bubble method (Levy 1964). A washout

curve and functional system volumes were determined (Bartholomew *et al.*

1981). Flow rates for all trials were set to approximately 20% of chamber

volume per minute (Chappell *et al.* 1995). One day chicks were tested in a

small-chamber system with volume of 1.60 L (meter flow rate = 0.335 L•min^{-1})

and 5 d chicks in a larger 2.8 L system (meter flow rate = 0.590 L•min^{-1}).

Sampling Procedures

Twelve chicks at each age were tested. Chicks of known age were

collected 2 or 3 at a time on the day prior to metabolic testing. Chicks tested at

1 d were therefore collected on the day of hatch, while chicks tested at 5 d were

collected at 4 d old. Chicks were transported, by van, in warmed boxes (36° C)

to the University of Manitoba where they were held in a brooder set at 36° C.

Upon arrival at the lab, chicks were fed a fish-based meal prepared for a local

mink farm (Evans 1994). Chicks did not receive additional food until metabolic

tests were completed, the next day. This feeding regime ensured that chicks

were moderately hungry (deprived) for metabolic tests, and reduced

complications due to the heat increment of feeding (Stack and Rossi 1988).

Water was provided (minimum of 5 times per day), via eyedropper throughout

the holding period. Chicks were returned to their nests the day following

metabolic tests.

Each chick was tested at only one age, though both types of solicitation were tested for each chick. The order of testing chicks was determined randomly. The mass of the chick, barometric pressure and room temperature were recorded before and after each trial. The average of these values was used for calculations.

In all trials, body temperature (T_b) was recorded continuously (to the nearest $0.1°$ C) with two thermocouple probes; one inserted approximately 2 cm. into the cloaca, the other taped to the back of the chick. The chamber temperature was monitored with an additional probe attached to the copper coil (see below). All thermocouples, as well as output from the oxygen analyser and a call event recorder were fed to the same data logger and recorded every 3 s. An additional output from the oxygen analyser and a thermocouple taped to the copper chamber coil were connected to a chart recorder for continuous visual record. Two microphones were placed in the chamber. One was inserted through the chamber lid and connected to a sound-operated relay that activated an Esterline Angus event recorder and an event channel on the data logger. The other (miniature) microphone was connected via an amplifier to a speaker near the chart recorder. The latter ensured that I could detect the appropriate call type, which was then manually noted on the chart.

Before starting a test, the mass of each chick, (to the nearest 0.1g) was obtained with an electronic balance and temperature probes were attached as quickly as possible, minimizing the amount of time (usually < 5 min) chicks were

exposed to room temperature. Chicks were then held in the chamber at 36°C and allowed to reach steady state (defined as a minimum of 15 min with O_2 varying by no more than 0.1%, Espira and Evans 1996). Once achieved, steady state baseline measures for determination of standard metabolic rate (SMR) were taken every 3 s for an average of 16 min ($\pm$ 0.7 min, n = 12). Baseline measures were immediately followed by tests of both forms of solicitation.

Heat solicitation by 1 d chicks was initiated by briefly running 20°C water through the coil. Coil temperature, which was under my control at all times, was switched back to 36°C as soon as calling began. This cold challenge was brief enough to have only minimal effects on cloacal and back temperature (maximum back temperature decrease during trial = 1.1° C, with a 0.5 °C decline in cloacal temperature). Preliminary tests with incipiently endothermic 5 d chicks indicated that 20°C coil temperature led to increases in oxygen consumption in the absence of heat solicitation or overt changes in activity (similar trends were not seen in the 1 d chicks). Because of the potential confound between incipient endothermy at 5 d (Evans 1984a) and the metabolic cost of solicitation, cooling was not used to initiate heat solicitation with this group. Heat solicitation at 5 d and food solicitation for both ages were sampled opportunistically, whenever given continuously (mean $\pm$ s.e. number of calls: 1 d heat, 34 $\pm$ 6 ; food, 93 $\pm$ 20: 5 d heat, 28 $\pm$ 9; food 39 $\pm$ 8). Spontaneous heat squawks are normally given in the absence of heat stress (eg. Evans 1990).

Tests on a particular chick were concluded when oxygen measures for heat and food solicitation and a final baseline (minimum of 10 minutes of silence and inactivity following all solicitation bouts) had been obtained. Because of the opportunistic nature of obtaining most calls and the final baseline measures, trial times varied (range 89 to 169 min.) from chick to chick.

Comparisons of $\dot{V}_{O_2}$, calculated as described above, were made across heat and food) and between ages. Two-factor (age, response type) analysis of variance tests with repeat measures on one factor (response type; Maxwell and Delaney 1990) were conducted using Statistix 4.1 analytical software. For analysis the two silent periods were treated as separate response types.

Estimates of Hourly Energy Expenditure

Two estimates of hourly energy expenditure were calculated in an attempt to place the above $\dot{V}_{O_2}$ measures in an ecological context. Though approximate, these measures do reflect the ecological costs of offspring solicitation. The first estimate (total $\dot{V}_{O_2}$) integrates time and $\dot{V}_{O_2}$ measures for each activity (silence, heat and food solicitation) to obtain a measure of oxygen consumed per hour of normal activity. The second estimate is simply the baseline $\dot{V}_{O_2}$ for one hour without solicitation. This latter measure is equivalent to the amount of oxygen which would be consumed per hour if solicitation is a

cost-free endeavor. The difference between total and baseline expenditure estimates serves as a measure of the incremental costs of solicitation.

Time budget data (Chapter 1) were used to calculate time spent soliciting each resource (number of bouts per hour multiplied by mean bout duration) and time spent silent per hour. As the ages of chicks studied in the field (Chapter 1) and the lab do not match I averaged 0 and 2 d, and 4 and 6 d time budget values to correspond with 1 and 5 d oxygen consumption measures. Oxygen consumed per hour was calculated by multiplying these time estimates by $\dot{V}_{O_2}$ for each activity. Energy equivalents were then calculated by converting hourly oxygen consumption to joules (conversion: 20.08 J / ml O_2 [Stack and Rossi 1988]). Finally, an estimate of the extra food required due to solicitation cost was determined (conversion: 5.5 kJ / g fresh mass of fish [Brugger 1993]).

Call Loudness

The loudness (dB) of heat squawks and food begs associated with resource solicitation was also determined in the laboratory. Fourteen chicks at each age, collected and transported as described above, were sampled. A decibel meter (B-weighted, 'fast' scale) was held at the tip of the soliciting chicks' bill and 10 readings were manually recorded for each solicitation type. The average of these calls for each bird and call type was used for statistical analysis. Two-factor ANOVAs (Maxwell and Delaney 1990) with repeat measures on call type was used to determine effects of age and call type.

Results

Oxygen Consumption

Variance in $\dot{V}O_2$ during heat solicitation differed across ages, so statistical analysis was completed on log transformed data (Neter *et al.* 1990). Means ($\pm$ S.E.) of the non-transformed actual data are presented (Fig. 11).

Oxygen consumption differed between response types (initial and final base lines, heat and food solicitation: $F_{3,66} = 92.07$, $p < 0.0001$) but not between ages ($F_{1,22} = 3.29$, $p = 0.08$). There was a significant interaction between age and response type ($F_{3,66} = 10.91$, $p < 0.0001$; Fig. 11), owing to the greater disparity between response types at 5 d relative to 1 d.

Within age, paired comparisons (Bonferoni, $\alpha = 0.05$, Neter *et al.* 1990) indicated that for 1 d chicks the $\dot{V}O_2$ measures separate into two groups ($t_{33} > 2.807$, $p < 0.05$). The first includes the non-solicitation response types (initial and final baseline, $\bar{x} = 0.775$ ml $O_2 \bullet g^{-1} \bullet h^{-1}$), the second includes the two forms of solicitation (heat and food, $\bar{x} = 0.93$ ml $O_2 \bullet g^{-1} \bullet h^{-1}$). At 5 d $\dot{V}O_2$ is divisible into three groups. The two base measures again compose one group (initial and final baseline, $\bar{x} = 0.805$ ml $O_2 \bullet g^{-1} \bullet h^{-1}$) while the two types of solicitation separate from both the baseline and from one another (Fig. 11).

Figure 11. Oxygen consumption of 1 d and 5 d pelican chicks. Mean values (± s. e.) of active metabolic rate (AMR) for heat (solid bars) and food (open bars) solicitation are plotted. The horizontal dashed line represents a combined average of all SMRs (mean value of initial and final baselines at each age). Factorial increases over baseline (AMR / SMR) for heat and food solicitation by 1 d chicks are 1.21 and 1.18 respectively. Equivalent measures for 5 d chicks are 1.51 and 1.26 respectively.

$\dot{V}O_2$ (mL $O_2 \cdot g^{-1} \cdot hr^{-1}$)

Age (d)
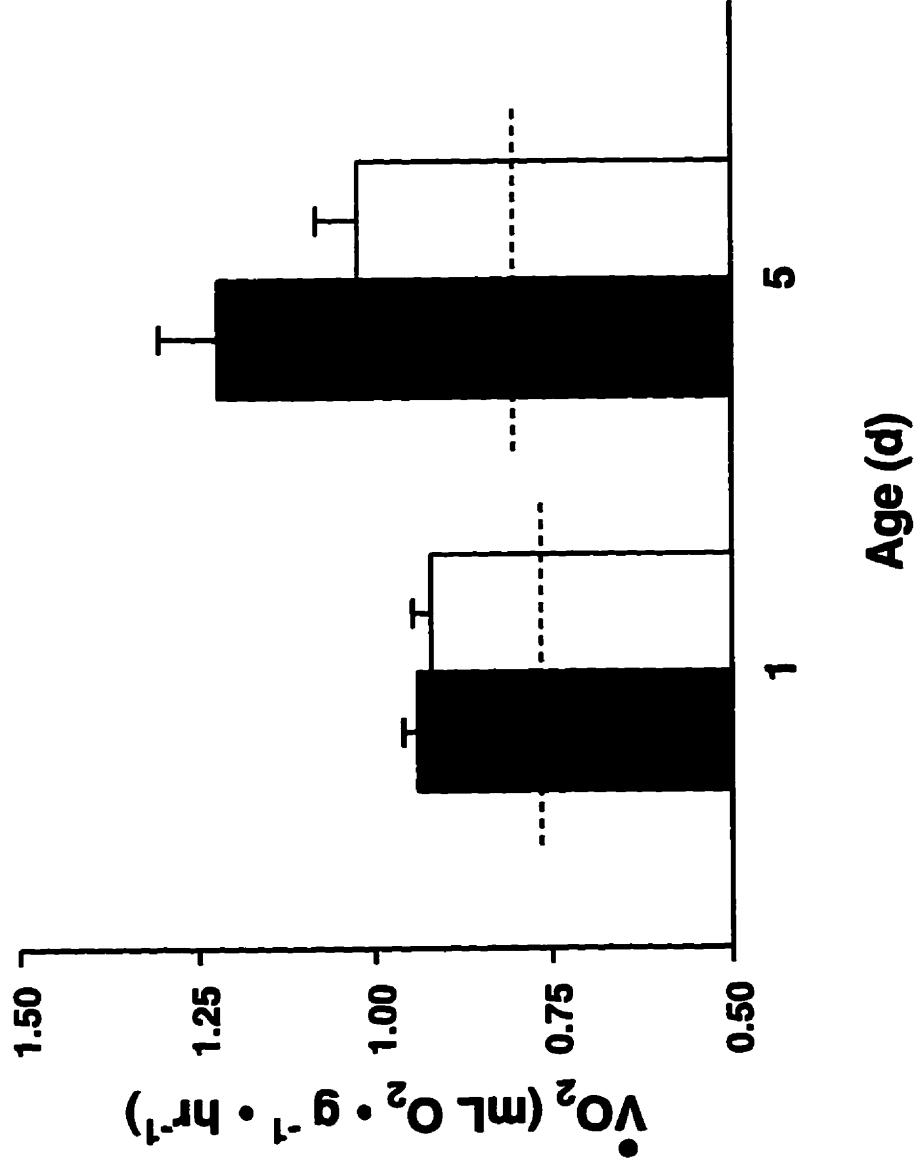
To determine if $\dot{I}_{O_2}$ differed between ages, I conducted one-factor ANOVAs (age) for each response type. There was a significant difference between ages for heat solicitation (5 d > 1 d, $F_{1,11} = 6.38$, $p < 0.03$), but not for food solicitation ($F_{1,11} = 0.26$, $p = 0.62$).

Hourly Energy Expenditure

The hourly increment of oxygen consumption due to solicitation (Table 10) and the food equivalent (g of fish) needed to compensate for the additional energy expended (Table 11) were both small. Based on these estimates, the total additional food required by a 156 g, 1 d pelican chick soliciting resources is 0.01 g per hour (0.12 g per 12 h day). Similarly, for a 408 g, 5 d pelican chick, the required increase in food delivery is 0.07 g of fish per hour (0.82 g per 12 h day).

Call Loudness

Older chicks gave significantly louder calls than did young chicks (2-way ANOVA, repeat measures on call type; $F_{1,26} = 12.52$, $p = 0.0015$). At both ages, heat solicitation was louder than food solicitation ($F_{1,26} = 54.12$, $p < 0.0001$; Fig. 12). These differences were consistent for all combinations of factors (interaction term, $F_{1,26} = 0.04$, $p = 0.85$).

Table 10: Incremental oxygen consumption associated with resource solicitation by young pelican chicks. Oxygen consumption is the product of time per behaviour and $\dot{V}'_{O_2}$. Total oxygen consumed is the sum of consumption for heat, food and resting. Base-line is the estimated oxygen consumption under the assumption that solicitation carries no energetic cost ($\dot{V}'_{O_2}$ = SMR). Hourly increment is the difference between Total and baseline oxygen consumption.

Age	Behaviour	Time / Behaviour (h)	$\dot{V}'_{O_2}$ (ml $O_2 \cdot g^{-1} \cdot h^{-1}$)	Oxygen Consumption (ml $O_2 \cdot g^{-1}$)	Hourly increment (ml $O_2 \cdot g^{-1}$)
1 Day	Heat	0.06	0.94	0.056	
	Food	0.09	0.92	0.083	
	Resting (SMR)	0.85	0.775	0.659	
	Total (Σ)			0.792	
	Baseline	1.00	0.775	0.775	0.017
5 Day	Heat	0.06	1.22	0.073	
	Food	0.10	1.02	0.102	
	Resting (SMR)	0.84	0.805	0.676	
	Total (Σ)			0.851	
	Baseline	1.00	0.805	0.805	0.046

Table 11: Energy and food equivalents for additional oxygen consumed during resource solicitation by young pelicans. Food equivalents are the hourly increase in food delivery required to offset energetic expenditure of solicitation. Food equivalents are standardized for chick mass.

Age	Cost Estimate		
	Oxygen Increment[1] $(ml\ O_2 \cdot g^{-1})$	Energy Equivalent $(j \cdot g^{-1})$	Food Required $(g\ of\ fish \cdot hour^{-1} \cdot g^{-1})$
1 Day	0.017	0.341	$6.2 \cdot 10^{-5}$
5 Days	0.046	0.924	$16.8 \cdot 10^{-5}$

[1] Refer to Table 10 for derivation of this column

Figure 12. Loudness (decibels) of vocalizations associated with solicitation of heat (solid bars) and food (open bars) by 1 d and 5 d pelican chicks.
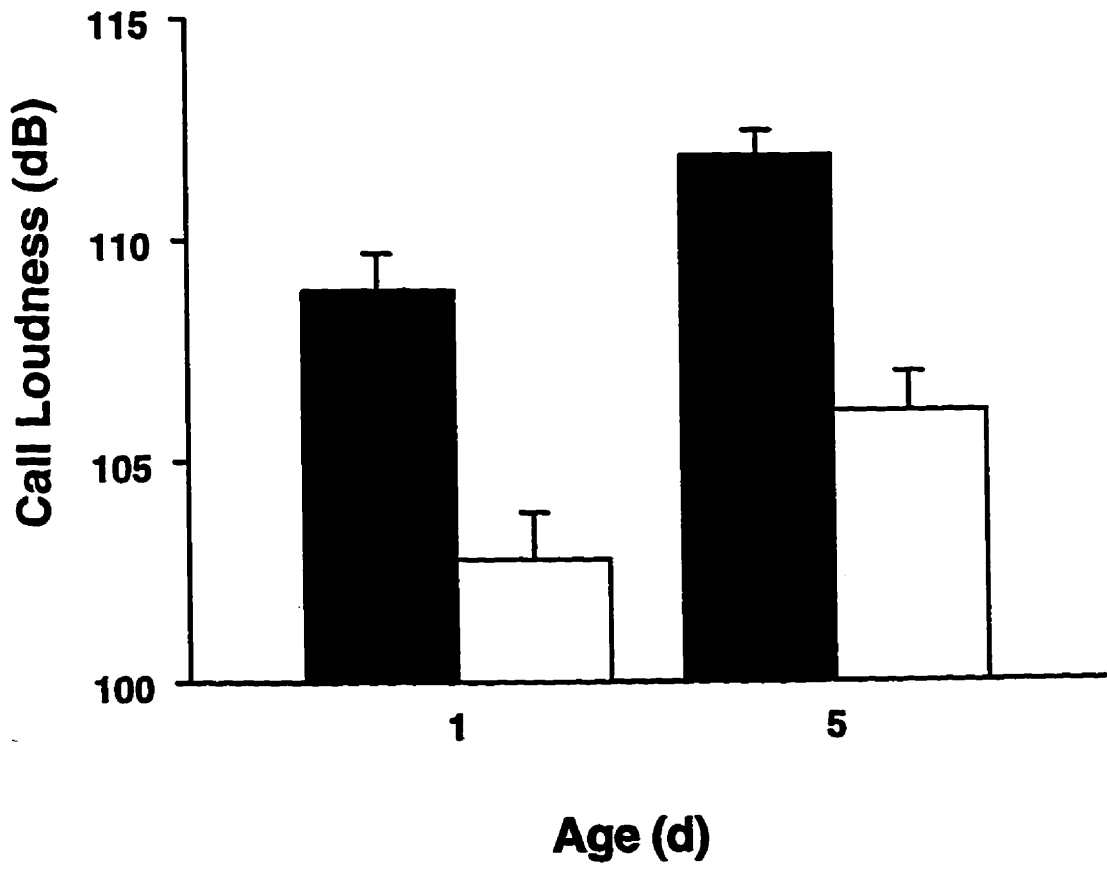
Discussion

POC and honest signalling theory both predict that the solicitation of care by young will be costly. These costs can arise either through direct energy expenditure or through increased predation risk (Harper 1986; Redondo and Castro 1992; Haskell 1994; Godfray 1995b). I found that the energetic cost of solicitation by white pelicans is small. At 1 and 5 d, the hourly increase in oxygen consumed (per g) due to solicitation was 0.017 and 0.046 mL respectively. At each age these values translate into an estimate of less than one tenth of a gram of additional food per hour to compensate for solicitation costs (Table 11). Exact measures of food delivery at these ages is not available but at 1 d chicks are likely fed in excess of 40 g and 5 d chicks in excess of 100 g daily (based on estimates from growth). Thus solicitation costs account for a small fraction of the total food intake of these chicks. This finding, combined with low predation risk, which is largely independent of solicitation (Evans and Knopf 1993), suggests that the direct costs of signalling need by white pelican chicks are negligible. Consequently, the prediction of both models that solicitation should be costly is open to doubt.

The estimates of additional food required by chicks are, at least partially, dependent on the ambient conditions chicks experienced in the lab. Tests of oxygen consumption over a broad range of conditions which mimic the natural thermal environment have yet to be completed. Caution is therefore advised

when assessing these estimates. In addition, the possible stress imposed on chicks by transport from the field was not specifically controlled. However, this factor should only impact the absolute measures. Relative comparisons will likely remain valid.

The notion that reliable signals will be costly stems from Zahavi's (1975) ground breaking work on the topic. Zahavi (1975, 1977) argued signal costs should be great enough to prohibit similar signalling by lower quality individuals. Grafen (1990), Godfray (1991, 1995a) and Johnstone and Grafen (1992) have all presented honest signalling models and all agree that signals must be costly to be reliable. Recently, empirical workers investigating the problem of signal reliability have clearly interpreted "costly" to mean large detectable costs, in absolute empirical terms (Eberhardt 1994; Chappell et al. 1995; McCarty 1996; Borgia 1996; Kilner and Johnstone 1997).

The observed factorial scope ($\dot{V}\,o_2$ solicitation : $\dot{V}\,o_2$ baseline) of solicitation (range 1.2 to 1.5) by pelican chicks is comparable to, though slightly higher than, previous work with nestlings of several passerine species (increases of 1.05 to 1.27; McCarty 1996). These increments fall between those for Carolina Wrens (scope up to 5.27) and crowing in roosters (1.15; Horn et al. 1995) and red jungle fowl (changes not detectable; Chappell et al. 1995). However, soliciting pelican chicks fall well below the factorial scope of adult, displaying sage grouse (up to 17; Vehrencamp et al. 1989) or vocalizing adult frogs and insects (20 - 30; Ryan 1988).

The range of costs noted above indicate that signal cost is variable across and within groups. It is likely that a range of factors influence signal costs. Of these, signal rate is of particular interest. The observed rates of signalling differ greatly across laboratory studies of avian signal cost. Wrens were observed to sing every 1 to 3 s (Eberhardt 1994), passerine nestlings begged on average every 2 to 4 s (McCarty 1996), jungle fowl crowed every 26 s to 2 min (Chappell et al. 1995) while roosters crowed every few minutes (Horn et al. 1995). As expected, the observed factorial scopes generally decline with declining signal frequency. The vocalizations associated with solicitation by pelican chicks in the lab were given once every 2 s for heat and 3.5 s for food at both ages. These rates are similar to the begging rate of passerine nestlings (McCarty 1996) and the song rates of wrens (Eberhardt 1994). The relative rate of solicitation by pelicans falls intermediate to other studies -- as did their observed factorial scope.

Signal loudness is also an important correlate of signal cost (Ryan 1988). Heat squawks of pelicans were louder than food begs (Fig. 12). Combined with the greater call rate for this resource, it is expected that the effort associated with a given duration of soliciting heat would exceed that of food. For both ages examined in the lab, the oxygen consumption of heat solicitation exceeded that of food solicitation (Fig. 11). The costs of solicitation therefore appear to be proportional to effort (loudness and rate). These observations support both POC

and honest signalling models to the extent that they predict increasing signal cost with increasing effort.

Increases in solicitation costs across age were observed for both resources, but increases for heat exceeded those for food. It is noteworthy that the cost increases for heat are not due to the thermoregulatory responses associated with chilling periods during tests. Only 1 d chicks were briefly cold challenged (see Methods), thus, if incipient endothermy (Hill 1992) influenced oxygen consumption it could have inflated the cost of heat solicitation at this age but not at 5 d, when chicks were not chilled. Such an increase, if it occurred at 1 d, would have had the effect of reducing differences in oxygen consumption for heat solicitation between 1 and 5 d. Thus, changes in the cost of heat solicitation over age must reflect real biological differences. This potential confound could not influence the rate of oxygen consumption associated with food solicitation as all of these measures were obtained at stable temperatures. Thus the cost differences between heat and food solicitation must also be reflective of true biological differences.

Similar to field studies, it is possible that a part of the increases through time of solicitation cost observed in the lab are related to chick development. However, as changes were unequal between resources it is also likely that strategic aspects of signalling are reflected in these increases. Thus, the observed changes in solicitation cost may have important implications for conflict and honest signalling models.

Dawkins and Guilford (1991) have forwarded the view that honesty is corrupted (i.e. dishonest signals are substituted) when communication costs can be reduced. Increasing signal costs therefore should tend to reinforce the honesty of a communication system. The increase in cost of heat solicitation over age found here could therefore be expected to enhance signal honesty as chicks develop. However, the patterns of heat solicitation by young pelicans in the field (Chapter 1) do not support these theoretical expectations. Based on increases in solicitation and declines in parental response I concluded that there was an increase with age in parent-offspring conflict over the provisioning of additional heat during the first two weeks post hatch (Chapter 1). If older offspring are in conflict with their parents over providing additional heat and manifest this conflict by using manipulative signals (Trivers 1974, Mock and Parker 1997), then honesty is actually corrupted with increasingly costly signals.

Consistent with this interpretation, honest solicitation for food was maintained despite low overall costs and relatively stable energetic expenditure. Based on consistent parental responses which were offered in significantly less time I concluded that offspring and parent were interacting in a way consistent with honest signalling of need for additional food (Chapter 1). The limited change in cost through time associated with food solicitation apparently did not compromise the honesty of signals for this resource.

The recent work into signal cost has challenged the original assumptions of signal evolution. McCarty (1996) concluded that signalling models which

depend on high costs should be considered cautiously. Similarly, previous

empirical workers have suggested that honesty will come cheaply (Clutton-Brock

and Albon 1979). Alternately, Eberhardt (1994) has suggested that oxygen

consumption of singing wrens may be large enough to be considered "costly",

although she calls for continued research. Consensus on the costliness of

signals remains lacking. The findings of this study may help to clarify some of

these issues. The overall low costs found for solicitation in pelicans suggest that

signals of all kinds need not be prohibitively expensive (see also Borgia 1996).

Concurrently, the observed changes in cost through time indicate that honesty

may be maintained despite low costs while escalated costs may reflect conflict

between generations. Future theoretical works therefore need to carefully

consider the cost structures they imposed on conflicting and honest signalling

systems.

General Discussion

"If you get on the wrong track with the Mathematics for your guide, the only result is that you do not realize where you are and it may be hard to unbeguile you." You have to be on the right track for logic and mathematics to be useful. "To find the right track you must exercise faculties quite other than the logical -- Observation, and Fancy, and Imagination: accurate observation, riotous fancy, and precise imagination."

From, Discordant Harmonies

Daniel B. Botkin, 1990

and the words of G.E. Yule.

Three findings of this study suggest new theoretical directions which may aid our understanding of communication between generations. They are: the occurrence of honest solicitation early and apparently manipulative conflicting solicitation late in a care providing season, the occurrence of relatively more costly dishonest signals compared to honest signals, and finally the occurrence of a signalling system which is cheap overall. Each of these observations is in some way contrary to current theoretical explorations. In this section I attempt to address these discrepancies and indicate possible ways of reconciling the theory with findings. The ideas presented herein are not meant to be all inclusive or definitive but rather are suggestions of possible ways to envisage offspring solicitation which will hopefully serve as a starting point for further exploration.

Calls for Help or Fighting Words?

The observed pattern of honest solicitation early and conflicting solicitation late in the care-providing season raises two important theoretical questions. First, over which levels of care do offspring and parent disagree, and second, is solicitation during disagreements necessarily dishonest? These issues are closely related to one another and will be dealt with simultaneously.

Throughout this thesis I have assumed, but not addressed why, conflicting signals by offspring should be dishonest. To appreciate why this might be the case it is necessary to consider why young pelicans appear to conflict over continued care only when a resource is being weaned. In his definitive work, Trivers (1974) first defined weaning conflict and then showed theoretically that conflict could arise prior to the termination of care. Accordingly, all amounts of care are thought to be grounds for potential battles (Trivers 1974). However, the behavioural patterns of white pelicans indicate that conflict before weaning is of limited significance. More importantly, the patterns of solicitation and provisioning in pelicans suggest that early delivered resources differ fundamentally from later delivered resources.

Life history theory assumes (e.g. Parker and Macnair 1978) that parents have a lifetime total amount of care (M) to invest in offspring. Optimal parents provide an equal portion (m) of this total (M) to each of their young. It is recognized that, for many species, the amount of care destined for a single young (m) can not be delivered in one bout of parental effort. Thus m must be

further partitionable into subunits (c). During a lifetime parents repeatedly provide care (c) until they have invested (m) units in each offspring (Fig. 13). Once parents have invested their lifetime resources (M) their reproductive lives come to a close.

Trivers' (1974) models explore conflicts which arise over single care giving bouts (instantaneous model) and the achieved cumulative care of a breeding season (weaning model). These conflicts are closely related to the way investment is partitioned by life history theory. Instantaneous conflicts arise from offspring attempting to influence the magnitude of individual bouts of care (c) while weaning conflicts are defined by an offspring's attempts to obtain levels of investment which exceed the seasonal parental optimum (P or m, Fig. 14). Instantaneous conflicts are those disagreements involving offspring attempts to influence the distribution of 'their own' resources, while weaning conflicts arise when a particular offspring attempts to acquire resources destined for its siblings. These conflicts are distinct because they differ both in terms of relative timing and because only disagreements at weaning potentially lead to adjustments in cumulative care received by young.

Based on the above arguments, resources delivered to offspring are naturally partitioned into early and late by the onset of weaning. The early, pre-weaning phase of care is a period of mutually agreed upon investment (Hamilton 1964; Trivers 1974) in which parents are expected to continue delivering resources (Fig. 15). Therefore early instantaneous conflicts for additional care

Figure 13. The lifetime resources parents can dedicate to reproduction (M).
Each non-conflicting offspring receives an equal portion of this total (m).
Parents which divide their parental effort in this way produce n offspring. Care is
provided in small amounts (c) through time. The cumulative effect is to provide
an optimal amount of care (m). In theory, offspring can conflict either over the
magnitude of a particular bout of care (c) or, later, over the total amount of care
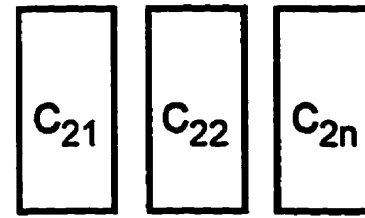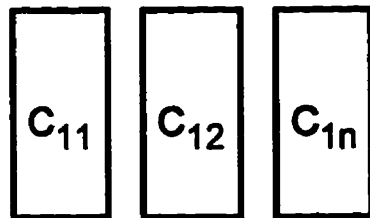they receive (m).

$$M = \boxed{m_1 \;\big|\; m_2 \;\big|\; m_3 \;\big|\; m_n}$$

$$m_1$$

$$m_2$$

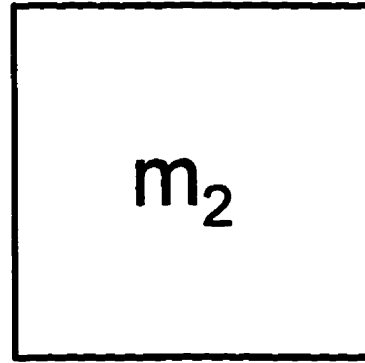$$c_{11} \quad c_{12} \quad c_{1n}$$
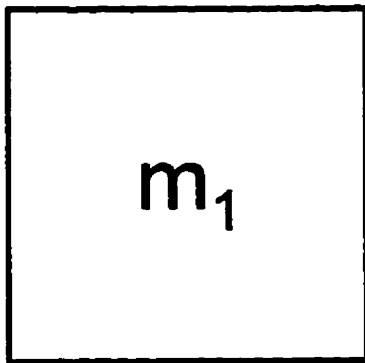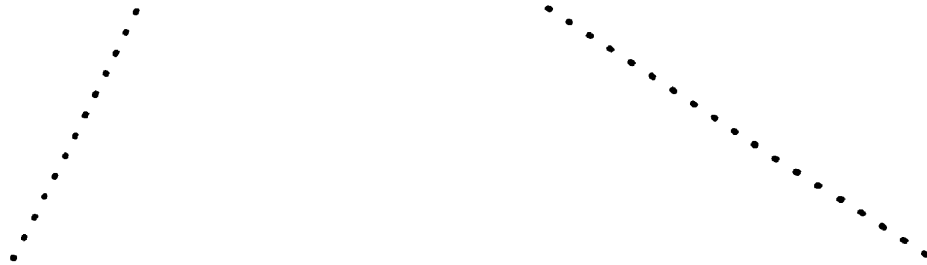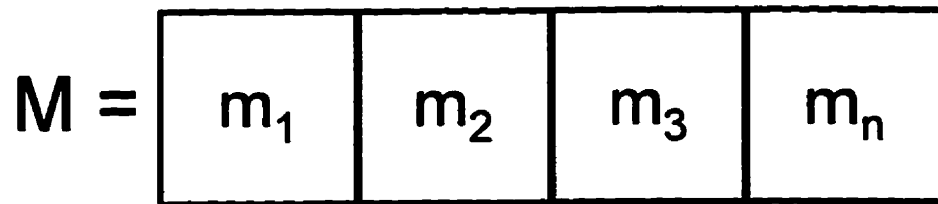
$$c_{21} \quad c_{22} \quad c_{2n}$$

Figure 14. Parental care partitioned according to life history theory and as described by Trivers weaning conflict model. Upper boxes represent the amount of care predicted for offspring by life history theory. The lower panel follows Trivers' (1974) weaning conflict model. The declining solid line represents B/C through time. Horizontal and vertical lines indicate selection boundaries as defined by inclusive fitness (Hamilton 1964). Offspring initially conflict over the way care is partitioned through time (instantaneous conflict over the magnitude of c) but do not yet acquire care which would not have otherwise been provided. As the profitability of providing care (B/C) declines parents begin to wean their offspring. During weaning, offspring attempt to obtain care which exceeds the parental optimum (P, according to Trivers; m, according to life history). Successful offspring, therefore, acquire care which otherwise would have been delivered to their siblings. Parental inclusive fitness is reduced in such cases and intense conflict is predicted.
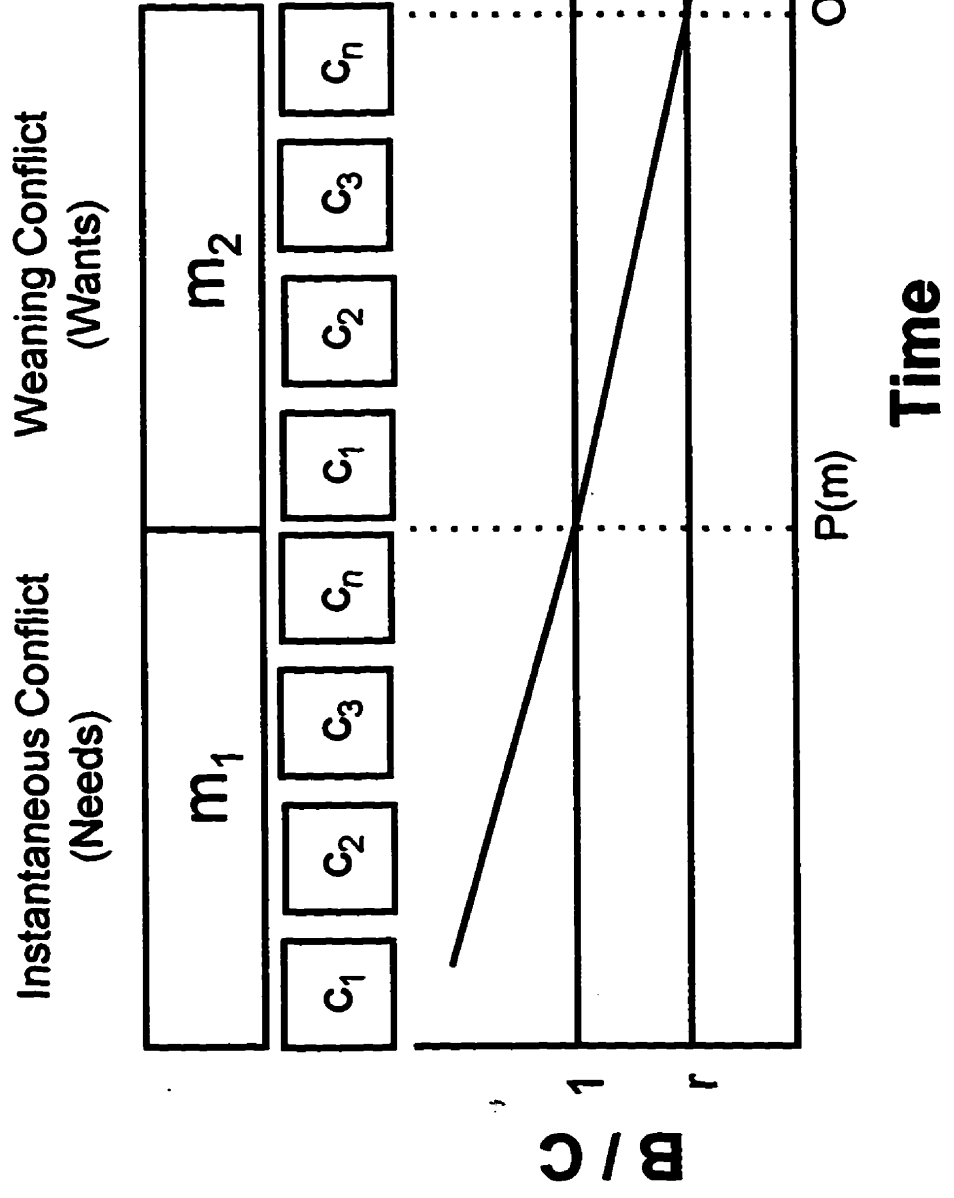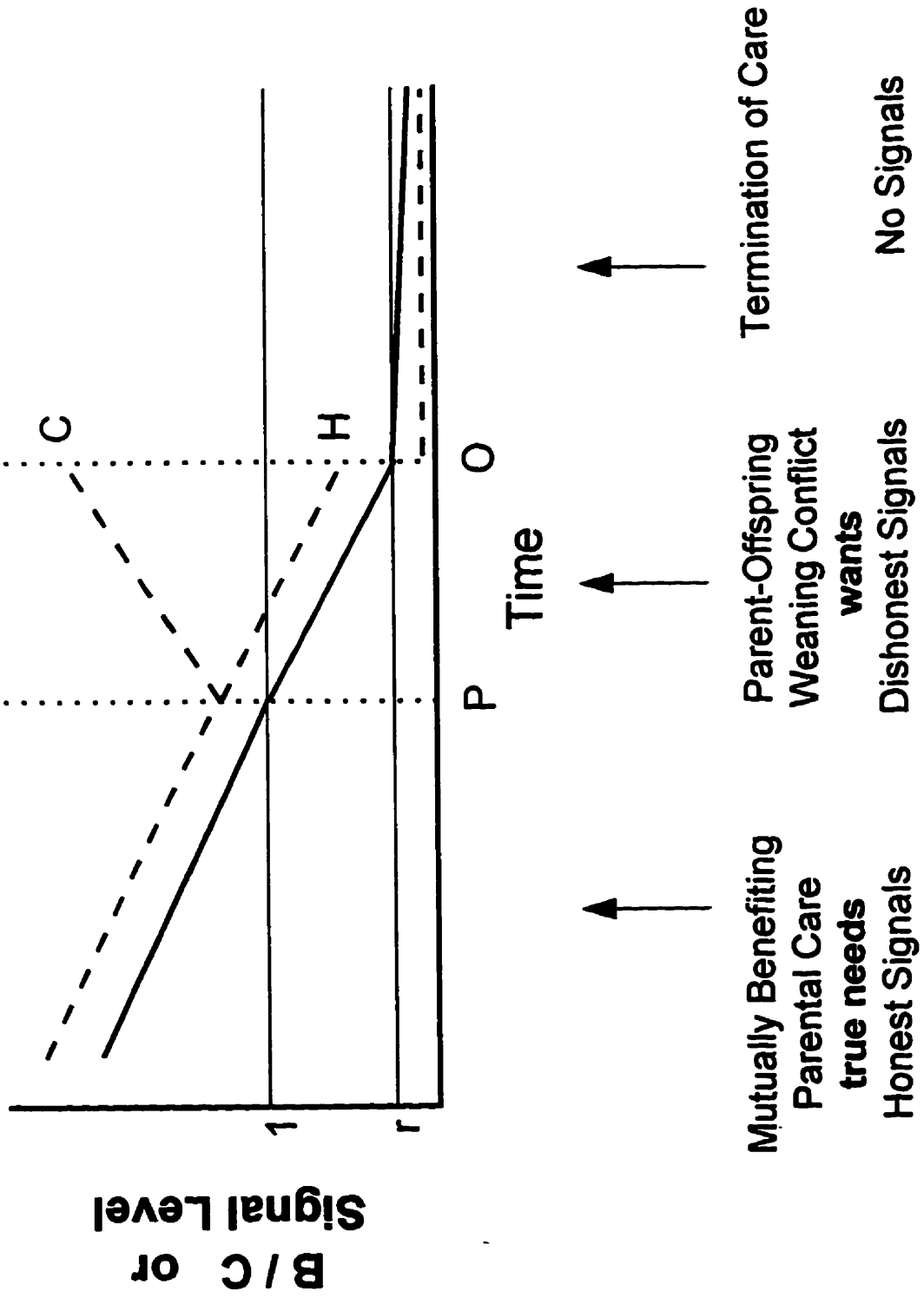
Figure 15. Theoretical changes through time in B/C (solid line) and corresponding changes in solicitation (dashed line). Honest signals are expected to reflect the B/C of continued care. When B/C > 1, parent and offspring both receive positive inclusive fitness payoffs and continued care is favoured by both parties. Inexpensive and largely cooperative honest signals of need can therefore be expected to evolve. When r < B/C < 1 levels of care are in the zone of weaning conflict. In this zone, honest offspring are expected to continue signalling at decreased intensity (H). Conflicting offspring can attempt to acquire additional care (wants) by misrepresenting their requirements through escalated, costly solicitation (C). Once B/C < r neither parent nor offspring favour additional care and solicitation is expected to terminate. Vertical dotted lines indicate optimal levels of care for parents (P) and offspring (O). Horizontal lines indicate the B/C limits of care for parents (1) and offspring (r).

Y-axis: B / C or Signal Level

Levels marked: C, H, V (intersections), and markers L, r

X-axis: Time (markers P, O)

Arrows and labels along the bottom:

Mutually Benefiting	Parent-Offspring	Termination of Care
Parental Care	Weaning Conflict	
true needs	**wants**	
Honest Signals	Dishonest Signals	No Signals

may not be profitable. The benefit of conflicting is the acquisition of additional care. But, care is already being provided (c) and is expected to continue until m is reached (Fig. 14). It is likely that conflicting at this pre-weaning phase will not lead to additional gain (it only alters c, Fig 14). Further, in white pelicans, during the first two weeks post hatch, the costs of soliciting heat (conflicting solicitation) increased greatly and exceeded the costs of soliciting food (honest solicitation). Given that conflicting early is likely not profitable, there is little to prevent the solicitation system from accurately reflecting needs of offspring. During these early phases parent and young may exchange accurate information (Godfray 1991) and cooperate to deliver appropriate levels of care. Further, as both parent and young receive positive inclusive fitness increments from care prior to weaning (Fig. 15), it is expected that honestly communicating needed care at this time would be relatively cheap (Dawkins and Krebs 1978; Krebs and Dawkins 1984; Maynard Smith 1994).

Weaning marks the transition from a period when both generations favour care to a period when only offspring benefit from continued provisioning. Prior to weaning, parental fitness increases because of indirect gains through offspring development and growth. If optimal parents are successful (as the label implies) then offspring survivorship and likelihood of reproduction must be assured (on average) given the level of care parents are selected to provide. In other words, the care provided prior to weaning is needed, for without continued early care, success is unlikely. Given that offspring needs are addressed once

the parents investment optimum (m) is achieved, it follows that conflicting during weaning only enhances offspring survivorship and/or future reproduction. Care given in the zone of weaning conflict, therefore addresses offspring 'wants' (Fig. 15). Such care is distinct from, and in addition to, agreed upon care which is provided to address offspring needs.

The solicitation of wants is manipulative because offspring must present these wants in a way which will be interpreted by parents as signals of need. Such signals are, by definition, dishonest. I have postulated (Fig. 15) that honest signals reflect the profitability (B/C) of continued care. The zone of weaning conflict is approached through time because profitability declines. Honest signals therefore also decline. In the zone of weaning conflict, B/C continues to decline and honest signals are expected to follow (H, Fig. 15). Presumably, parents are selected to not respond to these low level signals. Offspring can however, deceptively increase their signals to levels which previously resulted in resource delivery (C, Fig. 15). These increases are manipulative because the resulting signal falsely indicates that the profitability of continued care is high. It is costly because of the required escalation and because offspring are now attempting to acquire resources from resistant (Krebs and Dawkins 1984) parents which are selected to terminate care.

In essence, honesty is effective prior to weaning but is replaced by manipulative signalling when offspring strive to exceed this level of care and achieve their own optimum. Parent and offspring may cooperate by cheaply

exchanging valuable (Stephens 1989) information early, but communication turns manipulative as offspring are weaned. Manipulation is a costly tactic which is employed only when parents are no longer selected to provide care. At this time offspring have the incentive (benefit) of possibly acquiring levels of care which otherwise would not have been provided. Honesty therefore gives way to manipulation as selection on parents limits provisioning and offspring attempt to increase the duration and extent of care.

Quality or Condition? Explaining low cost solicitation.

To this point I have addressed solicitation costs primarily in relative terms. It is, however, also necessary to understand why solicitation by pelicans is so inexpensive in absolute terms.

Theories which predict that communication requires high costs to maintain honesty (Zahavi 1975, Grafen 1990) deal with signals of quality. Signals of quality indicate the extent to which a signaller can provide resources (genes, food, strength) and therefore the costs which signallers can bear. Because these signallers are indicating the ability to pay costs, it is the costs which determine signal level (Fig 16, Quality). High quality individuals pay lower costs than low quality individuals (Zahavi 1975) and are consequently predicted to signal at greater levels. Within these systems individuals which have the most to contribute give the greatest signal thereby honestly indicating their superior quality.

Condition is the inverse of quality. Honest signals of condition are

Figure 16. Honest signalling models where signallers indicate their quality and condition. Individuals signalling quality are limited by the costs of the system. Highest quality individuals pay lower costs and can give greater signals. Individuals signalling their condition are limited by the benefits of the signalling system. Low condition individuals have greater needs than high condition individuals. Greater benefits are associated with individuals of low condition and these individuals signal at greater levels. Condition dependent signals of need do not require large costs to ensure that honest signal levels are maintained.

Quality

B or C

B

C_L

C_H

L   H

Signal Level

Condition

B or C

B_L

B_H

C

H   L

Signal Level
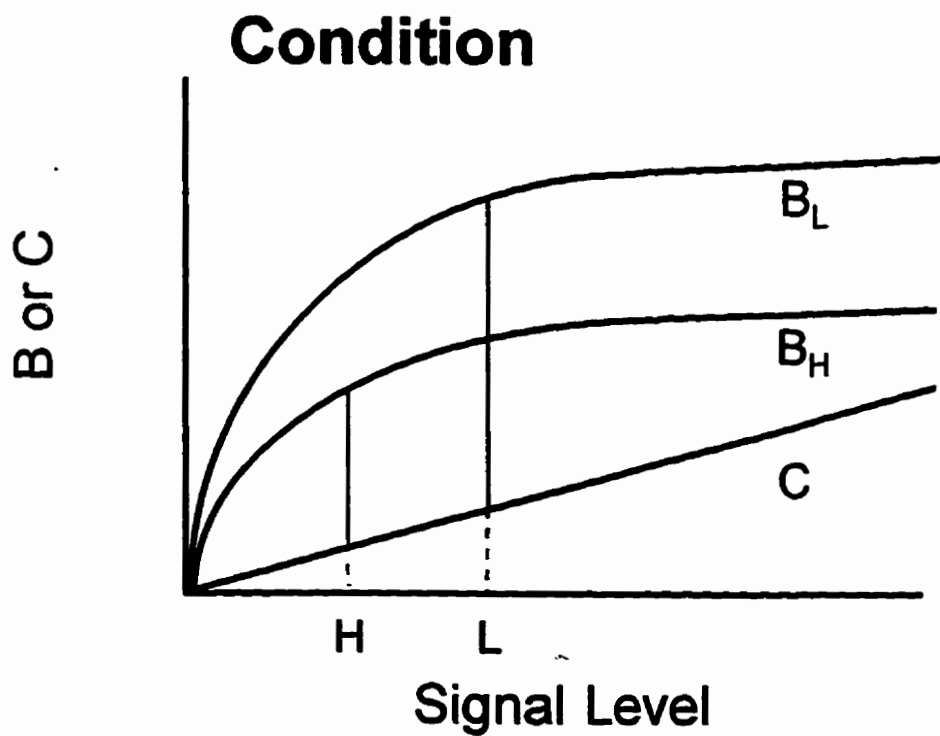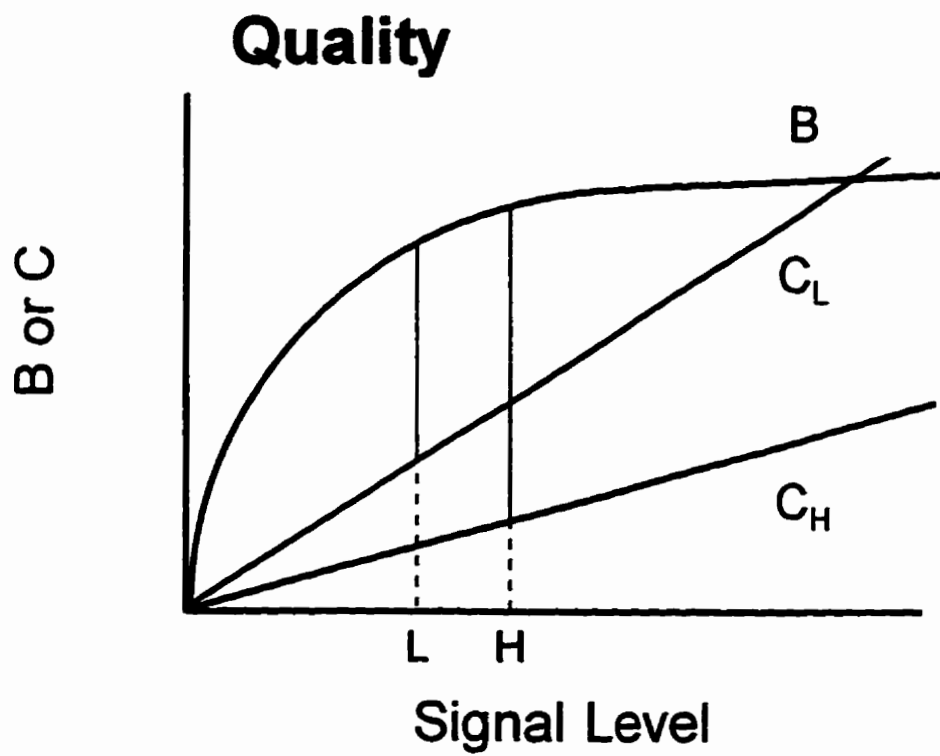
therefore maintained through a mechanism which is analogous to, though distinct from, that which ensures honest signals of quality. Individuals of low condition have high needs for resources. Conversely individuals of high condition have low needs for resources. Given that needs are directly proportional to benefits (Godfray 1991, 1995a) individuals of low condition would receive large benefits from receiving a resource. In the case of offspring soliciting resources needy young are indicating the benefits associated with receiving further care. Because low condition, needy young receive greater benefits from similar levels of care they can honestly indicate their needs with greater signal levels. High condition individuals indicate lower levels of need (i.e. lower benefits) through reduced signalling (Fig. 16, Condition).

Absolute costs can be low within such a benefit moderated communication system. Provided costs increase with increasing signal level (i.e. an optimal solution exists) honesty and a tendency towards cooperation can be maintained because it is benefits, not costs, which signallers are indicating.

The possibilities that signalling systems can have low costs, that honesty can be less costly than manipulation, and that only conflicts over resources delivered at, or following weaning are of importance are all supported by the observed behavioural patterns of white pelicans. These are new interpretations which require specific testing and investigation. However, they all provide alternate theoretical explanations for observed behaviours and may prove fruitful in testing and understanding parental care.

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Appendix

Figure A1: Mean (± s.e.) ambient air temperature for each age studied.