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Offspring Solicitation of Parental Care in American White Pelicans (*Pelecanus erythrorhynchos*)

BY

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of

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ABSTRACT

Recently hatched altricial nestlings rely on their parents for food and warmth. Honest signalling theory predicts that offspring produce reliable, yet costly, signals to communicate their current state of need to the parent. Parents respond to these signals to address the homeostatic requirements of their young. Although empirical studies on begging in various avian species support honest signalling theory, evidence is lacking on the pattern of development of this behaviour. A study designed to test whether spontaneous begging of young American white pelican (*Pelecanus erythrorhynchos*) chicks is influenced by feeding on a fixed schedule, as opposed to on demand, was conducted under controlled conditions. Training demand chicks to beg to receive food (reinforced learning) increased the total number of begs and begging bouts emitted by chicks but had little effect on bout structure. In the nest, a pelican chick would benefit if it learned from feeding patterns to probe its parents for optimal levels of food to ensure its growth and survival. Additional studies were undertaken to further assess honest signalling as it applied to young pelicans. When chicks were deprived of food they begged at higher levels, spent more time begging and emitted more calls per bout than demand or scheduled chicks, suggesting that begging reliably indicates a chick's nutritional need.

A second study investigated the interactive nature between a young pelican's nutritional need and warmth. Rearing chicks in a moderately chilled environment significantly reduced the total number of begs, bouts, calls per bout and increased squawks elicited by chicks, even though cold-reared chicks had a similar (or greater) need for food. Through the use of a negative feedback control system, honest signalling theory is conceptually extended to include interactive effects of thermal and nutritional need. The effects of feeding schedule and rearing temperature on chick growth are considered. Future research possibilities are discussed.

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GENERAL INTRODUCTION

Begging behaviour enables dependent offspring to receive food from parents (Kilner and Johnstone 1997). Selection should favour parental attentiveness to signals of need from the young because an offspring should be better able to assess its own needs than its parent can (Trivers 1974, Godfray 1991, 1995). As a result, parent and offspring may benefit if the offspring signals its somewhat cryptic state of need to the parent, which will appropriately enable an amount of food to be provided (Harper 1986, Hussell 1988).

Understanding the evolution of vigorous and conspicuous begging behaviour has been difficult because of the apparent costly nature of the display. Direct costs attributable to nestling begging can take the form of elevated predation risk and metabolic costs (Harper 1986, Godfray 1991, Haskell 1994, Kilner and Johnstone 1997). Begging calls of altricial nestlings are characteristically designed to attract the attention of parents, but at the same time they reveal the location of the nest to non-intended receivers, such as predators (Redondo and Arias de Reyna 1988, Redondo and Castro 1992a). For example, open-nesting magpie (*Pica pica*) broods experienced higher predation when their begging intensity increased (Redondo and Castro 1992a). Similarly, Haskell (1994) demonstrated that artificial nests on the ground that emitted playbacks of begging of Western bluebird (*Sialia mexicanus*) chicks were more frequently predated than silent nests. Predation costs are most likely to be shared among the entire brood (Sullivan 1989) but it is speculated that nestlings with the highest begging levels are more at risk (Redondo and Castro 1992a).

Measurements of the energetic costs associated with avian vocal displays, such as begging behaviour, are rare. Most measurements of energy costs of vocal displays have been performed on ectothermic frogs and insects, which experience a 5- to 30-fold increase in oxygen consumption when vocalizing (Ryan 1988). However, the energy cost associated with crowing in junglefowl roosters (*Gallus gallus*) did not differ significantly from average oxygen consumption levels before or after bouts (Chappell et al. 1995). Horn et al. (1995), however, found a 15% cost of crowing. Furthermore, the energy cost of vocalizations in roosters is lower than costs associated with feeding, drinking and preening (Chappell et al. 1995). A small energy cost associated with vocalizations for heat and food solicitation has also been observed in American white pelicans (*Pelecanus erythrohynchos*, Daniels 1997). Recently, McCarty (1996) reported a 1.05-times and 1.27-times increase in resting metabolic rate for begging nestling European starlings (*Sturnus vulgaris*) and tree swallows (*Tachycineta bicolor*), respectively. Leech and

Leonard (1996) also observed a similar 1.28-increase in energy expenditure in begging tree swallow nestlings, as has a study involving nestling house wrens (*Troglodytes aedon*, 1.27-times resting metabolic rate, Backman and Chappell 1998). Even though these values of the energetic cost of begging appear to be low (McCarty 1996, 1997), they are probably underestimates. This bias may have arisen because active metabolic rates were recorded when chicks did not beg constantly (Kilner and Johnstone 1997, Chappell and Backman 1998). It therefore seems premature to suggest that begging has little energy cost (Verhulst and Wiersma 1997, Weathers et al. 1997). In addition, a low cost associated with begging may still significantly affect a developing young's energy budget by reducing critical amounts of energy available for growth and survival (Verhulst and Wiersma 1997). Competition among siblings also may result in additional selection to increase begging costs (Parker and Macnair 1978).

Various theories have attempted to describe how such an apparently costly behaviour like begging in nestlings has evolved. Parent-offspring conflict (Trivers 1974), which suggests that nestlings evolve exaggerated begging behaviour as a tactic to obtain a larger portion of resources than their parents have been selected to provide, is one possibility. This views begging as the outcome of genetic conflicts of interest between a parent and its offspring, and between offspring themselves (present or future). Once parents appropriately respond to begging nestlings, selection will favour an increase in begging to the point where benefits of additional increases in begging are outweighed by the costs (Harper 1986).

More recently, ESS models (Godfray 1991, 1995) derived from biological signalling theory (Zahavi 1975, 1977, Grafen 1990, Maynard Smith 1991, Johnstone and Grafen 1992) have provided an alternative explanation to the resolution of parent-offspring conflict by focusing on the behavioural level. At equilibrium, offspring produce honest but costly signals of need, and the parent responds in proportion to the intensity of this accurate information about the condition of its young (Godfray 1991, 1995). The benefits of extra resources are assumed to increase with need (Godfray 1991) and cost of begging is an increasing function of intensity of begging (Godfray and Parker 1992) or need (Redondo and Castro 1992b). In this case, nestlings will be selected to increase begging levels to their own optimal level of resources, but direct and indirect (loss of inclusive fitness when successful begging deprive siblings of food) costs ensure the maintenance of honest advertisement of need (Godfray 1991, 1995, but see Dawkins and Guilford 1991, Johnstone and Grafen 1993, Maynard Smith 1994). Godfray's (1991, 1995) models also predict an increase in offspring begging when solicitation costs are reduced, thereby providing a theoretical explanation for higher begging levels found in species that experience less predation (Redondo and Arias de Reyna 1988) and have a low degree of relatedness among members of a brood (e.g. mixed parentage or brood parasitism, Briskie et al. 1994).

There has been growing support for Godfray's (1991) prediction that signal intensity or rate is a reliable indication of need. Calling by dependent young for brooding warmth from a parent or a surrogate has been reported in studies with ring-billed gulls (*Larus delawarensis*) and herring gulls (*L. argentatus*), domestic chicks (*Gallus domesticus*) and American white pelicans (Wiebe and Evans 1994, Evans 1994, Espira and Evans 1996, Bugden and Evans 1997, Safiniuk and Evans, unpubl. data). As well, domestic chicks and embryos in pipped eggs of American white pelicans and both gull species can vocally regulate body temperature under controlled laboratory conditions (Evans 1988, 1990a, Evans et al. 1994, 1995). In the field, exposed embryos and young chicks call at a higher rate, and parents respond by brooding (Evans 1992). Domestic chicks produce more distress calls upon chilling, and in turn elicit parental brooding (Kaufman and Hinde 1961, McBride et al. 1969). A similar graded response to chilling has been documented in various altricial rodents (Sewell 1968, 1970, Okon 1970, Allin and Banks 1971, Blake 1992), where ultrasounds produced by stressed pups result in their retrieval and the restoration of warmth by a parent (Sewell 1968, 1970). An increase in calling rates upon chilling in these species supports honest signalling theory (Evans 1994, Evans et al. 1995, Safiniuk and Evans, unpubl. data).

Young birds beg more vigorously when food-deprived (short-term hunger, Kilner and Johnstone 1997, but see Ricklefs 1992, Welham and Bertram 1993). An increase in begging intensity with hunger has been demonstrated in glaucous-winged gulls (*L. glaucescens*, Henderson 1975), ringed-billed gulls (Conover and Miller 1981, Iacovides and Evans 1998), great tits (*Parus major*, Bengtsson and Ryden 1983, Kolliker et al. 1998), pied flycatchers (*Ficedula hypoleuca*, Gottlander 1987), blue-footed boobies (*Sula nebouxii*, Drummond and Chavelas 1989), American robins (*Tardus migratorius*, Smith and Montgomerie 1991), red-winged blackbirds (*Agelaius phoeniceus*, Whittingham and Robertson 1993), pigeons (*Columba livia*, Mondloch 1995), yellow-headed blackbirds (*Xanthocephalus xanthocephalus*, Price and Ydenberg 1995, Price et al. 1996) and tree swallows (Leonard and Horn 1996). Studies on food-deprived piglets (*Sus scrofa*) yielded similar results (Weary and Fraser 1995). Also, begging levels fell after additional food was provided to great tits (Bengtsson and Ryden 1983) and magpies (Redondo and Castro 1992b). Prior to the development of postural and vocal begging displays, young (less than four days old) domestic canaries (*Serinus canaria*) display their pink mouths to solicit food from their parents (Kilner 1997). Kilner (1997) found that as canary nestlings were increasingly deprived of food, their mouths became more intensely coloured. Even though the above studies suggest that the animal's need is related to its begging intensity, it remains unclear if nestling begging is exaggerated (Leonard and Horn 1996).

If begging is an honest signal of chick need then it is expected that parents will respond appropriately to increased levels of nestling begging (Kilner and Johnstone 1997). Playbacks of taped begging calls of hungry offspring increased parental feeding rates in zebra finches (*Peophila guttata*, Muller and Smith 1978), great tits (Bengtsson and Ryden 1983), puffins (*Fratercula arctica*, Harris 1983), red-winged blackbirds (Burford et al. 1998, but see Clark and Lee 1998) and yellow-headed blackbirds (Price 1998). Similarly, higher begging levels in hungry or food-deprived broods have been associated with an increase in the number of feeding trips in a variety of species (Henderson 1975, Ricklefs et al. 1985, Hussell 1988, Stamps et al. 1989, Smith and Montgomerie 1991, Stamps 1993, Whittingham and Robertson 1993, Bolton 1995a, Leonard and Horn 1996, Hammer et al. 1999, but see Ricklefs 1987, 1992, Saether et al. 1993, Hammer and Hill 1994). Comparable results have been obtained for hungry piglets, where an increase in frequency and duration of food-related calls attract parental attention, which can lead to further feeding (Weary et al. 1996). As well, storm petrel (*Hydrobates pelagicus*) nestlings that received supplementary food were fed less frequently by parents (Bolton 1995b). Parents have also been observed to allocate food among their brood in proportion to the relative amounts of begging done by each chick (Bengtsson and Ryden 1983, Mondloch 1995, Price and Ydenberg 1995). When ring-billed gull chicks were experimentally muted, provisioning was deficient (Miller and Conover 1979). Furthermore, deafened parent doves (*Streptopelia risoria*) fed their young less (Nottebohm and Nottebohm 1971). In addition, canaries provide more food to chicks with redder mouths (Kilner 1997).

Recent evidence in yellow-headed blackbirds (Price et al. 1996), ring-billed gulls (Iacovides and Evans 1998) and piglets (Weary and Fraser 1995) has shown that long-term (body mass or condition) deprivation of food, in addition to short-term (hunger) deprivation, increases the intensity of begging behaviour. Furthermore, blackbirds (Price et al. 1996) and gulls (Iacovides and Evans 1998) in poor condition begged at a higher rate than individuals in good condition during intervals of short-term deprivation. This result is not surprising because offspring in low condition would have greater need, and at a proximate level could be more affected by bouts of short-term deprivations and therefore would signal to their parents that they value food more highly. Great tit nestlings, underweight from infestation with ectoparasites, more than doubled their begging rate, and male parents fed them more (Christe et al. 1996). Sows were also observed to respond appropriately to their piglets' long-term needs (Weary and Fraser 1995). The integration of both short-term and long-term need in begging behaviour seems to be a critical component in honest signalling for food.

Several confounding factors may influence the positive correlations cited above between chick begging intensity and parental feeding decisions (Redondo and Castro 1992b, Kilner and Johnstone 1997). For example, begging levels of one nestling may influence the begging levels of its nest mates (Harper 1986, Godfray 1995). Among eight cotingid species, single-chick broods had lower absolute begging intensities than broods of two or more (Harper 1986). Stamps et al. (1989) reported similar results between singletons and two- to five-chick broods of budgerigars (*Melopsittacus undulatus*), and Price (1996) found relatively higher begging levels in four-chick broods than three-chick broods. In addition, nestling zebra finches increased their begging frequency when exposed to playbacks of begging (Muller and Smith 1978). Furthermore, begging intensity of nestling song sparrows (*Melospiza melodia*), American robins, and yellow-headed blackbirds increased in response to higher levels of begging in their siblings (Reed 1981, Smith and

Montgomerie 1991, Price and Ydenberg 1995, Price et al. 1996). However, no such effect was found in European starlings (Kacelnik et al. 1995, Cotton et al. 1996). Also, a few studies have found that nestlings that begged sooner were more likely to be fed (Smith and Montgomerie 1991, Teather 1992, Price and Ydenberg 1995, Leonard and Horn 1996).

Factors other than begging intensity may also influence parental distribution of food among nestlings (Redondo and Castro 1992b, Kilner and Johnstone 1997). Among many passerine species, hatching asynchrony can create significant size and subsequent competitive asymmetries among nestlings where needier later-hatched chicks may beg at relatively higher rates, but are out-competed by their quieter, larger, but physically superior siblings (Richter 1984, Greig-Smith 1985, Drummond et al. 1986, Blanco et al. 1996). This competition between nestlings intensifies when food is in short supply (Drummond et al. 1986, Drummond and Chavelas 1989, Machmer and Ydenberg 1998). Recent evidence, however, suggests that in some avian species (e.g. red-winged blackbirds), a hormonal mechanism may work in opposition to the potential size and competitive asymmetries brought about by hatching asynchrony (Lipar et al. 1999). Parents may use various non-vocal criteria to allocate resources among their offspring (Redondo and Castro 1992b). In some species larger chicks are fed more because they reach higher (Smith and Montgomerie 1991, Teather 1992, Leonard and Horn 1996) and position themselves closer to preferred locations for feeding (Reed 1981, Greig-Smith 1985, Drummond et al. 1986, Gottlander 1987, Smith and Montgomerie 1991, McRae et al. 1993, Kilner 1995, Kacelnik et al. 1995, Blanco et al. 1996). These results suggest that the outcome of sibling competition, rather than begging effort, may influence parental feeding decisions. However, female budgerigars selectively fed their smallest nestlings (Stamps 1993). Similar parental favouritism toward smaller nestlings have been observed in North-Atlantic puffins (Johnsen et al. 1994) and rhinoceros auklets (*Cerorhinca monocarata*, Bertram et al. 1996), but not in pied flycatchers (Gottlander 1987).

The American white pelican is an ideal species for observing offspring solicitation of parental care. Offspring exhibit two unique vocalizations, one for solicitation of food and the other for warmth, from an attentive brooding parent (Evans 1992). The first chapter of this thesis focuses on the development of, and the effects of food deprivation on, begging in American white pelicans. Once increased begging levels were observed to be correlated with increased need for food (chapter 1 deprivation results), it was possible to attempt to extend Godfray's honest signalling model to include interactive effects between heat and food in dependent young pelicans, which was the main objective in chapter 2. This thesis was written using a manuscript format, where each chapter represents an independent study.

CHAPTER 1: BEGGING IN AMERICAN WHITE PELICANS: DEVELOPMENT AND EFFECTS OF FOOD DEPRIVATION

INTRODUCTION

Adult pelicans commonly nest far from their foraging sites, with a daily round trip between the two areas commonly being greater than 100 km (Evans and Knopf 1993). Prey (usually fish) is carried to the nest where it is regurgitated to the offspring. During the first 2-3 weeks after hatching, a single parent attends the nest while its partner forages, with nest-reliefs occurring once a day (O'Malley and Evans 1982). When a parent is at the nest it provides food, warmth and protects the young from neighbours (colonial nests are densely packed) and predation by gulls (Evans and Knopf 1993).

Young pelicans emit long series of begging calls to initiate parental feeding (Evans 1992, pers. obs.). They face an unpredictable meal frequency and quantity, as the parent cryptically has a finite load of food in its gut that may pre-determine the frequency or amount of food that is delivered to the chick during a given day. It seems logical therefore that it would benefit the young to "test" the parent by begging relatively more frequently than the average number of meals actually received. At the same time, it should benefit the parent to determine when it is time to respond. Pelican parents respond with provisioning behaviour to only 20 to 50% of chick begging bouts (Evans 1992, Daniels 1997). By provisioning only after a chick has begged extensively, the parent can presumably ensure that the chick is honestly in need and, indeed, would consume the food if it is delivered, thereby minimizing apparent costs associated with parental feeding, such as the physical act of regurgitation and kleptoparasitized food (pers. obs.).

Previous studies with young herring gulls (Evans 1979) and ring-billed gulls (Evans 1980) suggested that nestlings learn to limit begging to the food-providers that were most likely to reward their behaviour. Conditioned responses have also been observed in the begging calls of great tits (Ryden 1982) and cactus wrens (*Campylorhynchus brunneicapillus*, Ricklefs 1967). In addition, Drummond and Osorno (1992) found that smaller, second-hatched booby nestlings (*Sula nebouxii*) learned to be subordinate to their larger, older sibling when begging. Further, begging rates in young budgerigars (Stamps 1993) and great tits (Davies 1978) are affected by previous experience with provisioning parents, thereby suggesting they are able to assess food reinforcement schedules. Therefore, it is possible that pelican chicks could learn from parental feeding patterns to beg in a way that enables them to eventually be fed optimally, possibly as a result of the appropriate information being signalled to the parent.

Begging behaviour in birds is clearly becoming a complex area of research, yet evidence is lacking on possibly the most fundamental issue, that is, the pattern of development of this behaviour. A study designed to test whether or not spontaneous begging of young American white pelican chicks changes in duration, rate or number of bouts per unit time as a result of feeding chicks on a fixed schedule versus on demand was conducted under controlled conditions. A previous attempt to raise chicks to beg normally when hand-reared in the lab, from hatching onwards, was unsuccessful (Evans, pers. comm.). Therefore, this study used field-reared chicks beginning at 3 days of age, which begged normally under laboratory conditions (Evans, pers. comm.), to explore whether or not reinforcement of begging by feeding chicks in response to their begging influences the early development of begging behaviour. If begging is enhanced by being reinforced with food when it occurs, chicks trained on demand should beg longer, have a higher rate of begging, and/or produce more begging bouts than chicks given food on a fixed schedule.

Additional studies on different species are needed to further assess Godfray's model as it applies to a specific species (e.g. pelican chicks). Therefore, studies were undertaken to observe the effects of varying levels of short-term deprivation on various aspects of chick begging. Chicks that are deprived of food should beg longer, have a higher rate of begging, and exhibit more begging bouts than their well-fed counterparts. In addition, the influence of different feeding schedules on subsequent chick growth and development was evaluated.

METHODS

Three-day old field-reared American white pelican chicks were collected (under provincial permit) from breeding colonies on East Shoal Lake, Manitoba, Canada (see O'Malley and Evans 1980 for a map and description of the study area). Hatch date was estimated through observation of courtship flights (Evans and Cash 1985) in April, 1997, thereby reducing the need to enter the colony before chicks were required. Pelicans lay a modal clutch of 2 eggs, but rear only one chick (Evans and Knopf 1993). To minimize effects on productivity, in all cases only the larger first-hatched, or A-chick, was collected from 2-chick nests. Upon hatching, each chick was numbered on its back with a black marker.

Chicks were randomly assigned to holding pens back in the lab at the University of Manitoba. Three pens were partitioned by an opaque barrier, into 2 chambers, each measuring 36.5cm x 21.0cm x 32.9cm high. Pens were constructed of standardized plywood with wire-mesh floors and a Plexiglass sheet on top (so chicks could be observed). A hole large enough for a hand to fit through was cut on each side of the pen. These holes were used during feedings, and were otherwise covered by insulating Styrofoam. Pens were regulated for light (14 h light, 10 h dark) using a 15-watt light bulb. Pens were dark from

2200 h to 0800 h. Each pen was heated with a 100-watt light bulb placed below the floor. A miniature fan was placed below the floor to circulate the warm air to the upper holding chamber via flexible conduits. A thermostat, controlling the 100-watt light bulb, was used to maintain a pen temperature of 35.0±.5°C on days 3 - 6, 33.5±.5°C on days 7 - 9 and 32.0±.5°C on day 10 (just above thermoneutrality at these respective ages, Evans, pers. comm.), which ensured most calls given by the chicks were begs and not cold-induced squawks (Conover and Miller 1981, Evans 1992, 1994).

Three testing pens closely resembled the individual compartments of the holding pens, each appropriate to hold one chick. A microphone was fitted into a hole in the Plexiglass above the chick that activated a sound-operated relay and a custom-built call discriminator switch that automatically distinguished, by call duration, food begs from significantly shorter heat squawks given by the chick (see sonograms in Evans 1992). Spontaneous begging coming from each of the three test pens were recorded on an event data logger for analysis and monitored manually during testing using a hand-held counter to provide a cumulative visual output needed for some feeding schedules (see below).

All chicks were spoon-fed a fish-based protein diet, prepared by a local mink farm as used in previous lab-rearing studies of this species (e.g. Evans 1994). During feedings, water was provided using an eye dropper, in sufficient amount (estimated to be 2 ml) to maintain feces in the liquid state typical of naturally reared chicks.

Three treatment groups were set up: (1) chick fed on a fixed schedule (group 1), (2) chick fed on demand (group 2) or, (3) chick experienced food deprivation on testing days but otherwise fed on demand on non-test days (group 3). Group 1 chicks acted as a control group for experimental group 2 chicks, which tested effects of reinforcing begging bouts by feeding on demand. In addition, group 2 chicks acted as a control for the experimental group 3 chicks, for testing effects of short-term deprivation. Twenty-seven chicks (n=9 for each treatment group) were used in this study, with 3 chicks starting anew each day (1 per treatment) for the first 3 days per group of 9 subjects. Every 9 days a new group of 9 chicks was started. To meet the desired sample size, 27 days of testing (3 rotations of 9 days for each group of subjects) were required.

Feeding Methods During Rearing

The amount of food a chick received was determined by the cumulative mass of the spoon, dish, and food before feeding minus the cumulative mass of all these variables combined with spillage, if any, after feeding was complete. The amount of food provided for all groups was equated as closely as possible (mean ± SE = 5.8 ± 1.2% daily difference between treatment groups, range = 0.3% - 9.5%

more g of food provided for demand versus deprived chicks on day 5 and for demand versus scheduled chicks on day 8, respectively) to avoid confounding effects of differing total food eaten on subsequent begging levels.

Group 1 chicks were fed on a fixed schedule four times a day (Schaller 1964) during both test and non-test days. Feedings for this group were provided at 0900 h, 1200 h, 1600 h and 2000 h (i.e. at the end of daytime testing hours 1, 4, 8 and 12, respectively, see below). Group 2 chicks were fed on demand, starting as soon as chick mass was taken, shortly after 0800 h. Chicks in this group were fed only after a threshold number of begs were produced. For chicks of 3-6, 7-9, and 10 days of age, 200, 250 and 300 begs were required, respectively, before food was provided (based on nest monitoring during field preliminary studies in 1996). The number of begs given by these chicks were counted from the output provided by the manual counter, and used to maintain the demand feeding schedule. Group 3 chicks were treated the same as group 2 chicks. When demand-fed birds begged they were fed to satiation, which was determined as the point when the bird refused to eat additional food. For scheduled birds, an equivalent amount was fed. During the light-on period of testing (daytime), which lasted for 14 h (until 2200 h), birds continued to be fed on schedule (group 1) or demand (group 2 and 3).

Test Procedure

Simultaneous tests of 3 chicks (1 per treatment) were conducted, thereby controlling for any possible confounding seasonal or other temporal effects on chick begging. Each chick was tested on day 4, 7 and 10. Chicks were balanced among the 3 test cages to minimize possible confounding effects of any differences in the pens. Testing duration was approximately 24 h (see below). One chick from each of the 3 treatment groups was taken from its holding pen and placed in 1 of the 3 darkened test cages at 2200 h (coinciding with the normal onset of the dark cycle). At 0800 h the following morning, lights were turned on (light schedule hours: 0800 h to 2200 h) and each chick was weighed to the nearest 0.1g and culmen length was measured to the nearest 0.1mm at this time. Direct measures of mass and culmen length allowed for a measured comparison of growth and development in chicks.

Feeding schedules during testing for groups 1 and 2 were the same as during non-test days (see above). Group 3 chicks were provided with 1 initial feeding given on demand, and then were deprived of food for the remainder of the test. If a group 3 chick failed to reach the age-related threshold amount of begs for feeding in the first 2 h, they were then fed, thus ensuring a subsequent total deprivation period of 12 h. Deprived chicks were fed after the test day was completed (2200 h) to ensure overnight survival. After testing was completed each day, all chicks were weighed again (group 3 chicks were weighed before their "after 2200 h" feeding). All non-test chicks were weighed and measured similarly.

After tests involving each chick were completed, chicks were given to trained Zoology Department Animal Holding staff and euthanized with carbon dioxide overdose. Canadian Council of Animal Care regulations were met in all procedures during this study.

Data Analysis

Information in the data logger, which consisted of the time (to the nearest second) of all begging calls that were given during testing for each chick, were downloaded onto a Microsoft Excel spreadsheet. For analysis, a food calling bout was defined as any group of beg calls (or a single beg call) that was preceded and followed by 20s of silence, which is approximately 10 times the interval between successive begs (Daniels 1997). Several begging variables among chicks in the 3 treatment groups were analyzed. These variables included total number of begs and bouts, average bout duration (s), average number of calls in a single bout, average rate of calling (calls/min) within bouts and mean interbout duration (s). Hourly and overall daily summaries of these call parameters were obtained automatically from the spreadsheet with the aid of a customized Visual Basic program developed specifically for these data sets (R.M. Evans, pers. comm.). For hourly summaries, when chicks did not produce any begs during a particular hour, no value was provided for mean bout duration, number of calls in a bout, number of calls per minute within a bout, and mean interbout duration. If begging bouts in a particular hour only contained one call, they were not assigned a mean bout duration or calls per minute value.

During the daytime test period (0800 h to 2200 h), call variables were analyzed separately under overall (totals for entire 14 h daytime test period) and hourly (1 h to 14 h, respectively) time periods. As chicks in the three groups were independent, ANOVA tests without repeat measures on treatments were used for statistical analysis of call variables and food eaten on test days. Changes over age and time (for hourly analysis only) used a repeat-measures analysis (Winer 1971).

For the hourly analysis between groups, nonparametric Kruskal-Wallis tests were used when variances and sample sizes were unequal. Within groups, chick begging frequency (begs/hr) during daytime versus nighttime test periods were compared for each test age using Wilcoxon Signed Rank tests. ANOVA tests without repeat measures on treatment were used to analyze total daily amounts of food consumed by chicks, chick mass and culmen length during the 8-day rearing period (days 3 - 10). All statistical tests were conducted using

Statistix (version 4.1, Analytical Software).

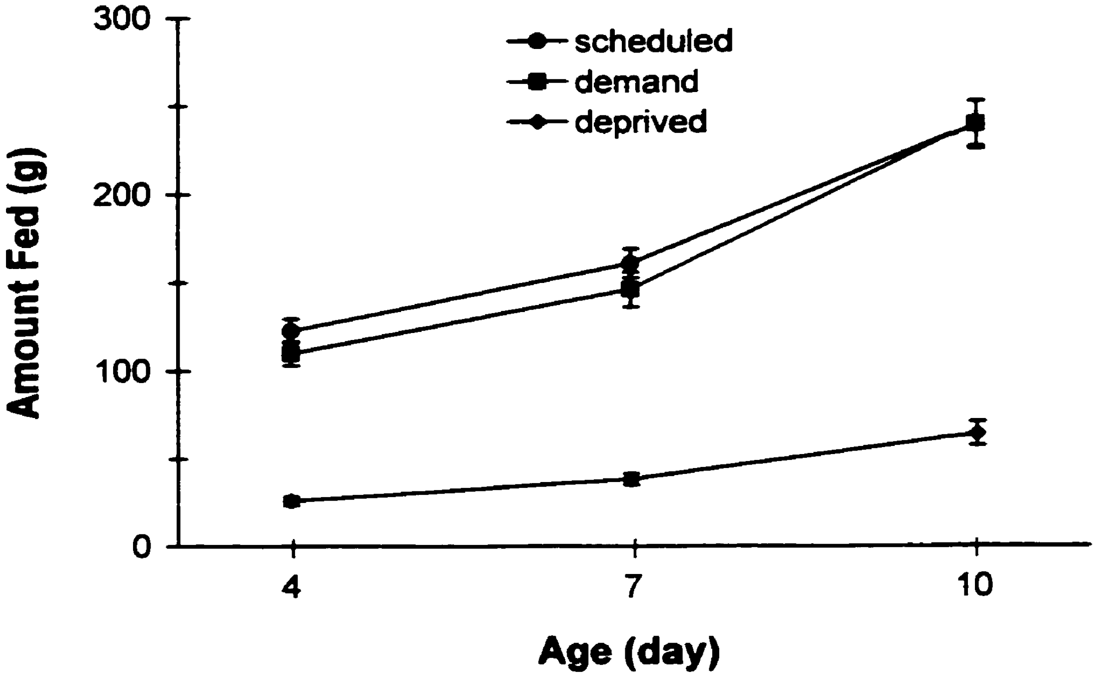
RESULTS

Distribution of Food on Test Days

Daily amount of food provided. Deprived chicks received significantly lower overall amounts of food than chicks in the other two treatment groups (Fig. 1, 2-way ANOVA, repeat measures on age, Tukey's paired comparisons test, alpha = 0.05: deprived < demand = scheduled, $F = 126.12$, $df = 2, 48$, $p < 0.0001$). Younger chicks ate lower daily amounts of food than older chicks under all test conditions (day 10 > day 7 > day 4, $F = 152.37$, $df = 2, 48$, $p < 0.0001$) This difference was most evident for scheduled and demand chicks (age x treatment interaction, $F = 14.13$, $df = 4, 48$, $p < 0.0001$).

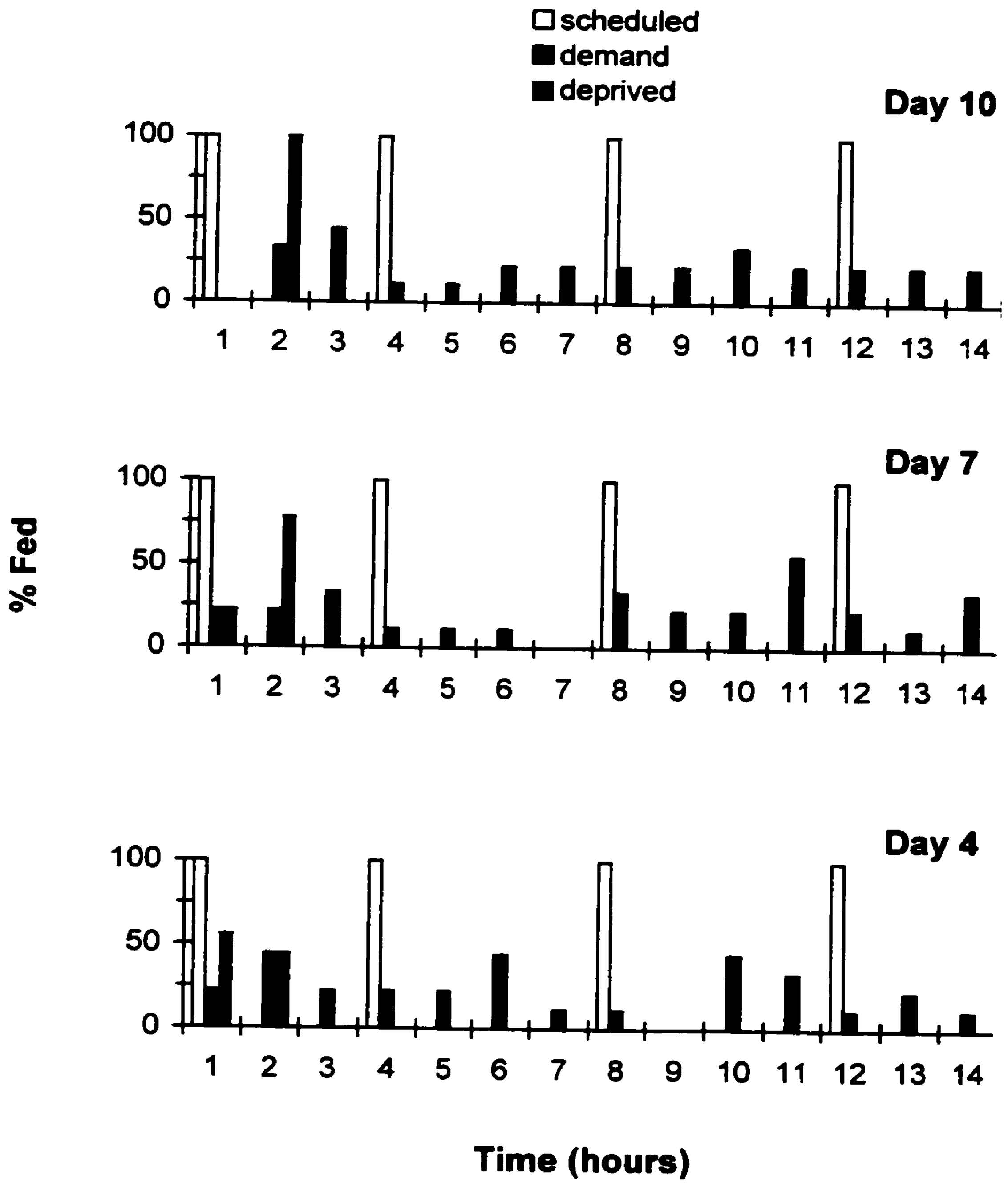
Feeding frequency. Chicks in the 3 treatment groups were fed at different hourly frequencies throughout the daytime test period from 0800 h to 2200 h (hour 1 to hour 14, respectively, Fig. 2). At all ages, chicks fed on a fixed schedule (group 1) were fed four times a day, once at 0900 h, 1200 h, 1600 h and 2000 h (the end of hour 1, 4, 8 and 12, respectively). It was not necessary to force-feed scheduled chicks as they willingly ate the food that was presented to them. Demand chicks (group 2) were fed 3.15 ± 0.17 (mean ± SE) times a day (range = 2.00 - 5.00, $n = 27$). Chick age did not have a significant effect on the number of

Figure 1. Daily amount of food provided (g, mean ± SE) on test days for scheduled, demand and deprived chicks (n = 9 for each treatment group at each test age).



300
200
100
0
Amount Fed (g)
scheduled
demand
deprived
4
7
10
Age (day)

Figure 2. Proportion (%) of chicks fed in each treatment group (scheduled, demand and deprived) during hourly time intervals throughout the daytime test period from 0800 h to 2200 h (hour 1 to hour 14, respectively, n = 9 for each treatment group for every hour at each test age).


☐ scheduled
■ demand
■ deprived
Day 10
Day 7
Day 4
100
50
0
% Fed
1 2 3 4 5 6 7 8 9 10 11 12 13 14
Time (hours)

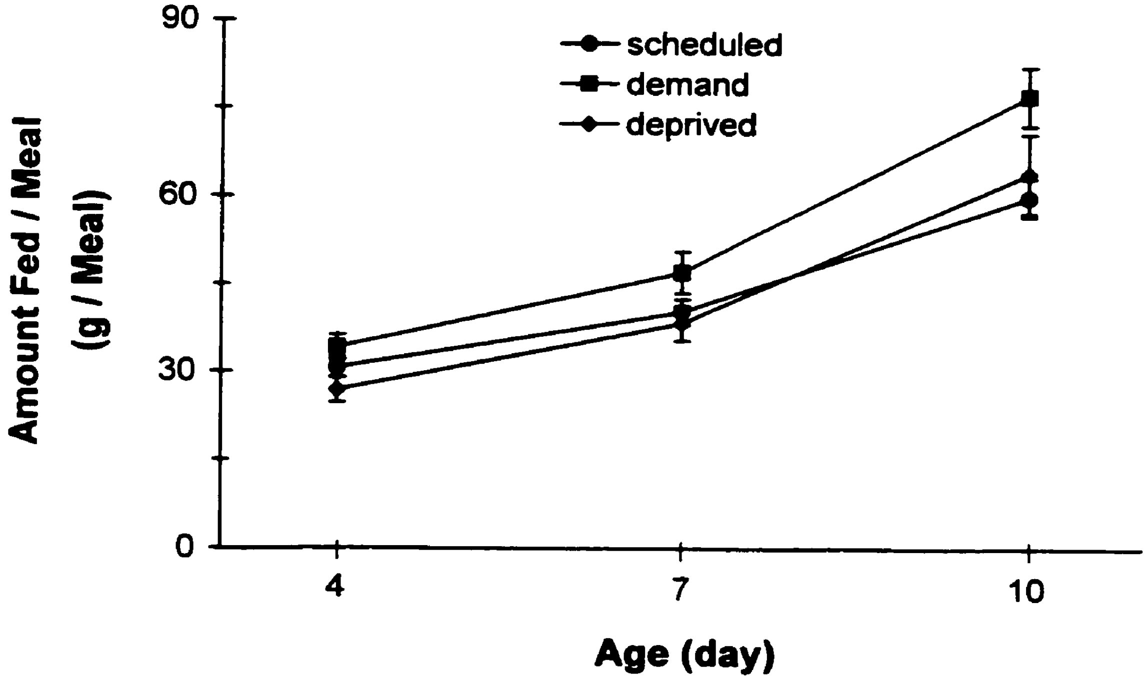
feedings demanded (1-way ANOVA, $F = 0.05$, $df = 2, 24$, $p = 0.9551$). On day 10, all demand chicks preferred to begin feeding after 0900 h (hour 2) and, as a group, continued to demand food at a relatively consistent hourly interval throughout the test day (Fig. 2). At every age, deprived chicks (group 3) were fed only once in either hour 1 or 2 before their deprivation period began. As chicks grew, they tended not to feed until the second hour (Fig. 2).

Amount of food provided per meal. On average, demand chicks were provided with significantly more food per meal than chicks in the other two treatment groups (Fig. 3, $F = 4.23$, $df = 2, 217$, $p = 0.0156$). The amount of food consumed by chicks during each meal increased with age ($F = 78.73$, $df = 2, 217$, $p < 0.0001$).

Chick Begging Frequency During Daytime Versus Nighttime Test Periods

During the daytime (light-schedule hours: 0800 h to 2200 h), chicks begged at a frequency of mean ± SE = 82.4 ± 14.0, 65.3 ± 9.0 and 64.8 ± 8.3 begs/hr on day 4, 7 and 10, respectively. During the nighttime (dark cycle: 2200 h to 0800 h), chicks begged at a frequency of 1.3 ± 0.5, 6.8 ± 2.0, and 6.2 ± 1.7 begs/hr on day 4, 7 and 10, respectively (daytime versus nighttime: Wilcoxon Signed Rank Test, $p < 0.0001$ for day 4, 7 and 10 tests). As chicks at all ages

Figure 3. Amount of food provided per meal (g/meal, mean ± SE) on test days for scheduled, demand and deprived chicks (n = 9 for each treatment group at each test age).


90
60
30
0
Amount Fed / Meal
(g / Meal)
scheduled
demand
deprived
4
7
10
Age (day)

rarely begged at night the analysis of overall begging variables was limited to the daytime test period.

Analysis of Begging Variables During the Daytime Test Period

Begs produced by chicks. During the day, deprived chicks begged more than scheduled and demand chicks (Fig. 4, $F = 37.14$, $df = 2, 48$, $p < 0.0001$). When scheduled and demand chicks were analyzed separately, demand chicks begged more often than scheduled chicks ($F = 11.46$, $df = 1, 32$, $p = 0.0038$). The overall main effect of age was not significant ($F = 2.39$, $df = 2, 48$, $p = 0.1024$), but there was a significant interaction between age and treatment ($F = 3.19$, $df = 4, 48$, $p = 0.0212$), with deprived chicks begging more at day 4 than at day 10 (day 7 = day 4 > day 10 = day 7, $F = 3.92$, $df = 2, 16$, $p = 0.0412$, total number of begs produced with respect to age was not significant in either demand or scheduled chicks: $F = 0.89$, $df = 2, 16$, $p = 0.4313$, $F = 0.72$, $df = 2, 16$, $p = 0.5001$, respectively).

Begging bouts produced by chicks. Treatment had a highly significant main effect on the number of begging bouts produced by chicks (Fig. 5, $F = 36.17$, $df = 2, 48$, $p < 0.0001$), with deprived chicks producing more bouts than demand chicks, whereas scheduled chicks produced the least number of bouts (deprived > demand > scheduled). Older chicks produced more bouts than younger chicks (day 10 = day

Figure 4. Overall number of begs (mean ± SE) produced by scheduled, demand and deprived chicks during the daytime test period (14 h) at each test age (n = 9 for each treatment group at each age).

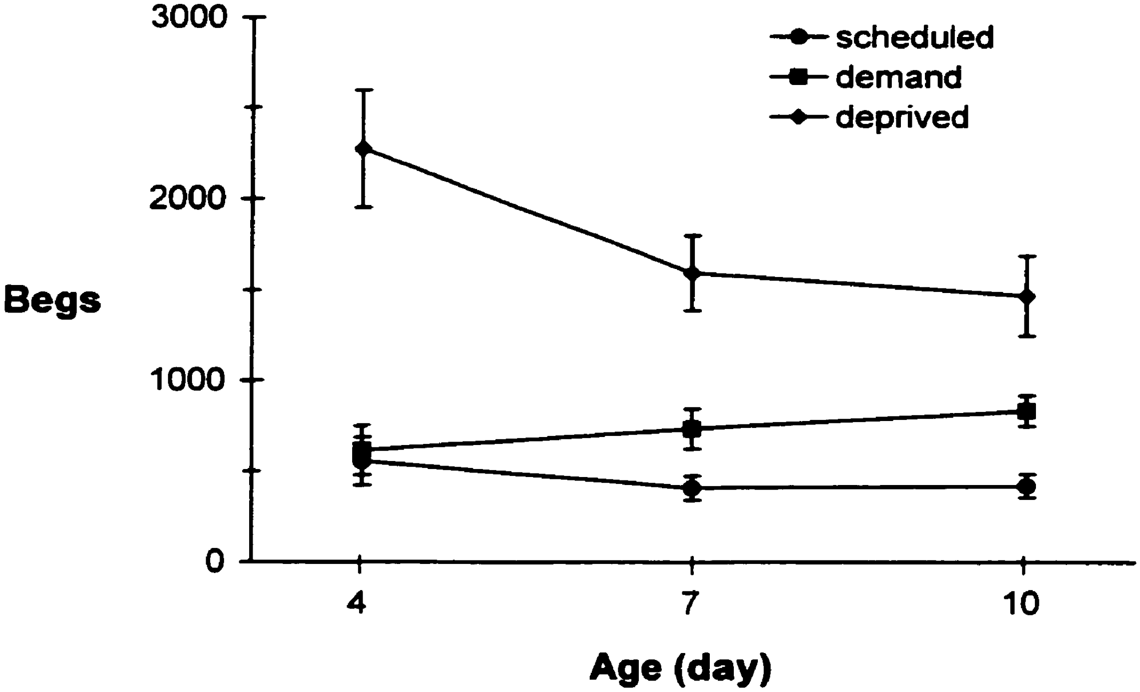
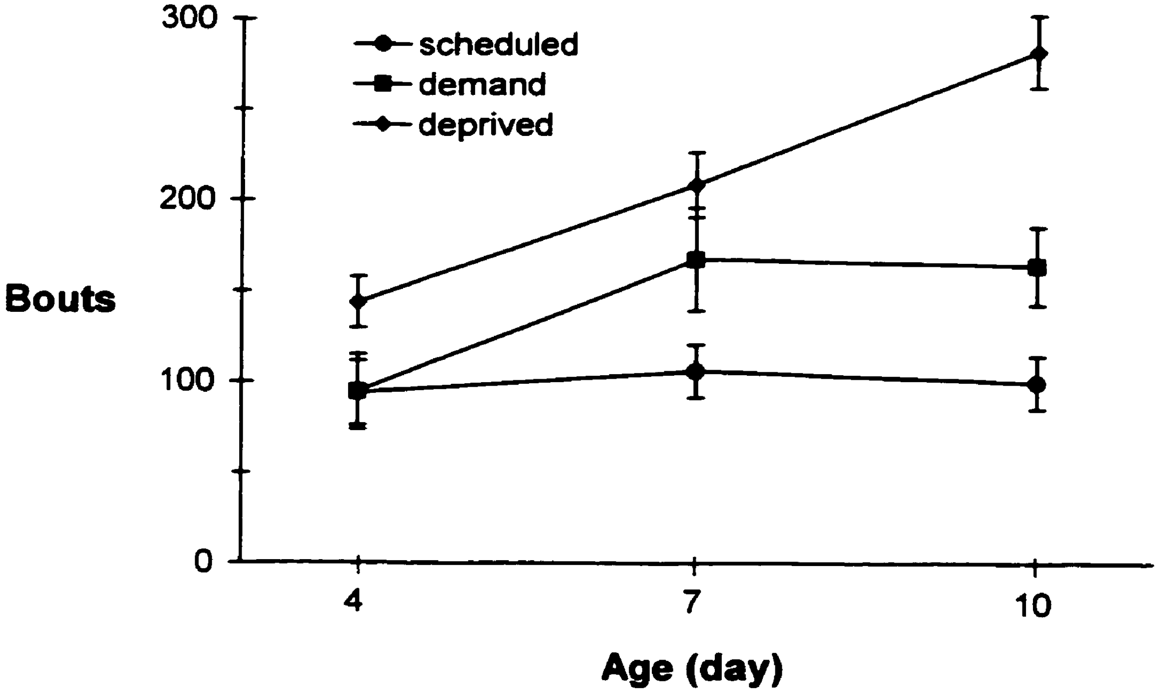

3000
2000
1000
0
Begs
4
7
10
Age (day)
scheduled
demand
deprived

Figure 5. Overall number of begging bouts (mean ± SE) produced by scheduled, demand and deprived chicks during the daytime test period (14 h) at each test age (n = 9 for each treatment group at each age).



scheduled
demand
deprived
300
200
100
0
Bouts
4
7
10
Age (day)

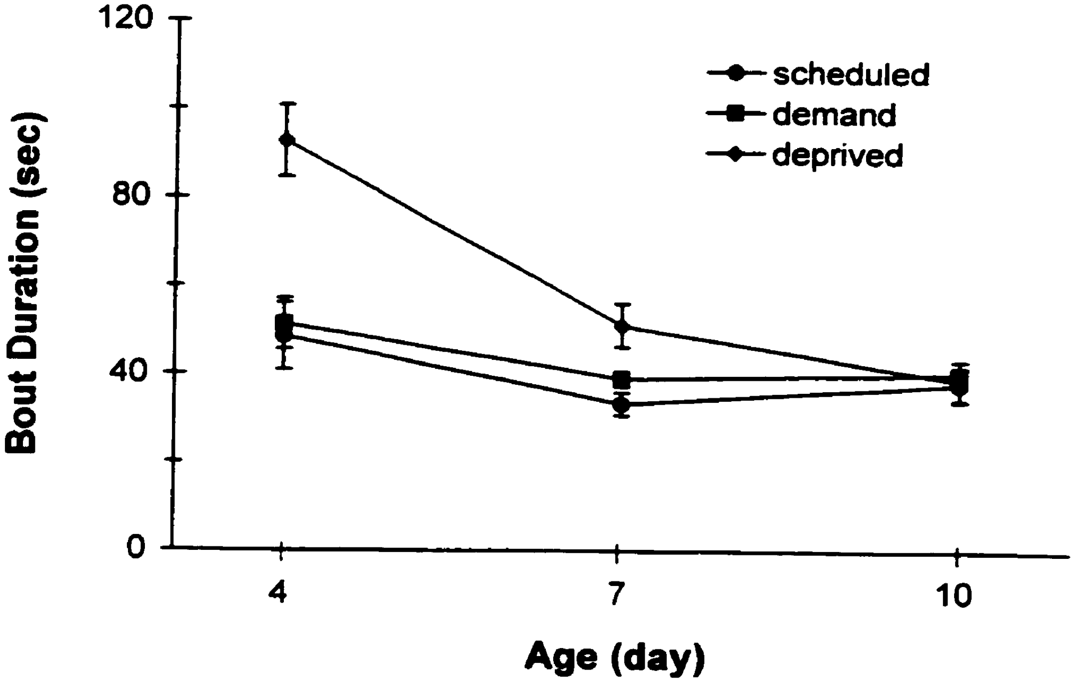
7 > day 4, F = 9.48, df = 2, 48, p = 0.0003), but this effect was most prominent among deprived chicks (age x treatment interaction, F = 2.97, df = 4, 48, p = 0.0284).

Mean bout duration (s). The overall main effects of treatment and age were highly significant (Fig. 6, deprived > demand = scheduled, F = 10.69, df = 2, 48, p = 0.0005, day 4 > day 7 = day 10, F = 27.71, df = 2, 48, p < 0.0001). There was also a significant interaction between treatment and age (F = 7.49, df = 4, 48, p = 0.0001), where at younger ages deprived chicks maintained longer bouts than chicks in the other two treatment groups.

Calls per bout. Both treatment and age significantly influenced the number of calls produced per bout (Fig. 7, main effect of treatment, deprived > demand = scheduled, F = 18.19, df = 2, 48, p < 0.0001, main effect of age, day 4 > day 7 = day 10, F = 23.23, df = 2, 48, p < 0.0001). Similar to mean bout duration results, at younger ages deprived chicks produced more begs per bout than chicks in the other two treatment groups (interaction between treatment and age, F = 10.90, df = 4, 48, p < 0.0001).

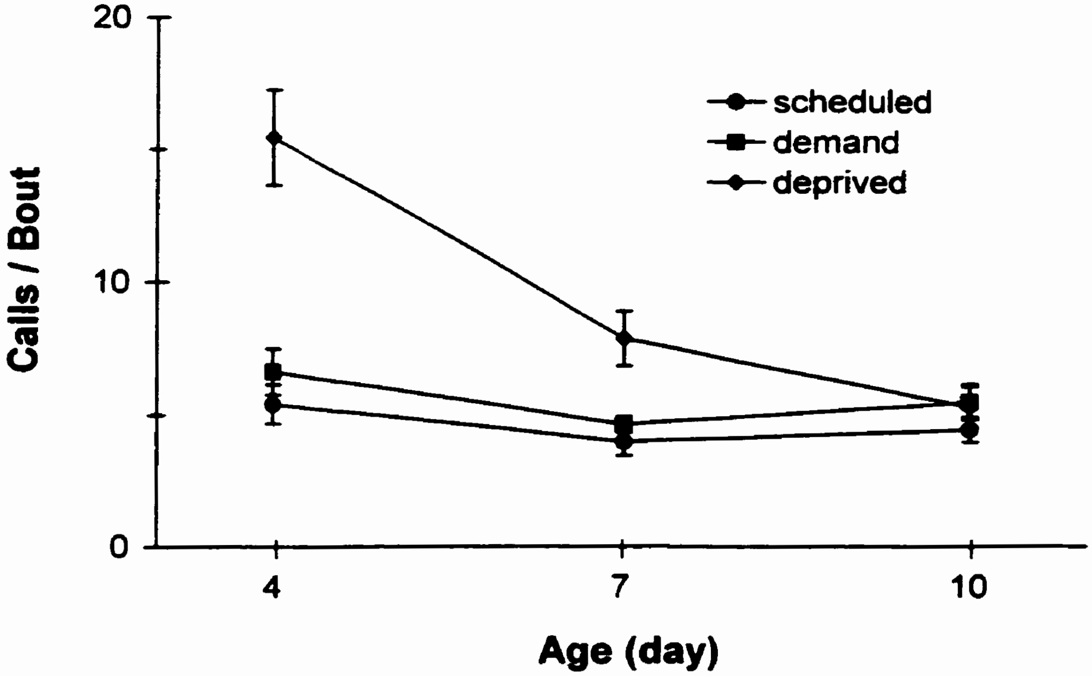
Calls per minute within bouts. Chicks from all three treatment groups called at a similar rate (calls/minute) during their begging bouts (Fig. 8, F = 1.36, df = 2, 48,

Figure 6. Overall mean bout duration (s, mean ± SE) maintained by scheduled, demand and deprived chicks during the daytime test period (14 h) at each test age (n = 9 for each treatment group at each age).



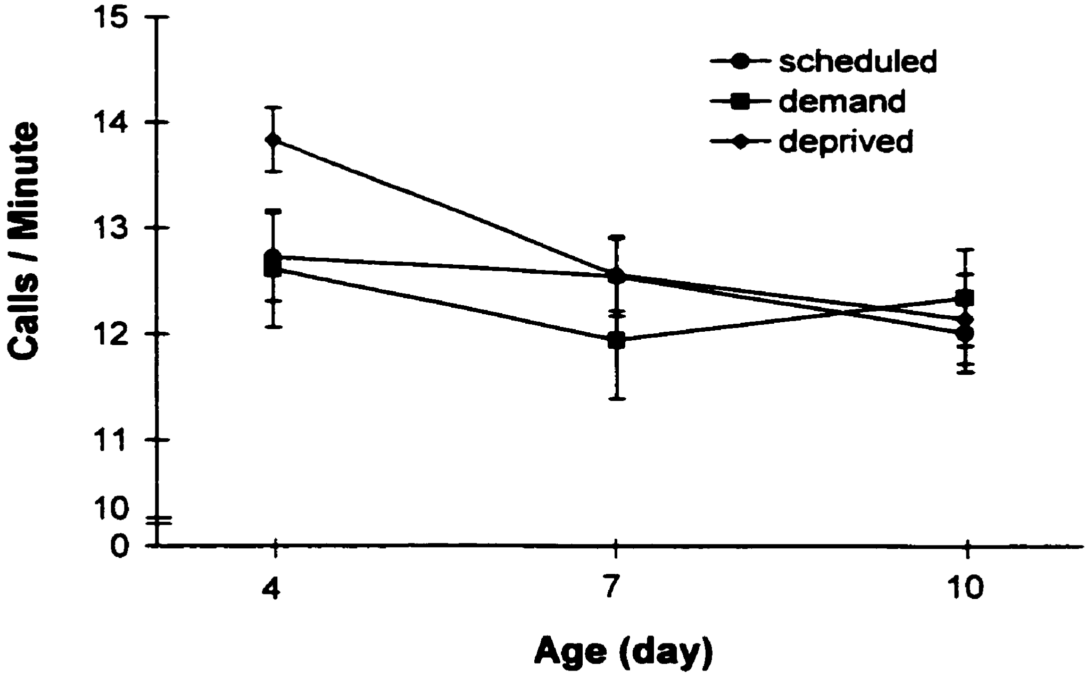
120
80
40
0
Bout Duration (sec)
4
7
10
Age (day)
scheduled
demand
deprived

Figure 7. Overall number of calls produced per bout (mean ± SE) by scheduled, demand and deprived chicks during the daytime test period (14 h) at each test age (n = 9 for each treatment group at each age).



20
10
0
Calls / Bout
4
7
10
Age (day)
scheduled
demand
deprived

Figure 8. Overall number of calls produced per minute within bouts (mean ± SE) by scheduled, demand and deprived chicks during the daytime test period (14 h) at each test age (n = 9 for each treatment group at each age).


15
14
13
12
11
10
0
Calls / Minute
4
7
10
Age (day)
scheduled
demand
deprived

$p = 0.2751$). This result was consistent among all ages (interaction between treatment and age, $F = 0.98$, $df = 4, 48$, $p = 0.4282$). Chicks did, however, beg at a relatively higher rate within bouts at day 4 than at day 10 (day 7 = day 4 > day 10 = day 7, $F = 3.56$, $df = 2, 48$, $p = 0.0361$).

Mean interbout duration (s). Scheduled chicks had longer mean interbout durations than demand chicks, whereas deprived chicks averaged the lowest durations of silence between begging bouts (Fig. 9, main effect of treatment, scheduled > demand > deprived, $F = 18.84$, $df = 2, 48$, $p < 0.0001$). This difference was consistent among all ages (interaction between treatment and age, $F = 0.44$, $df = 4, 48$, $p = 0.7809$). Mean interbout durations of all chicks were longer at 4 days ($F = 4.47$, $df = 2, 48$, $p = 0.0166$).

Hourly Analysis of Begging Variables During the Daytime Test Period (1 to 14 hours)

Begs produced by chicks. It should be noted that when testing began, chicks from all three treatment groups were hungry as they were not fed during the night. This is reflected in relatively high begging levels during the initial hours of testing (Fig. 10). Hourly chick begging levels were significantly different over time (3-way ANOVA, repeat measures on age, $F = 22.48$, $df = 13, 624$, $p < 0.0001$). This difference was most evident for deprived

Figure 9. Overall mean interbout duration (s, mean ± SE) maintained by scheduled, demand and deprived chicks during the daytime test period (14 h) at each test age (n = 9 for each treatment group at each age).

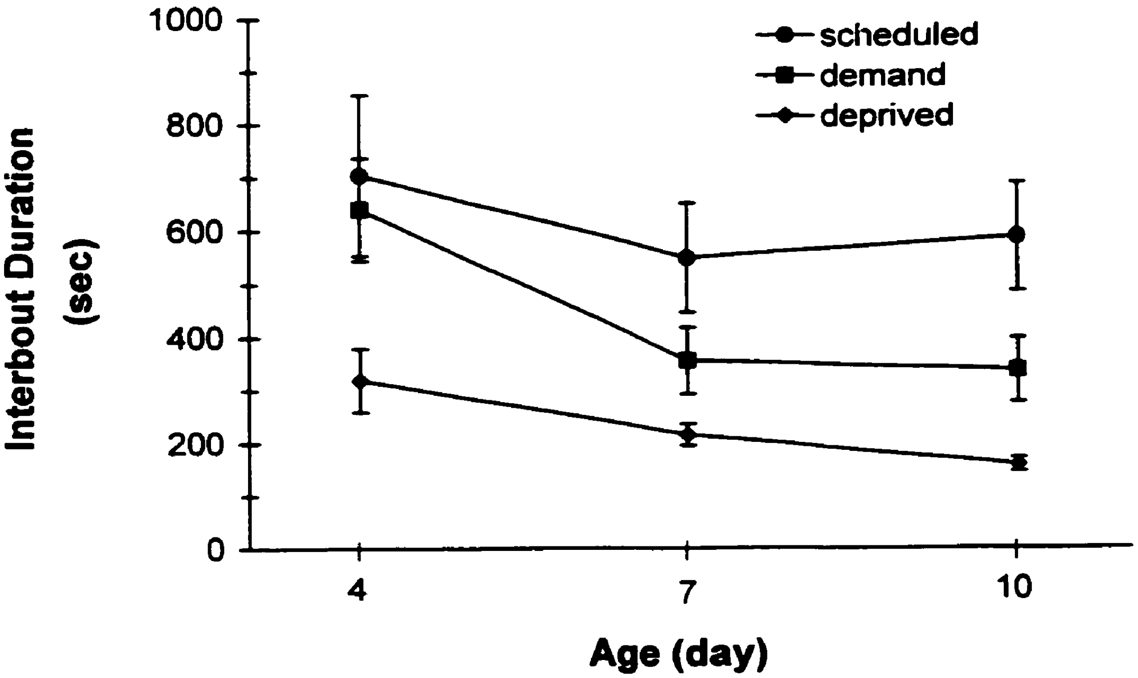
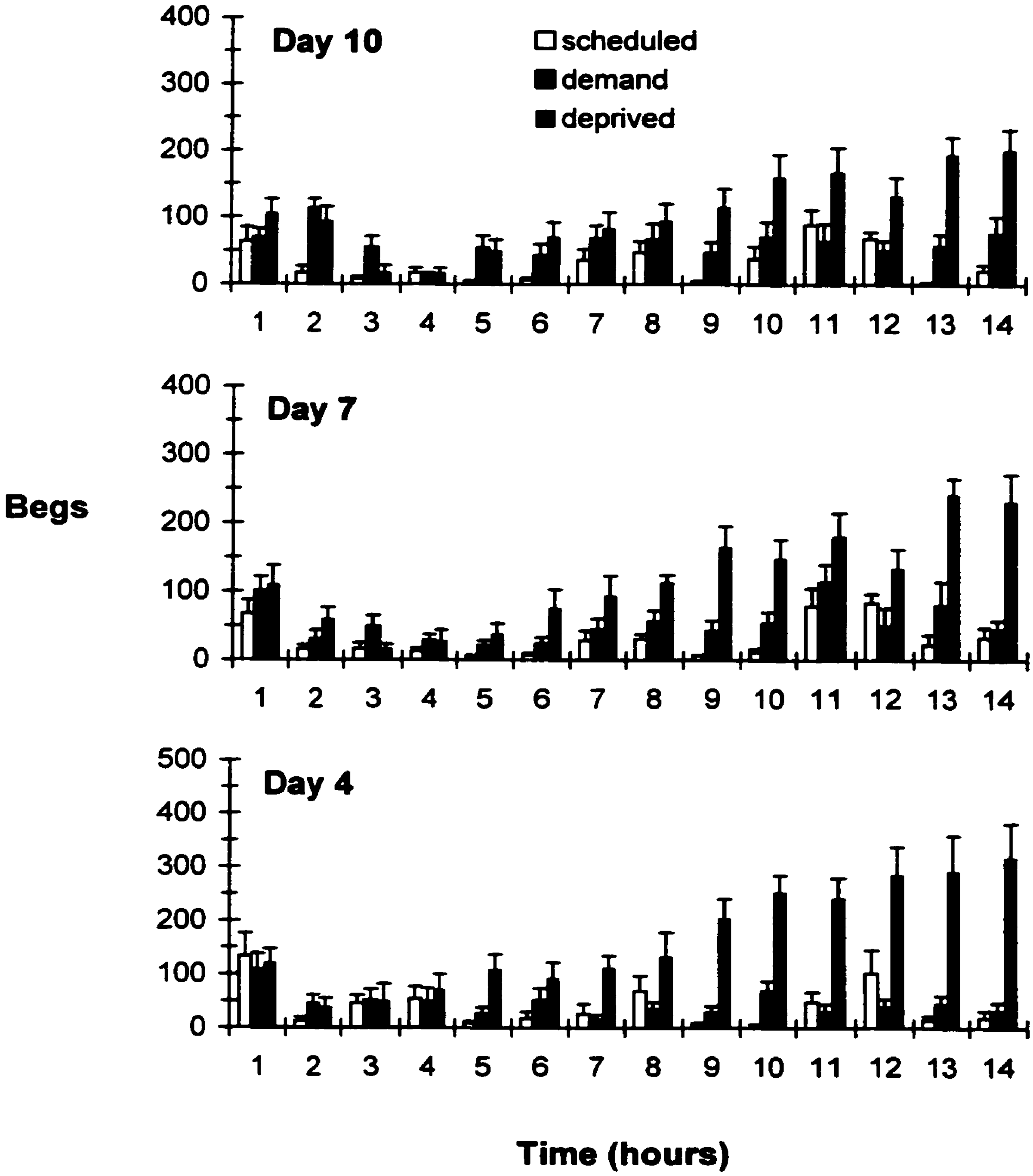

Interbout Duration (sec)
1000
800
600
400
200
0
scheduled
demand
deprived
4
7
10
Age (day)

Figure 10. Number of begs (mean ± SE) produced by scheduled, demand and deprived chicks during hourly time intervals throughout the daytime test period from 0800 h to 2200 h (hour 1 to hour 14, respectively, n = 9 for each treatment group for every hour at each age).

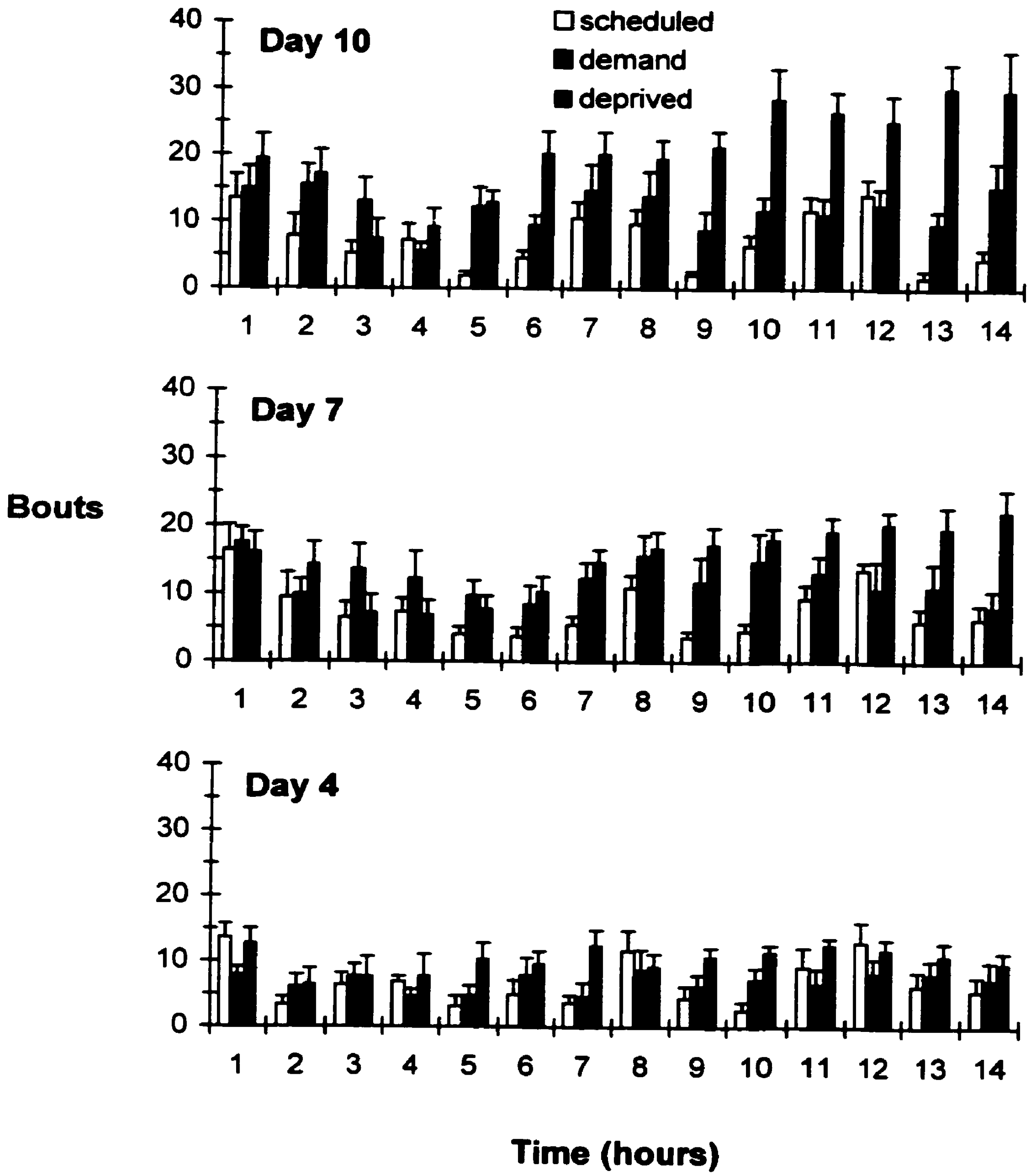

Day 10
☐ scheduled
■ demand
■ deprived
Day 7
Day 4
Begs
0
100
200
300
400
500
1
2
3
4
5
6
7
8
9
10
11
12
13
14
Time (hours)

chicks as they noticeably increased their begging effort as test time (deprivation time) proceeded (interaction between time and treatment, F = 14.70, df = 26, 624, $p < 0.0001$). For scheduled chicks, the pattern of begging corresponded to their feeding schedule (compare to Fig. 2) as chicks gradually increased their begging until they were fed, after which, begging levels decreased and then the cycle repeated (Fig.10). A similar situation occurred in demand chicks, but because different demand chicks were fed at various times throughout the day (Fig. 2) a cyclical pattern of begging in the grouped data was less apparent. The interaction between time and age was significant (F = 1.68, df = 26, 624, p = 0.0193), as younger chicks begged more than older chicks.

Deprived chicks generally produced significantly more hourly begs than demand and scheduled chicks (deprived > demand = scheduled, F = 37.69, df = 2, 624, $p < 0.0001$). Hourly begging levels were similar among all ages (F = 2.26, df = 2, 624, p = 0.1150), but there was a significant interaction between treatment and age (F = 3.15, df = 4, 624, p = 0.0224), as deprived chicks decreased their hourly begging effort as they became older.

Begging bouts. Time had a highly significant main effect on the number of begging bouts recorded (Fig. 11, F = 11.03,

Figure 11. Number of begging bouts (mean ± SE) produced by scheduled, demand and deprived chicks during hourly time intervals throughout the daytime test period from 0800 h to 2200 h (hour 1 to hour 14, respectively, n = 9 for each treatment group for every hour at each age).

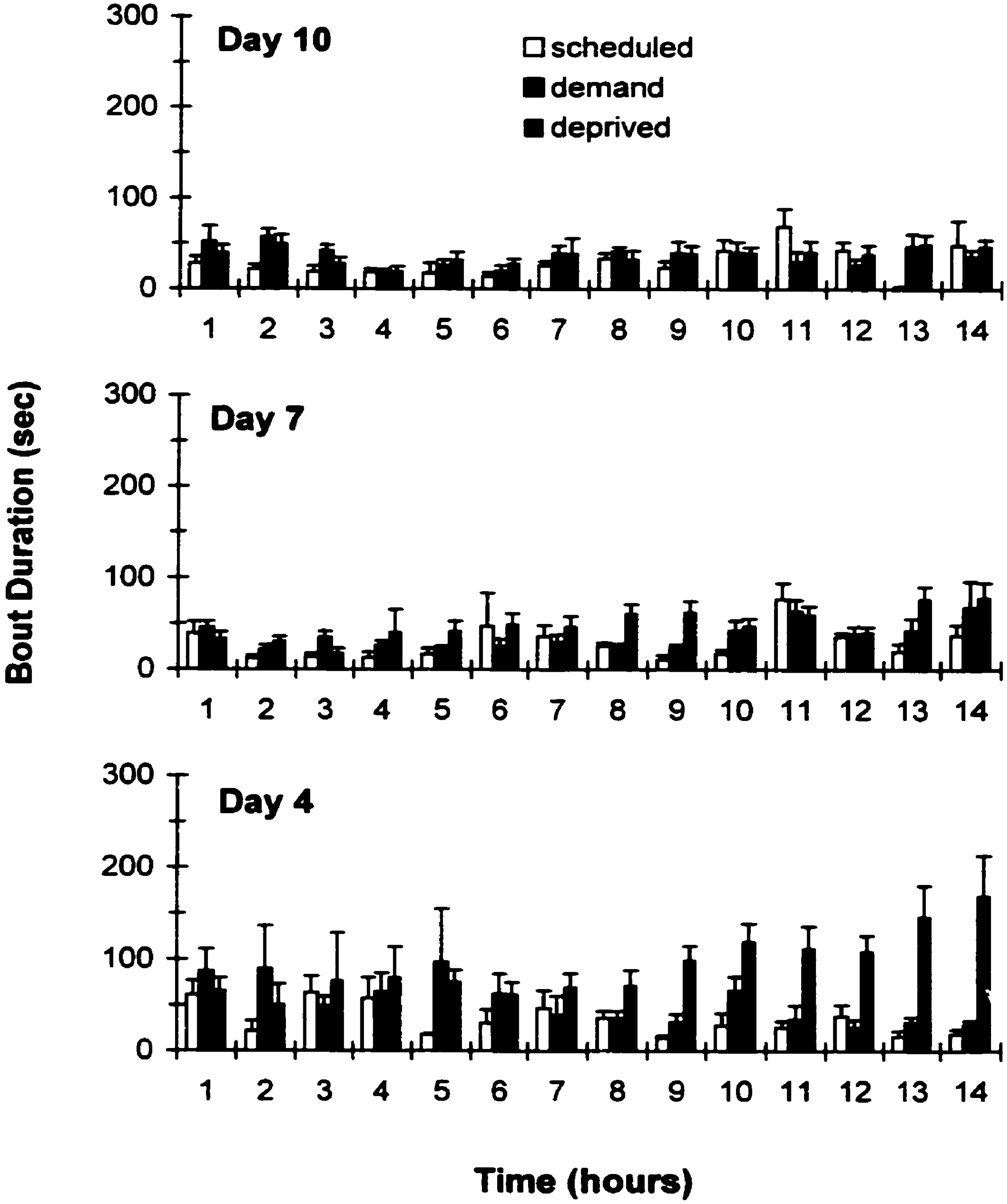

Day 10
☐ scheduled
■ demand
■ deprived
Day 7
Day 4
Bouts
40
30
20
10
0
1 2 3 4 5 6 7 8 9 10 11 12 13 14
Time (hours)

df = 13, 624, $p < 0.0001$), with chicks producing significantly more begging bouts toward the end of the test day (and during the first hour of testing). Again, this difference was mainly attributable to the deprived chicks (time x treatment interaction, F = 5.67, df = 26, 624, $p < 0.0001$), and was consistent among all ages (time x age interaction, F = 1.45, df = 26, 624, p = 0.0710).

Deprived chicks produced more hourly bouts than demand chicks, whereas scheduled chicks produced the least number of bouts per hour (deprived > demand > scheduled, F = 38.15, df = 2, 624, $p < 0.0001$). Older chicks produced more bouts each hour than younger chicks (day 10 = day 7 > day 4, F = 9.75, df = 2, 624, p = 0.0003). This trend was especially apparent among deprived chicks (F = 3.02, df = 4, 624, p = 0.0265).

Mean bout duration (s). On day 4, mean hourly bout durations were significantly different over time only among deprived birds, which maintained longer bout durations toward the end of the test day (Fig. 12, unequal variances and sample sizes, Kruskal Wallis, deprived: H = 22.50, df = 13, p = 0.0481, demand: H = 13.70, df = 13, p = 0.40, scheduled: H = 13.36, df = 13, p = 0.42). Chicks from all three treatment groups had significantly different hourly

Figure 12. Mean bout duration (s, mean ± SE) maintained by scheduled, demand and deprived chicks during hourly time intervals throughout the daytime test period from 0800 h to 2200 h (hour 1 to hour 14, respectively). No value for mean bout duration was provided for any particular hour when chicks did not produce a single beg or only gave 1 beg per bout. Mean ± SE hourly sample size for each treatment group at day 4, 7 and 10 were as follows: scheduled n = 5.4 ± 0.5, 5.9 ± 0.4 and 5.7 ± 0.7, demand n = 6.1 ± 0.4, 7.1 ± 0.3 and 7.4 ± 0.3, deprived n = 7.9 ± 0.4, 8.0 ± 0.4 and 8.2 ± 0.4, respectively.


Bout Duration (sec)
Day 10
☐ scheduled
■ demand
■ deprived
Day 7
Day 4
300
200
100
0
1 2 3 4 5 6 7 8 9 10 11 12 13 14
Time (hours)

bout durations at day 7 (scheduled: $H = 32.41$, $df = 13$, $p = 0.0021$, demand: $H = 27.07$, $df = 13$, $p = 0.0122$, deprived: $H = 31.08$, $df = 13$, $p = 0.0033$). On this day, scheduled chicks, and to a lesser extent demand chicks, had longer bout durations prior to, rather than after, their scheduled and demand feedings, respectively (see Fig. 2 for feeding times). Again, demand chicks gradually increased their hourly bout duration with increasing hunger. Only scheduled birds had significantly different hourly bout durations during the course of testing on day 10 (scheduled: $H = 26.73$, $df = 13$, $p = 0.0135$, demand: $H = 19.90$, $df = 13$, $p = 0.0977$, deprived: $H = 17.93$, $df = 13$, $p = 0.1601$).

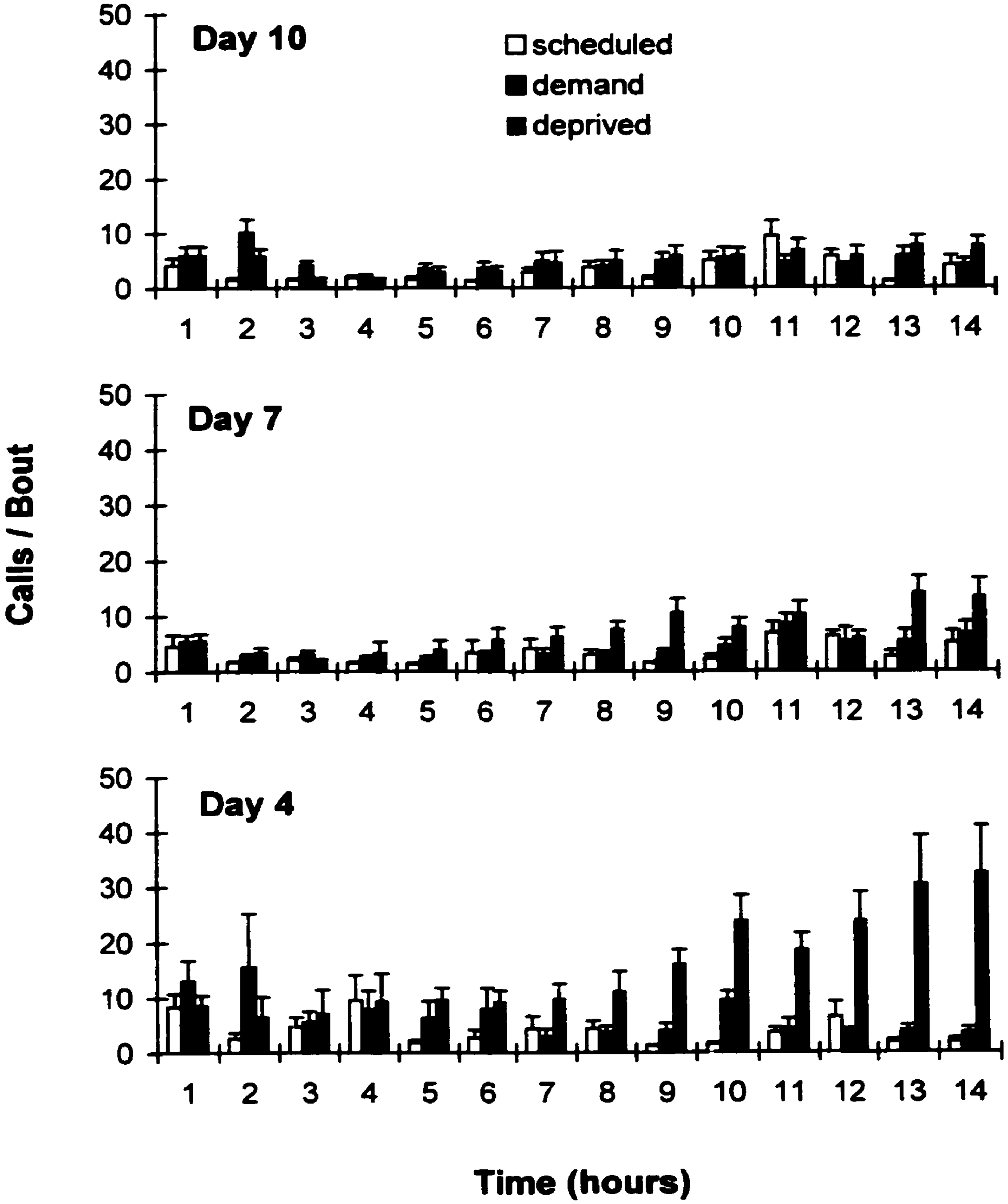
Treatment significantly influenced chick hourly bout duration at all ages (day 4: deprived > demand = scheduled, $H = 56.10$, $df = 2$, $p < 0.0001$, day 7: deprived > demand > scheduled, $H = 42.00$, $df = 2$, $p < 0.0001$, day 10: demand = deprived > scheduled = demand, $H = 7.10$, $df = 2$, $p = 0.0287$). In deprived birds, younger chicks had significantly longer mean hourly bout durations than older chicks (deprived: day 4 > day 7 > day 10, $H = 64.38$, $df = 2$, $p < 0.0001$, age not significant for demand and scheduled chicks: $H = 4.40$, $df = 2$, $p = 0.1110$, $H = 2.56$, $df = 2$, $p = 0.2784$, respectively).

Calls per bout. On day 4, deprived chicks progressively produced more calls per bout throughout the test day (Fig.

13, $H = 40.46$, $df = 13$, $p = 0.0001$), however, neither demand nor scheduled chicks produced significantly different numbers of calls per bout over time (demand: $H = 18.24$, $df = 13$, $p = 0.1486$, scheduled: $H = 21.53$, $df = 13$, $p = 0.0630$). On days 7 and 10, scheduled chicks produced significantly more calls per bout during hours leading up to their feeding times, especially before 0800 h (i.e. end of hour 12, day 7: $H = 24.74$, $df = 13$, $p = 0.0250$, day 10: $H = 39.74$, $df = 13$, $p = 0.0002$). At these ages, deprived chicks, following the initial few hours of testing (i.e. before the actual deprivation period began), gradually increased the number of calls per bout (day 7: $H = 49.15$, $df = 13$, $p < 0.0001$, day 10: $H = 45.75$, $df = 13$, $p < 0.0001$). Number of calls per bout did not differ significantly over time in 7- and 10-day old demand chicks (day 7: $H = 21.34$, $df = 13$, $p = 0.0666$, day 10: $H = 15.91$, $df = 13$, $p = 0.2539$).

A highly significant effect of treatment on hourly number of calls produced per bout was present at all three ages (day 4: deprived > demand > schedule, $H = 76.00$, $df = 2$, $p < 0.0001$, day 7: $H = 53.49$, $df = 2$, $p < 0.0001$, day 10: $H = 26.97$, $df = 2$, $p < 0.0001$). Only deprived chicks produced significantly different hourly number of calls per bout over age ($H = 54.87$, $df = 2$, $p < 0.0001$), where younger chicks had uttered more calls per bout than older chicks

Figure 13. Number of calls produced per bout (mean ± SE) by scheduled, demand and deprived chicks during hourly time intervals throughout the daytime test period from 0800 h to 2200 h (hour 1 to hour 14, respectively). No value for calls per bout was provided for any particular hour when chicks did not produce a single beg. Mean ± SE hourly sample size for each treatment group at day 4, 7 and 10 were as follows: scheduled n = 7.4 ± 0.4, 7.7 ± 0.3 and 8.1 ± 0.4, demand n = 7.5 ± 0.3, 8.3 ± 0.2 and 8.4 ± 0.2, deprived n = 8.5 ± 0.2, 8.6 ± 0.2 and 9.0, respectively.

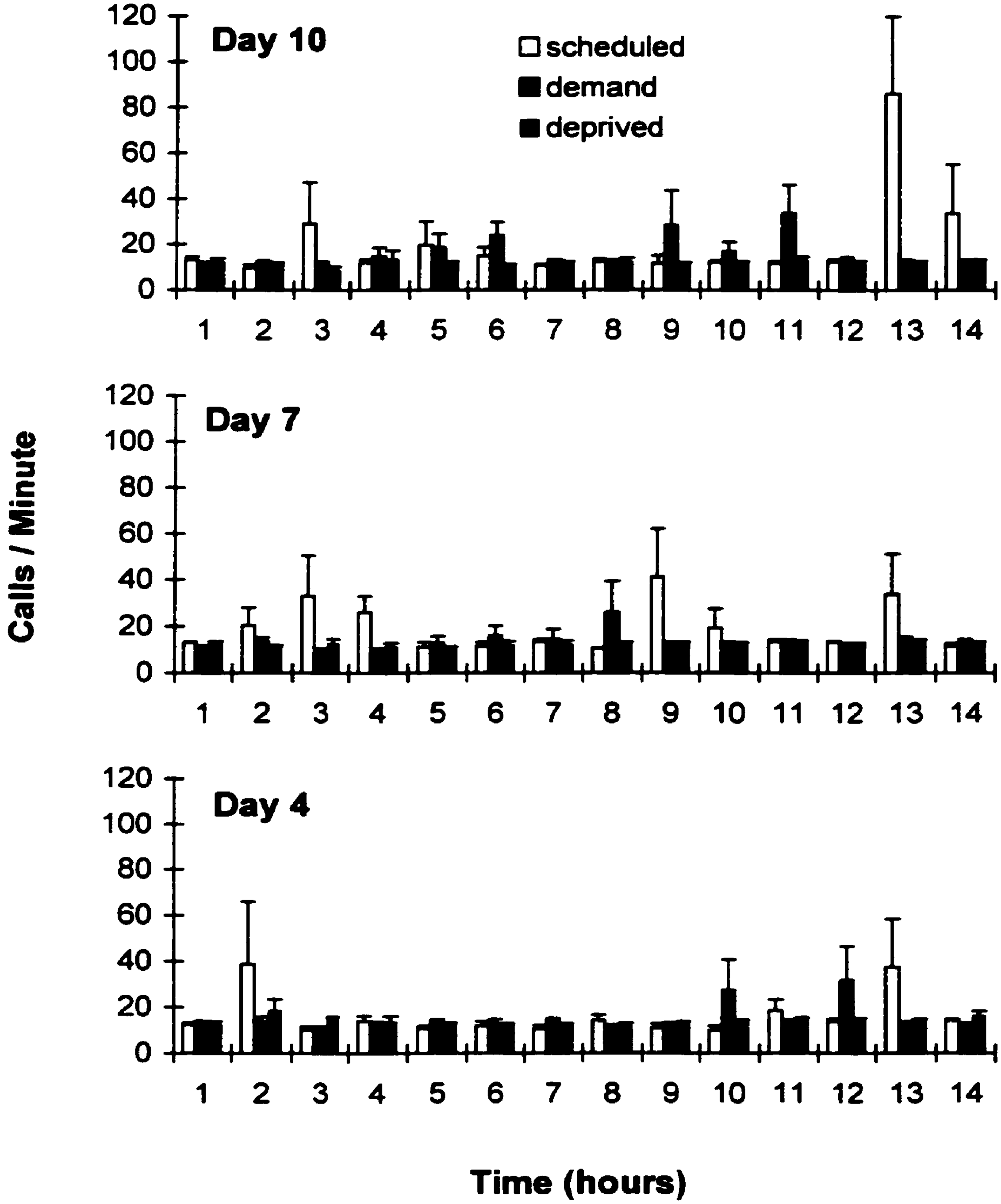

Day 10
□ scheduled
■ demand
■ deprived
Day 7
Day 4
50
40
30
20
10
0
1
2
3
4
5
6
7
8
9
10
11
12
13
14
Calls / Bout
Time (hours)

(day 4 > day 7 > day 10, age not significant for demand and scheduled chicks: $H = 3.24$, $df = 2$, $p = 0.1980$, $H = 0.0946$, $df = 2$, $p = 0.9434$, respectively).

Calls per minute within bouts. At all ages, scheduled and demand chicks called at relatively consistent rates (calls/min) within bouts throughout the test day (Fig.14, scheduled and demand chicks on day 4: $H = 14.62$, $df = 13$, $p = 0.3314$, $H = 13.41$, $df = 13$, $p = 0.4164$, day 7: $H = 20.35$, $df = 13$, $p = 0.0867$, $H = 16.80$, $df = 13$, $p = 0.2087$, day 10: $H = 13.23$, $df = 13$, $p = 0.4304$, $H = 12.57$, $df = 13$, $p = 0.4812$, respectively). These chicks occasionally produced very short bouts with unusually high calling rates (e.g. 2 calls in a bout that lasted 1s yielded a calling rate of 120 calls per min) when followed by scheduled, and to a lesser extent demand, feedings (see Fig. 2). Although not significantly different, testing hours that included these short bouts had relatively higher overall calling rates. For deprived chicks, calling rate was significantly different over time only on day 4, even though an overall trend (increasing or decreasing) was not apparent over time ($H = 31.46$, $df = 13$, $p = 0.0029$, calls/min was not significantly different on day 7 or day 10: $H = 17.17$, $df = 13$, $p = 0.1916$, $H = 13.00$, $df = 13$, $p = 0.4482$, respectively).

Treatment had a significant effect on hourly number of

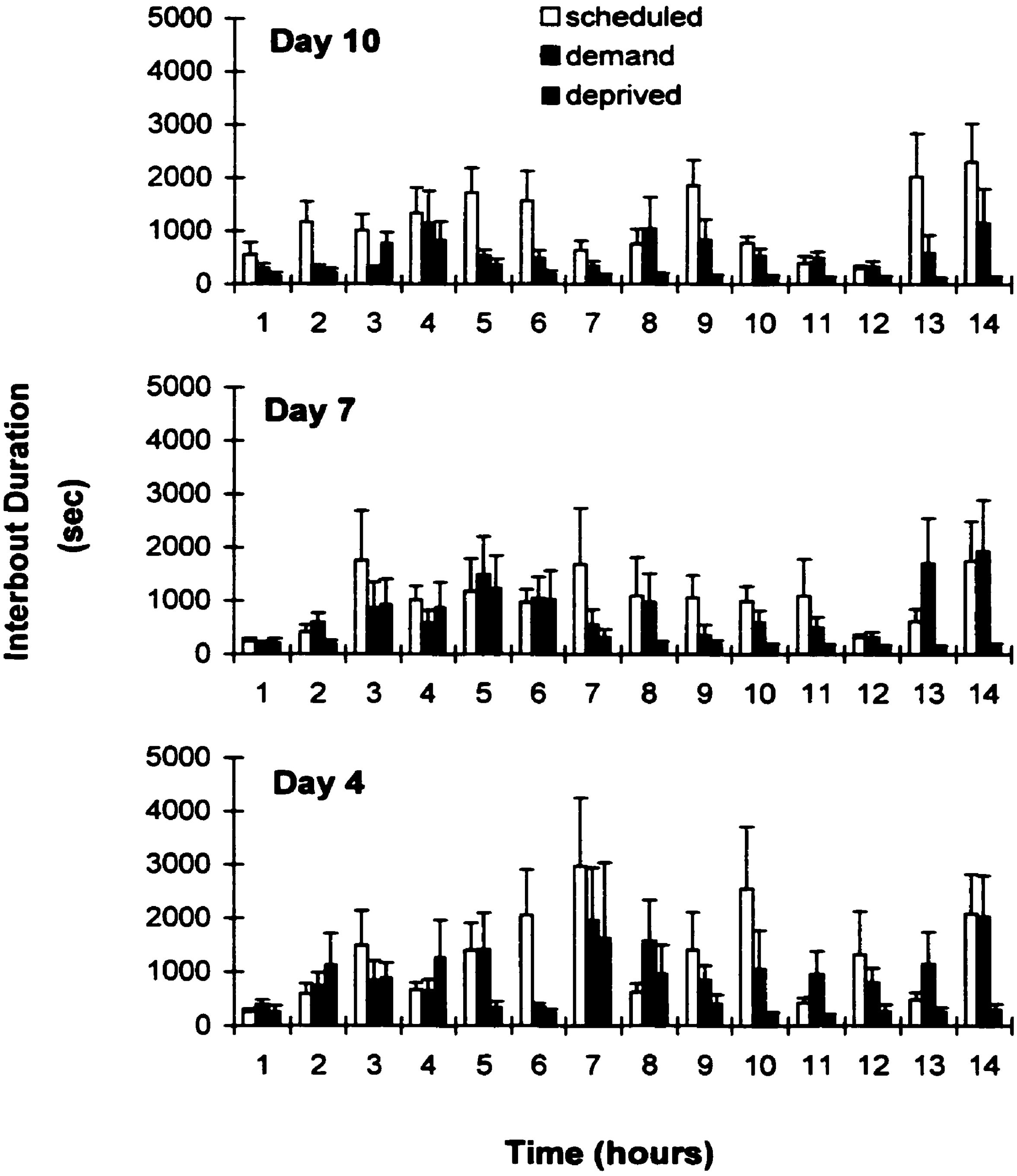
Figure 14. Number of calls produced per minute within bouts (mean ± SE) by scheduled, demand and deprived chicks during hourly time intervals throughout the daytime test period from 0800 h to 2200 h (hour 1 to hour 14, respectively). No value for number of calls per minute was provided for any particular hour when chicks did not produce a single beg or only produced 1 beg per bout. Mean ± SE hourly sample size for each treatment group at days 4, 7 and 10 were as follows: scheduled n = 5.4 ± 0.5, 5.9 ± 0.4 and 5.7 ± 0.7, demand n = 6.1 ± 0.4, 7.1 ± 0.3 and 7.4 ± 0.3, deprived n = 7.9 ± 0.4, 8.0 ± 0.4 and 8.2 ± 0.4, respectively.


Day 10
□ scheduled
■ demand
■ deprived
Day 7
Day 4
Calls / Minute
Time (hours)
0
20
40
60
80
100
120
1
2
3
4
5
6
7
8
9
10
11
12
13
14

calls produced per minute during begging bouts on day 4 (demand = deprived > scheduled = demand, H = 8.01, df = 2, p = 0.0182) and day 7 (deprived = scheduled > demand = deprived, H = 8.55, df = 3, p = 0.0139), but not on day 10 (H = 5.58, df = 2, p = 0.0614). Younger deprived chicks called at higher hourly rates than older chicks (day 4 > day 7 = day 10), while day 4 demand chicks produced significantly more calls per minute within hourly bouts than 7-day old chicks (day 10 = day 4 > day 7 = day 10, H = 8.99, df = 2, p = 0.0112, scheduled chicks did not produce significantly different hourly calling rates during begging bouts over age: H = 3.49, df = 2, p = 0.1748).

Mean interbout duration (s). Time had a significant effect on hourly mean interbout duration in scheduled chicks at all three ages (Fig. 15, day 4: H = 25.83, df = 13, p = 0.0179, day 7: H = 30.50, df = 13, p = 0.0040, day 10: H = 31.25, df = 13, p = 0.0031). Interbout durations did not differ significantly over time at any age in demand chicks (day 4: H = 7.56, df = 13, p = 0.8873, day 7: H = 16.98, df = 13, p = 0.2003, day 10: H = 15.67, df = 13, p = 0.2672). At all ages, chicks in the deprived group generally maintained shorter interbout durations before their deprivation period began (ie. hour 1 and 2) and during the later hours of their deprivation period when begging was most intense (see Fig. 4, day 4: H = 24.28, df = 13, p = 0.0286, day 7: H = 45.82,

Figure 15. Mean interbout duration (s, mean ± SE) maintained by scheduled, demand and deprived chicks during hourly time intervals throughout the daytime test period from 0800 h to 2200 h (hour 1 to hour 14, respectively). No value for mean interbout duration was provided for any particular hour when chicks did not beg. Mean ± SE hourly sample size for each treatment group at day 4, 7 and 10 were as follows: scheduled n = 7.4 ± 0.4, 7.7 ± 0.3 and 8.1 ± 0.4, demand n = 7.5 ± 0.3, 8.3 ± 0.2 and 8.4 ± 0.2, deprived n = 8.5 ± 0.2, 8.6 ± 0.2 and 9.0, respectively.


Day 10
Day 7
Day 4
□ scheduled
■ demand
■ deprived
Interbout Duration (sec)
Time (hours)
0
1000
2000
3000
4000
5000
1
2
3
4
5
6
7
8
9
10
11
12
13
14

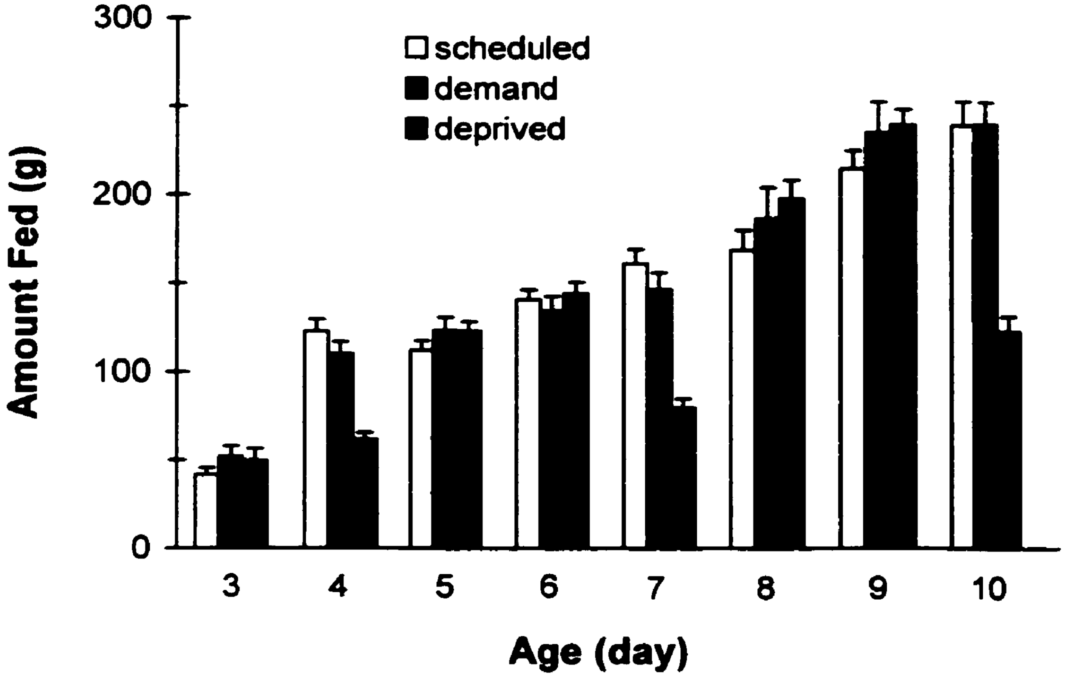
df = 13, $p < 0.0001$, day 10: H = 54.20, df = 13, $p < 0.0001$).

On day 4, deprived chicks maintained significantly shorter hourly mean interbout durations than chicks in the other two treatment groups (deprived > demand = scheduled, H = 33.64, df = 2, $p < 0.0001$). Chicks from all three treatment groups had significantly different hourly interbout durations on days 7 and 10 (day 7: deprived < demand < scheduled, H = 49.33, df = 2, $p < 0.0001$, day 10: deprived < demand < scheduled, H = 85.27, df = 2, $p < 0.0001$). Age significantly influenced hourly mean interbout durations in deprived and demand chicks (H = 30.32, df = 2, $p < 0.0001$: H = 14.76, df = 2, $p = 0.0006$, respectively), as younger chicks had longer periods of silence between begging bouts than older chicks (day 4 > day 7 = day 10 for both deprived and demand chicks). Hourly interbout durations were similar among all ages in scheduled chicks (H = 1.72, df = 2, $p = 0.4238$).

Analysis of Food Consumed by Chicks and Subsequent Chick Growth During the Eight-Day Rearing Period (Days 3 to 10)

Total daily amounts of food consumed by chicks. Owing to the nature of their feeding regime on test days (days 4, 7 and 10), chicks that were reared in the deprived treatment group were fed, on average, lower amounts of food than scheduled and demand chicks (Fig. 16, F = 9.38, df = 2, 168,

Figure 16. Total daily amounts of food consumed (g, mean ± SE) during the eight-day rearing period (days 3 - 10, inclusively) by scheduled, demand and deprived chicks (n = 9 for each treatment group at each age). The relatively low recorded levels of daily food eaten by day 3 chicks were a result of their late-afternoon arrival from the field. Totals for deprived chicks on test days (days 4, 7 and 10) include their feeding after the test (deprivation) period concluded immediately after 2200 h.



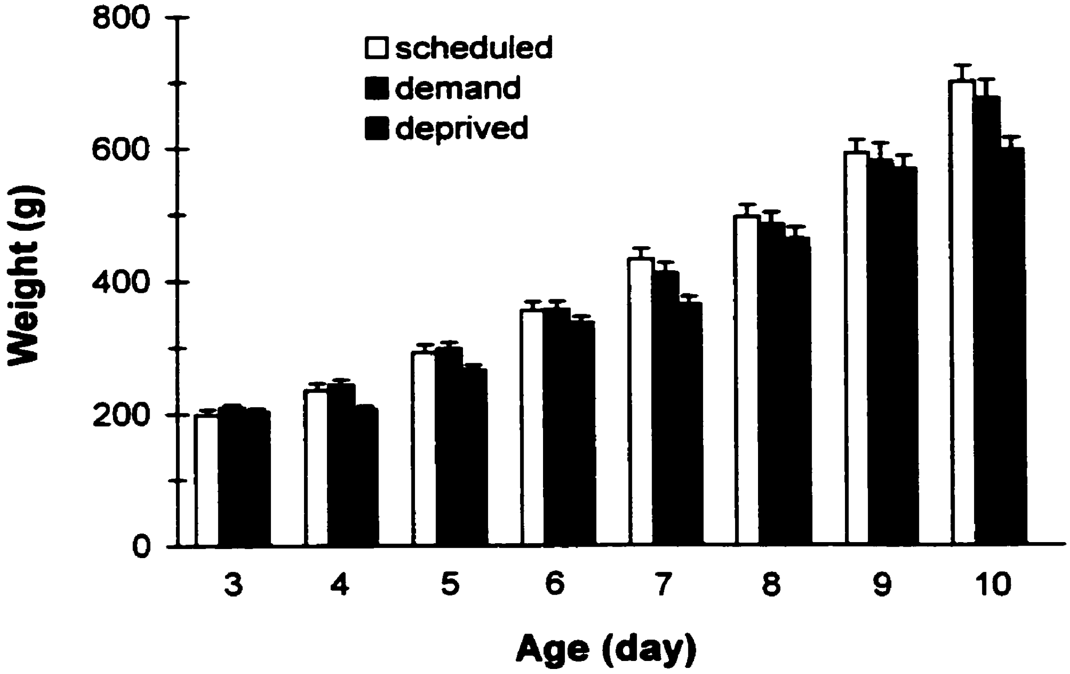
☐ scheduled
■ demand
■ deprived
Amount Fed (g)
300
200
100
0
3
4
5
6
7
8
9
10
Age (day)

$p = 0.0010$). In general, as chicks grew older they consumed more food ($F = 137.44$, df = 7, 168, $p < 0.0001$), however, this trend was interrupted on test days as deprived chicks were fed only once before and once after their deprivation period during daytime testing (see methods for details, age x treatment interaction, $F = 11.89$, df = 14, 168, $p < 0.0001$).

Chick growth. Overall, chick mass (g) did not differ significantly between treatment groups (Fig. 17, $F = 2.44$, df = 2, 168, $p = 0.1082$) and consistently increased with age ($F = 845.69$, df = 7, 168, $p < 0.0001$). However, as expected, deprived chicks gained little compared to scheduled and demand chicks during test days ($F = 3.23$, df = 14, 168, $p = 0.0002$).

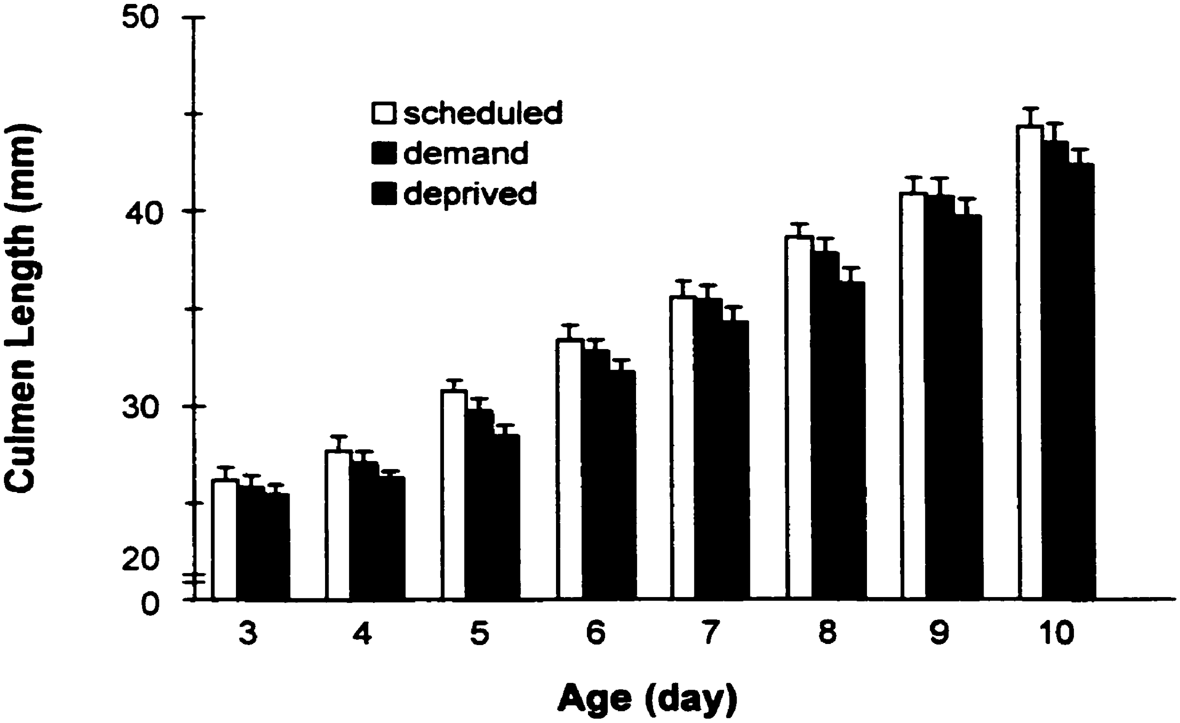
Treatment did not significantly influence chick culmen length (mm, Fig. 18, $F = 1.72$, df = 2, 168, $p = 0.2004$). Culmen growth increased steadily with age ($F = 680.75$, df = 7, 168, $p < 0.0001$), and any minor differences between treatment groups remained relatively constant over time (interaction between treatment and age, $F = 0.52$, df = 14, 168, $p = 0.9173$).

Figure 17. Daily weights (g, mean ± SE) of scheduled, demand and deprived chicks during the eight-day rearing period (days 3 - 10, inclusively, n = 9 for each treatment group at each age).



800
600
400
200
0
Weight (g)
□ scheduled
■ demand
■ deprived
3
4
5
6
7
8
9
10
Age (day)

Figure 18. Daily culmen lengths (mm, mean ± SE) of scheduled, demand and deprived chicks during the eight-day rearing period (days 3 - 10, inclusively, n = 9 for each treatment group at each age).


50
40
30
20
0
Culmen Length (mm)
□ scheduled
■ demand
■ deprived
3
4
5
6
7
8
9
10
Age (day)

DISCUSSION

Feeding Schedule and Development of Begging

Feeding chicks on demand as opposed to a fixed schedule increased general begging, although differences between the two groups were at times small and insignificant. However, these differences deserve consideration as they either increased or remained relatively consistent with age or over time. Confounding effects of food intake on subsequent begging levels seem unlikely as chicks from both treatment groups received similar amounts of food (Fig. 1). Therefore, training chicks to beg to receive food (reinforced learning) may have played a role in the observed enhanced begging of demand chicks. Previous studies on young budgerigars (Stamps 1993), great tits (Davies 1978, Ryden 1982), cactus wrens (Ricklefs 1967) and gulls (Evans 1979, 1980) have shown that, as with young pelicans, chicks are capable of assessing food reinforcement schedules. It would be beneficial for a pelican chick to learn to probe its parent (through the use of reliable signals of need, see below) for food in a fashion that will provide it with an optimal amount of food, thereby ensuring its own growth and survival.

Both demand and scheduled chicks produced virtually an identical total number of begs and bouts (of begging) at the start of rearing (Figs. 4 and 5, respectively), but as testing proceeded, demand chicks elevated their begging efforts with respect to scheduled chicks. The observed growing disparity between treatment groups most likely was a result of the aforementioned reinforced learning on behalf of chicks which were fed on demand. However, it may have been due to demand chicks having to beg longer to receive food, whereas scheduled chicks stopped begging when they were fed at their respective scheduled times (Fig. 10, compare to Fig. 2). Even though scheduled chicks begged at relatively lower levels than demand chicks, they did, however, continue to beg throughout the duration of testing. This suggests that raising pelicans on a fixed-feeding schedule could be a successful method for captive rearing.

Feeding schedule did not influence the duration of bouts (Fig. 6) or the number of calls emitted during bouts (Fig. 7) at any age. Therefore, demand chicks either quickly learned that extending the duration of begging bouts and/or increasing the frequency in which begs were elicited did not "pay off" with additional food rewards, or they simply did not experience the level of hunger of deprived chicks (see below). This is not to say that these begging variables were not affected by modest daily variations in hunger. Scheduled chicks, and to a lesser extent demand chicks, had longer bout durations (Fig. 12) and more calls per bout (Fig. 13) leading up to, rather than after, their scheduled and demand feedings on days 7 and 10, respectively. Daily and hourly interbout durations (Fig. 9 and 15) indirectly resulted from bout durations. Chicks from both treatment groups begged at similar rates (Figs. 8 and 14). Therefore, feeding chicks on demand as opposed to on a fixed schedule only increases absolute number of begs and bouts elicited by chicks, but does not affect bout structure itself. In the nest, the parent can presumably recognize and be assured that the chick is in need of food, only once it has begged extensively.

Food Deprivation and Implications for Honest Signalling Theory

In agreement with Godfray's (1991) "honest signalling" predictions, deprived chicks begged at higher levels (Figs. 4 and 5), spent more time begging (Fig. 6) and emitted more calls per bout (Fig. 7) than chicks that were fed on demand and on a fixed schedule, which suggests that begging is a reliable indication of a chick's nutritional need. Interestingly, as deprived chicks matured, they tended to engage in begging bouts more often, however, they happened to beg less during these respective bouts. Chicks may have adopted this strategy because the quantity, rather than the quality, of bouts could be a more successful tactic to attract parental attention to their state of need. Apparently little information about offspring need is provided by the rate at which chicks beg during a bout, as chicks in all three treatment groups generally maintained similar rates of calling (Fig. 8).

My results also imply that chick solicitation for food follows a graded response, as deprived chicks increased their begging effort when they were increasingly deprived of food (see Figs. 10 to 13), a phenomenon that has previously been documented in many different species (Kilner and Johnstone 1997, see General Introduction). In fact, elevated begging exhibited by scheduled and demand chicks as they approached their respective feeding times (and presumably became more hungry) is further evidence that begging is a reliable indicator of nutritional need. Field studies on American white pelicans have shown that parents respond appropriately to increases in chick begging, with more feedings taking place when lengthy bouts of calling were produced (Evans 1992, Daniels 1997).

Even though begging appears to be a reliable indicator of need for nourishment, contrary to assumptions made by biological signalling theory (Zahavi 1975, 1977, Grafen 1990, Maynard Smith 1991, Johnstone and Grafen 1992) and Godfray's (1991, 1995) honest signalling model, it may not be necessarily costly to produce (Maynard Smith 1994, Daniels 1997, Kilner and Johnstone 1997). Therefore, it may be possible that the parent and offspring mutually agree on the required level of care (e.g. in gulls, Evans et al. 1995). Maynard Smith's (1991, 1994) model demonstrated that low cost signals could evolve if there was an absence of conflict of interest between signaller and receiver. Kin relationships between parent and offspring may represent such a situation as both participants share a commmon interest, that being the chick's health and survival. Perhaps during the early nestling period there is very little or complete absence of parent-offspring conflict over the level of parental care required for the chick, while a weaning conflict (Trivers 1974) emerges during the termination of the nestling period.

An alternative explanation is that the parent is able or willing to respond to a low-cost signal. If a conflict of interest over parental resources does exist, it is still possible for a low-cost signalling system to be evolutionarily stable as long as the signaller and receiver interact repeatedly (Silk et al. 2000). A good example of such a situation is the interaction between a pelican parent and its chick during the nestling period. Evidence for low-cost honest signals exists, as rooster crowing vocalizations have been found to be relatively inexpensive to produce (Chappell et al. 1995), but are still considered to be an honest signal of fighting ability (Furlow et al. 1998).

Even though low metabolic costs are associated with chick begging (McCarty 1996, Leech and Leonard 1996, Daniels 1997, Bachman and Chappell 1998), absolute costs for a single begging call may increase as the deprivation period increases because less energy may be readily available as chicks become more hungry (and presumably weaker) over long periods of deprivation. This, taken together with the observed step-wise increase in number of begs produced during increasing deprivation, could be extremely costly to a chick with such a high level of need.

Even low cost signals could potentially have a significant effect on the energy budget of young chicks during critical growth and developmental periods (Verhulst and Wiersma 1997, Weathers et al. 1997). This is probably the case with a pelican chick, that usually is required to produce extensive bouts of begging (probing) before it is actually fed by the parent that constantly tends to the nest. Since chicks from all three treatment groups begged at similar rates (Figs. 8 and 14) within bouts, it appears that chicks always beg more or less at maximum intensity when they beg, no matter what the level of need. This finding contrasts with house wren nestlings, that worked at only half maximum effort during begging (Chappell and Bachman 1998). An explanation for this discrepancy is that wren chicks only beg a few times per hour and their parent, which is only present at the nest for brief feeding intervals, almost immediately responds to begging after arriving at the nest.

A fundamental question that should be addressed is, "What exactly does costly mean?". Presently, the term "costly" is arbitrarily set by researchers. It is important to keep in mind that when assessing costs one must include, in addition to metabolic costs of begging, potential costs of predation (Haskell 1994), loss of inclusive fitness when successful begs deprived siblings of food (Briskie et al. 1994, Godfray 1995) and physical competition with siblings may also elevate begging costs (Parker and Macnair 1978).

Although sibling competition (Smith and Montgomerie 1991, Price et al. 1996) and parent-offspring conflict (Trivers 1974) may act to increase or exaggerate begging levels, the hypothesis that begging is a reliable indicator of need (as shown with deprived chicks in this study) should not be ruled out (see Cotton et al. 1996). However, caution is required when interpreting these types of results (Iacovides and Evans 1998).

Effects of Feeding Schedule on Chick Growth

Chick mass did not differ significantly between treatment groups, but scheduled birds were slightly heavier than demand chicks near the end of testing (Fig. 17). A possible explanation for this result could be that scheduled birds simply did not have to work (beg) as hard as demand chicks in order to get fed (remember that both scheduled and demand chicks were fed very similar amounts of total food during the rearing period, Fig. 16). This result may support the notion that begging does indeed "drain" a chick's energetic pool, which in turn suggests that begging vocalizations are somewhat costly to produce (Godfray 1991, 1995, Verhulst and Wiersma 1997, Weathers et al. 1997). The lower body weights recorded for deprived chicks reflect their feeding regime on test days. Any significant differences between scheduled and demand chick weights from those recorded in the field (Evans 1997) can probably be attributed to the time of day in which field weight readings were recorded, that is, field measurements could have been taken just prior to, or just after a parental feeding.

Culmen length was similar among all treatment groups (Fig. 18). A study by Oyan and Anker-Nilssen (1996) has shown that in food-stressed Atlantic puffin chicks growth is preferrably allotted to features which are paramount for successful or quick fledging (e.g. head, brain, culmen, feet and wings). Perhaps then it is not surprising that culmen growth and development was not adversely affected in those chicks which experienced prolonged deprivation periods during testing days. The culmen enables a young, rather uncoordinated, altricial pelican chick to manipulate its food efficiently and acts as the pivot for an "anchor and drag" type of movement used for limited mobility. It is also used as a weapon when attacking or defending against its sibling during the brood-reducing period. Therefore culmen length can have an indirect influence on survival and determine whether or not a chick successfully fledges.

CHAPTER 2: INTERACTION BETWEEN HEAT AND FOOD IN DEPENDENT YOUNG AMERICAN WHITE PELICANS

INTRODUCTION

Offspring of altricial birds hatch in an immature state, thus relying heavily on their parents for food (Kilner and Johnstone 1997) and heat (Dawson and Evans 1957, 1960, Dunn 1975). To some extent, parents should be able to anticipate offspring need and provide appropriate levels of care. However, short-term variations in both need states are inevitable, and may go unnoticed by parents unless the offspring signals its current state of need to the parent (Harper 1986, Hussell 1988, Godfray 1995).

A recent model developed by Godfray (1991, 1995) suggests that dependent offspring honestly signal their true needs to parents. Central to his model are the assumptions that parents should provision young in relation to signal intensity and that signals are costly (Godfray 1991). Numerous empirical studies on various avian species that rear young that actively solicit food and/or heat from parents have shown that chicks produce reliable signals of need (with apparently minimal energetic expenditure but are potentially costly as they may attract the attention of predators) upon food deprivation (short- and long-term) and/or chilling (Kilner and Johnstone 1997, see General

Introduction for details regarding these studies). Parents generally respond to these signals in a way which appears to address the homeostatic requirements of their young (Kilner and Johnstone 1997, see General Introduction). Based on the results of these studies, it appears that the predictions of Godfray's honest signalling model are fairly accurate. However, in order to appreciate fully biological signalling systems in species whose chicks signal for both food and warmth during the nestling period, it is necessary to understand how the different need states influence one another. The present study will extend the scope of Godfray's honest signalling model by testing for interactions between nutritional need and warmth in young American white pelicans.

Newly hatched pelicans distinctively vocalize to solicit heat or food (Evans 1992). In the field, parents respond to cold-induced squawks and begging vocalizations with brooding and food-related behaviour, respectively (Evans 1992, pers. obs.). The rate in which cold-induced squawks are elicited is positively correlated with increased chilling (Evans 1994), and parents increase their brooding responses accordingly (Evans 1992). Begging levels also increased with food deprivation (see Chapter 1), and the probability of being fed is enhanced when longer bouts of calling are produced (Evans 1992). In these dependent young, both heat and food are obviously critical requirements for normal chick growth and development. Moreover, an important relationship between these two resources may also exist, that is, if food is provided with little heat, or heat is provided with little food, chick growth and development could be severely affected.

Pelicans generally raise only one chick. Two eggs are normally laid and both may hatch (a larger first-hatched A chick and a smaller, later-hatched B chick, with an approximately 2.5 day hatching interval), with only the older or more robust surviving an early brood reduction period (Evans and Knopf 1993). Nests are typically shallow with poorly defined rims, allowing chicks to periodically wander small distances away from the nest (Evans and Knopf 1993, pers. obs.), especially when the parent stands up to preen or tends to the needs of a single chick (Evans 1989). When young chicks are displaced beyond the immediate vicinity of the nest cup, they are rarely retrieved by their parents (pers. obs.). Given that a chick's motor capabilities are relatively undeveloped at such a young age (Evans and Knopf 1993), chicks may inadvertently remain exposed over extended periods of time. Young colony-reared pelican chicks, which are essentially ectothermic until they reach an age of two weeks (Evans 1984), have been observed to experience a general slowing of behaviour (as would a typical ectotherm) when exposed to modest low temperatures overnight. However, as long as ambient conditions were not too severe, this appeared to have no irreversible negative effects once they eventually returned to the nest (Evans, pers. comm.). If a chick was frequently displaced from the nest and subsequently chilled over time, it is quite possible that a general retardation in growth and development could occur. In fact, laboratory studies have shown that moderately chilled pipped eggs of American white pelicans, ring-billed gulls and domestic chickens experienced retarded embryonic development as hatching times significantly increased (Evans 1990b, 1990c). In extreme cases, however, if chicks are absent from the nest for too long of a period of time, they may become comatose and die from exposure (Evans and Knopf 1993).

Choi and Bakken (1990) have observed a similar effect of chilling on digestive responses in altricial red-winged blackbirds (*Agelaius phoeniceus*), where hunger contractions of the proventriculus in chicks decreased as ambient temperature was lowered. Numerous studies on ectothermic reptiles and amphibians have also pointed to the importance of ambient temperature on digestive processes (Skoczylas 1970). In the red spotted newt (*Notophthalmus viridescens*) and hibernating frogs (*Rana pipiens*), digestion takes up to 7 times longer at 5°C than at 25°C, or 20 times longer at 4°C than at 21°C, respectively (Gossling et al. 1980, Jiang and Claussen 1993). Temperature dependence of digestion in ectotherms has also been found in other species, for example in the grass snake (*Natrix natrix* L.), rubber boas (*Charina bottae*), fresh water turtles, and in American crocodiles (*Crocodylus acutus*, Skoczylas 1970, Lang 1979, Parmenter 1981, Dorcas et al. 1997). Moreover, when exposed to a cold environmental temperature, snakes may refuse food (Skoczylas 1970, Naulleau 1983).

Although less well studied than in ectotherms, digestion in young altricial birds that pass through an ectothermic stage is likely as dependent on temperature as it is in amphibians and reptiles. One avian study that has addressed the relationship between temperature, digestion and subsequent growth has been done on incompletely endothermic domestic chicks (*Gallus domesticus*, Osbaldiston 1966). Chicks reared at 7.2°C as opposed to 32.3°C experienced a 3-fold decrease in their digestive efficiency and grew at only half the rate as the warmer chicks (Osbaldiston 1966). Achieving a body temperature that is sufficient for normal digestion may be a crucial function during behavioural interactions between a chick and its parent (Theberge and West 1973), who provides the necessary resources (food and heat) for digestion and ultimately growth.

Of particular relevance to the overall relationship between need state and level of solicitation is that begging for food decreases in response to chilling in ring-billed gull and red-winged blackbird chicks (Conover and Miller

1981, Choi and Bakken 1990). A similar response has been observed in young pelicans (Evans 1994), but has not yet been studied in detail. Therefore, it appears that vocal thermoregulatory squawks, which solicit parental brooding that enables a chick to attain an optimal warm body temperature, may play an intricate role in a chick's overall ability to acquire food (Evans 1994). In addition, prior to the development of endothermy, preliminary tests suggested a young pelican's ability to compete for food may be reduced when it is moderately chilled (Evans pers. comm.). Therefore, the benefits of maintaining a high and stable body temperature seem to be fundamentally important to the early growth and development of pelicans, and could become critical to a chick's survival during the period of peak brood reduction (usually by end of first week) when sibling competition for resources is at its maximum (Cash and Evans 1986) but endothermy is poorly developed.

The main objective of the present study was to assess the interaction between a young pelican's need for food and heat, thereby attempting to broaden the scope of Godfray's (1991, 1995) honest signalling model. The study focused on the chronic effects of rearing temperature (warm versus cold) on the relative amounts of heat and food solicitation in young altricial American white pelicans. In addition to testing an important behavioural model, work on honest signalling has practical merit in the field of animal welfare assessment, where signals of need may provide useful cues to evaluate an animal's current state and well-being (Weary and Fraser 1995, Weary et al. 1996).

Specifically, this study tested whether heat, such as that solicited from a brooding parent, influenced begging behaviour, feeding response, competitive ability, and growth in thermally dependent young chicks. Chronic chilling was hypothesized to retard the development of normal begging while at the same time increase the number of squawks elicited by chicks and reduce overall growth, even when daily food intake was held constant between warm- and cold-reared chicks. In addition, the effect of direct chilling and warming on begging, feeding responses and competitive ability of warm and cold chicks, respectively, was investigated. Chicks (warm and cold) were expected to beg less and eat less food when they were fed under cool, as opposed to warm, conditions. Warm-reared chicks were predicted to be more successful competitors under both warm and cold test temperatures.

METHODS

American white pelican chicks were collected under provincial permit from a local breeding colony on East Shoal Lake, Manitoba, Canada (see O'Malley and Evans 1980 for description). In order to minimize disturbance to the colony, hatch date was approximated through observations of courtship flight (Evans and Cash 1985) during April, 1998. As in the previous study, only the larger first-hatched or A-chick was taken, thereby minimizing productivity loss as a second B-chick was left for the parent to rear (parents lay 2 eggs but normally rear only one chick, Evans and Knopf 1993). Upon entry into the breeding colony, three-day old chicks were selected based on their weight (approximately 190 g, Evans 1997). At this time, a number was drawn on each chick's back for identification purposes.

Chicks were placed in a portable incubator (held at 35.0±.5°C) and transported by van to the University of Manitoba. Upon arrival at the lab, chicks were randomly assigned to holding pens. Four pens were each divided into two chambers by an opaque barrier. Each chamber measured 36.5 cm x 21.0 cm x 32.9 cm high. As in the previous (1997) study, pens were constructed of standardized plywood with wire-mesh floors and a Plexiglass sheet on top (so chicks could be observed; the three holding pens used during the 1997 study were used again during this study, while the fourth holding pen was constructed in identical fashion). A hole large enough for a hand to fit through was cut on each side of the pen. These holes were used during feedings, and were otherwise covered by insulating Styrofoam. Once again, 15-watt light bulbs were used to regulate a 14 h light:10 h dark cycle in the pens. Pens were dark from 2200 h to 0800 h. Pen temperature varied between 35.0±.5°C and 27.5±.5°C, depending on treatment and chick age (see below). A portable floor heater was placed in the room which contained the warmer pens. To fine-tune temperature, all pens (warm and cold) were equipped with a 100-watt light bulb (controlled by a thermostat) and a miniature fan, both of which were placed below the pen floor. The fan circulated warm air through flexible conduits to the upper chamber.

Four testing pens (two warm and two cold) closely resembled the individual compartments of the holding pens, each appropriate to hold one chick. The three testing pens used during the 1997 study were used again during this study, while a fourth testing pen was constructed in identical fashion. On a given day of testing, three of these pens were equipped with a microphone that was placed into a hole in the Plexiglass above the chick. Calls produced by the chick activated a sound-operated relay and a custom-built call discriminator switch. As in 1997, the call discriminator automatically distinguished, by call duration, food begs from significantly shorter heat squawks given by the chick (see sonograms in Evans 1992). Spontaneous begging coming from each of the three test pens was recorded on an event data logger. Squawk calls produced by the chick were recorded manually using a hand-held counter at sampled intervals of 1 h before each daytime feeding (see below for exact times). In addition to these individual testing pens, a single large-chambered pen (no opaque barrier, 36.5 = 42.6 cm x 32.9 cm high), capable of housing 2 chicks at one time, was used for short-term competitive tests (see below).

Rearing Conditions

Feeding methods. Chicks were hand-fed a chopped fish-based diet obtained from a local mink farm (Evans 1994). All chicks were fed on a fixed schedule, four times a day (Schaller 1964), at every age during both test and non-test days. Feedings were provided at 0900 h, 1200 h, 1600 h and 2000 h (an identical feeding schedule was used for the scheduled birds in the 1997 study). Feeding chicks on a fixed schedule does not appear to adversely affect chick begging (see Chapter 1), and ensured that all chicks were fed four times each, every day.

As in the previous study, the amount of food a chick received was determined by the cumulative weight of the spoon, dish, and food before feeding minus the cumulative weight of all these variables combined with spillage, if any, after feeding was completed. To minimize possible confounding effects of differing total food eaten on subsequent begging levels and growth, the amount of food provided for both treatment groups (see below) was equated as closely as possible. Water was provided, via an eye dropper, during feedings to ensure feces remained in a natural liquid state.

Treatment groups. Upon arrival from the field, each chick was randomly assigned to one of two treatment groups which determined their rearing temperature. The first treatment group consisted of chicks being reared in a warm pen held at 35.0±.5°C, 33.5±.5°C and 32.0±.5°C on days 3 - 6, 7 - 9 and 10, respectively. These temperatures represent thermoneutral temperatures for chicks at these ages (Evans, pers. comm.). Chicks placed in the second treatment group were reared 4.5°C cooler in pens held below thermoneutrality, that is, at 30.5±.5°C, 29.0±.5°C and 27.5±.5°C on days 3 - 6, 7 - 9 and 10, respectively. Chicks raised at the warm temperatures acted as a control group for experimental cold chicks, which tested for chronic effects of mild chilling on begging and growth. In addition, the effects of direct short-term chilling (on warm birds) and warming (on cold birds) on begging, feeding and competitive ability of warm-and cold-reared chicks were determined (see below).

Test Procedure

Simultaneous testing of 3 chicks (at least one per treatment) was conducted using the warm and cold rearing rooms. Each chick was tested on days 4, 7 and 10. Chicks were balanced among the 3 call discriminators to minimize possible confounding effects of differential sensitivity of this equipment. In order to minimize movement of equipment between successive testing days, two testing pens were present in each room, even though only 1 of them might have been active on a given day.

Testing duration was approximately 24 h, starting at 2200 h and continuing to 2200 h the next day. At 2200 h on the evening of testing, three chicks were removed from their respective holding pen (either 2 cold and 1 warm, or vice versa) and placed in a darkened individual test pen (which coincided with the onset of the dark cycle) held at their respective rearing temperature. Lights were turned on at 0800 h (light schedule hours: 0800 h to 2200 h) the following morning. At this time, each chick was briefly removed from its testing pen and weighed, to the nearest 0.1 g, on an electronic balance. Feather (down) development and culmen length were also measured with calipers (to the nearest 0.1 mm). When assessing down development, length was measured at a standardized location on the chick's flank. Down development and culmen length acted as linear measurements of growth and development, while chick mass provided an estimate of these parameters (due to the possible presence of undigested food) for comparisons among warm- and cold-reared chicks.

During the daytime testing period (duration of 14 h), chicks from both treatment groups were fed 2 times under both warm and cool temperatures (in balanced order). Chicks were fed to satiation (determined as the point when the bird refused to eat additional food). It was not necessary to force-feed chicks as they spontaneously ate the food presented to them. When it was time for a chick to be fed under the opposite rearing temperature (e.g. cold chick fed under warm temperature), it was temporarily removed from its original testing pen (e.g. cold) and placed in a different testing pen, which was held at the opposite temperature (e.g. warm), where it was fed. The fourth testing pen (inactive) accommodated these "switched" feedings. Chick begging was counted manually during the "switched" feedings, and resumed automatically once the chicks were brought back to their original testing pens. On non-test days, chicks remained in holding pens (held at their respective rearing temperature) for all feedings.

The competitive ability of warm- and cool-reared chicks was assessed by determining which individual became most aggressive and obtained a pre-weighed amount of food (3, 4 and 6 g of food on days 4, 7 and 10, respectively, which was anticipated to be approximately 10% of average meal size at the appropriate ages, see Chapter 1) when warm- and cool-reared chicks were fed two at a time in weight-matched pairs. The outcomes of this test were scored as either a win, loss or a tie. These chicks were temporarily removed from their respective testing pens just prior to their 0900 h and 2000 h feeding and placed in a single large-chambered pen held at either the respective warm or cool temperature (tested in balanced order). A paired test was stopped if one chick (scored as a win) began to attack the other (scored as a loss), as is common during the brood reduction process at natural nests (Cash and Evans 1986, Evans and McMahon 1987, pers. obs.). Immediately after the competitive test was completed, chicks were returned to their original test pen where they were fed to satiation. After testing was completed each day, chicks had a second measurement of body weight taken. For all non-test chicks, weighing and measuring procedures were identical to that described for test chicks.

Twenty-four chicks, 12 per treatment group, were used. Similar to the study in Chapter 1, a testing period of 27 days (3 rotations of 9 days each) was required. At the beginning of each rotation, 3 chicks began testing anew each day (at least 1 chick per treatment) for the first 3 days per group of 9 subjects. Every 9 days a new group of 9 chicks was started. Unfortunately, 3 cold-reared chicks died during the duration of testing (one on day 6, 7 and 10) and were removed from the study. Upon completion of testing, chicks were given to trained Zoology Department Animal Holding staff to be euthanized with carbon dioxide overdose. Canadian Council of Animal Care regulations were followed throughout this study.

Data Analysis

All begging calls produced by chicks during testing (accurate to the nearest second) were downloaded from the data logger. For analysis, a begging bout was defined (as in Chapter 1) as any group of begs, including single begs, separated by 20 s (Daniels 1997). A time interval of 20 s between begs is approximately 10 times the interval between successive begs when chicks are calling strongly (Daniels 1997). As in the previous study, the effect of treatment on the total amount of begs and bouts produced by chicks, average bout duration (s), average number of calls in a bout, average rate of calling (calls/min) within bouts and mean interbout durations (s) were assessed using a customized Excel program (see Chapter 1 for details). If chicks only called once during begging bouts, they did not receive a value for mean bout duration or calls per minute for those particular bouts. To ensure that ingested food levels did not influence or confound the above begging variables, total daily amounts of food consumed by chicks from both treatment groups during the 8 day rearing period were compared. In addition, total amount of squawks produced during 1 h sampling periods before each scheduled feeding were compared between treatment groups.

To determine whether rearing temperature influenced chick growth and development, down length, culmen length and chick mass were compared between warm and cold chicks. Direct effects of chilling (in warm chicks) and warming (in cold chicks) on begging, feeding and competitive ability of warm- and cold-reared chicks were assessed.

As chicks in the two treatment groups were independent, ANOVA tests, with repeat measures on age, were used for statistical analyses of all variables except: chick begging frequency (begs/hr) during daytime versus nighttime test periods and weight comparisons between warm and cold birds in competitive tests on each test day, which used Wilcoxon Signed Rank tests and 1-way ANOVAs, respectively (Winer 1971). All statistical tests were performed using *Statistix* (Version 4.1 Analytical Software).

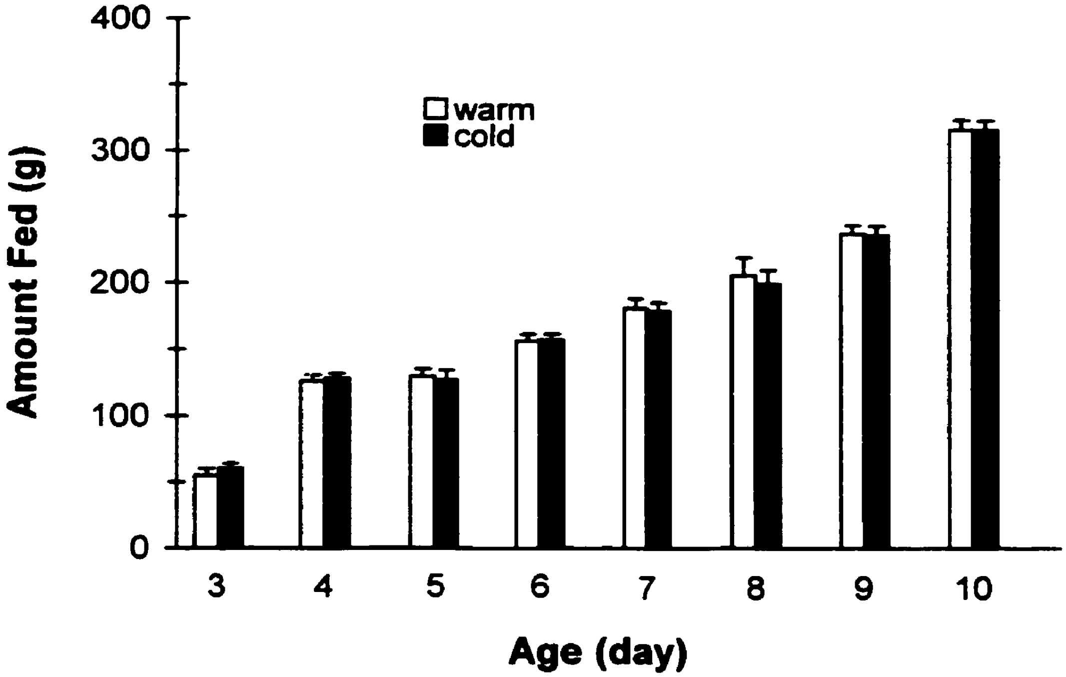
RESULTS

Distribution of Food

Total daily amounts of food consumed by chicks. Warm- and cold-reared chicks were fed on a fixed schedule, four times a day (once at 0900 h, 1200 h, 1600 h and 2000 h), at all ages during both test and non-test days. Chicks from both treatment groups readily ate the food that was presented to them, thereby eliminating any need for force-feedings. Warm- and cold-reared chicks consumed similar total daily amounts of food during the eight-day rearing period (Fig. 19, 2-way ANOVA, repeat measures on age, $F = 0.01$, $df = 1, 154$, $p = 0.9248$). Younger chicks ate lower daily amounts of food than older chicks ($F = 468.83$, $df = 7, 154$, $p < 0.0001$). The interaction between treatment and age was highly insignificant ($F = 0.24$, $df = 7, 154$, $p = 0.9733$).

It should be noted that because chicks from both treatment groups ate virtually identical daily amounts of food during test days, any potential confounding effects of variable food intake levels on subsequent begging were avoided. The mean ± SE amount of food consumed for each treatment group on days 4, 7 and 10 were: warm = 126.0 ± 4.4, 180.7 ± 7.3, 315.5 ± 7.3, cold = 127.9 ± 3.6, 178.6 ± 6.5, 315.0 ± 7.3, respectively.

Figure 19. Total daily amounts of food consumed (g, mean ± SE) during the eight-day rearing period (days 3 - 10, inclusively) by warm- and cold-reared chicks (n = 12 for both treatment groups at each age). The relatively low recorded levels of daily food eaten by day 3 chicks were a result of their late-afternoon arrival from the field.


400
300
200
100
0
☐ warm
■ cold
Amount Fed (g)
3
4
5
6
7
8
9
10
Age (day)

Total amount of food consumed by chicks under warm and cold test temperatures on test days. During testing, warm- and cold-reared chicks ate similar total amounts of food under both warm and cold test temperatures (Table 1, warm: $F = 0.28$, $df = 1, 44$, $p = 0.600$, cold: $F = 0.09$, $df = 1, 44$, $p = 0.7721$). When warm- and cold-reared chicks were analyzed separately, chicks from each treatment group also ate similar amounts of food when exposed to either warm or cold test temperatures (Table 1, warm: $F = 0.03$, $df = 1, 22$, $p = 0.8580$, cold: $F = 1.06$, $df = 1, 22$, $p = 0.3249$).

Chick Begging Frequency During Daytime Versus Nighttime Test Periods

During the daytime (light-schedule hours: 0800 h to 2200 h), chicks begged at a frequency of mean ± SE = 17.6 ± 4.4, 17.3 ± 3.2, 25.0 ± 6.8 begs/hr on days 4, 7 and 10, respectively. During the nighttime (dark cycle: 2200 h to 0800 h), chicks begged at a frequency of only 0.7 ± 0.2, 1.4 ± 0.4, 1.8 ± 0.4 begs/hr on days 4, 7 and 10, respectively (daytime versus nighttime: Wilcoxon Signed Rank Test, $p < 0.0001$ for day 4 and 10 tests, $p = 0.0001$ for day 7 test). As in the previous study (Chapter 1), the analysis of overall begging variables was limited to the daytime test period because of the small number of begs produced by chicks at all ages during the night.

Table 1. Amount of food consumed (g) by warm- and cold-reared chicks under both warm and cold test temperatures.

Age	Warm chicks		Cold chicks	
	Warm test temperature	Cold test temperature	Warm test temperature	Cold test temperature
Day 4	64.0 ± 2.5	62.1 ± 3.0	62.9 ± 3.0	65.1 ± 3.2
Day 7	94.6 ± 4.8	86.1 ± 3.3	84.5 ± 3.8	94.1 ± 6.2
Day 10	152.2 ± 6.3	164.1 ± 4.9	156.6 ± 3.6	157.1 ± 6.3

Note: Values are represented as means ± SEs of total amount of food consumed by chicks under both test temperatures during their respective test days. N = 12 for each cell.

Analysis of Begging Variables During Daytime Test Period

Begs produced by chicks. Warm-reared chicks begged more often than cold-reared chicks (Fig. 20a, F = 8.45, df = 1, 44, p = 0.0082), a result that was consistent at all ages (interaction between treatment and age, F = 0.76, df = 2, 44, p = 0.4721). Age did not have a significant effect on the number of begs produced by chicks (F = 0.96, df = 2, 44, p = 0.3891). The increase of begging observed in warm chicks on day 10 is somewhat misleading because on this day a single warm-reared chick produced 2137 begs, an amount which significantly increased the average begs produced for chicks in this group. When this particular chick was removed from the analysis, warm-reared chicks still produced significantly more begs than cold-reared chicks (Fig. 20b, F = 7.66, df = 1, 43, p = 0.0112). In fact, the difference between treatment groups remained relatively consistent over age (age x treatment interaction; F = 0.06, df = 2, 43, p = 0.9399), as warm birds begged approximately 2.2, 2.3 and 2.4 times more often than cold birds on days 4, 7 and 10, respectively.

As chicks immediately stopped begging when the Styrofoam panels covering the feeding holes were removed, an analysis on the total number of begs produced by chicks during feedings under both warm and cold temperatures was not possible.

Figure 20a. Overall number of begs (mean ± SE) produced by warm- and cold-reared chicks during the daytime test period (14 h) at each test age (n = 12 for both treatment groups at each age).

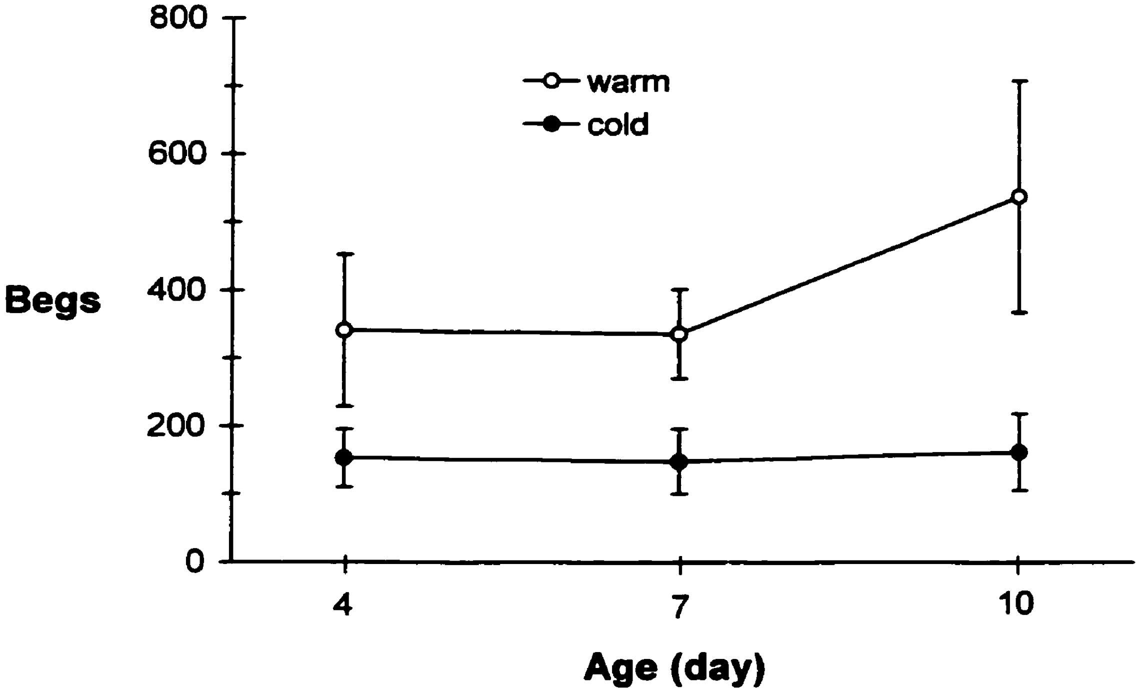
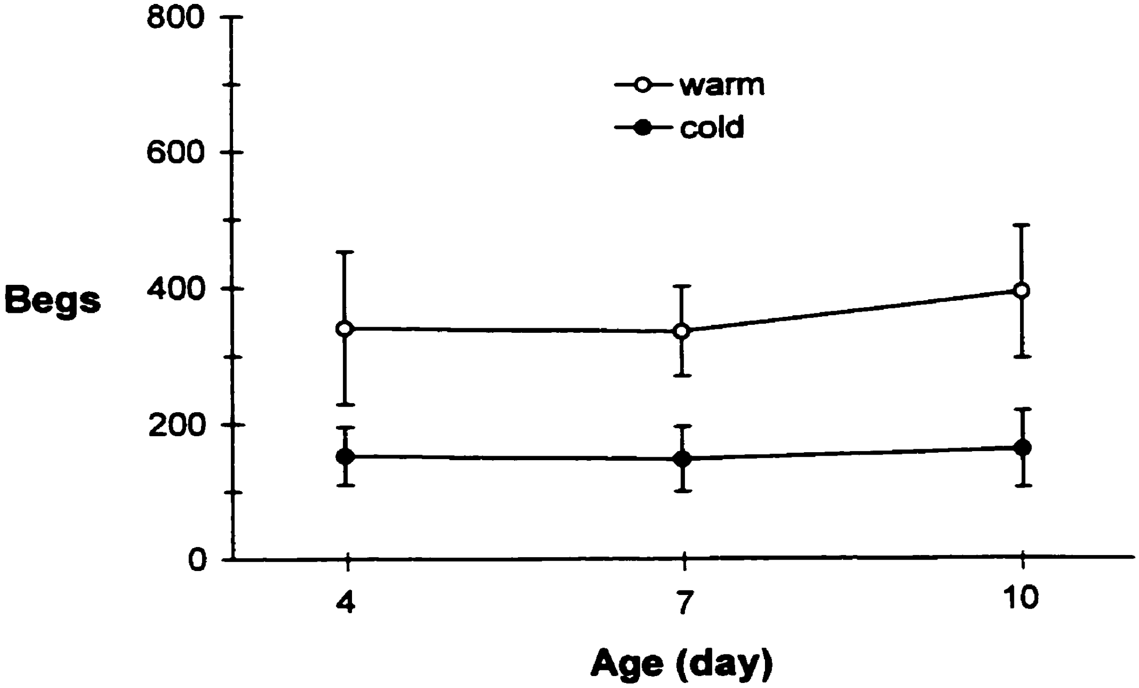

800
600
400
200
0
Begs
warm
cold
4
7
10
Age (day)

Figure 20b. Overall number of begs (mean ± SE) produced by warm- and cold-reared chicks during the daytime test period (14 h) at each test age after the day 10 warm-reared chick which produced 2137 begs was removed from the analysis (n = 11 for day 10 warm-reared chicks, n = 12 for chicks in both treatment groups at all other ages).


warm
cold
Begs
800
600
400
200
0
4
7
10
Age (day)

Begging bouts produced by chicks. Treatment had a significant main effect on total begging bouts produced by chicks, where warm-reared chicks produced a higher number of bouts than cold-reared chicks (Fig. 21, F = 11.48, df = 1, 44, p = 0.0026). The youngest chick age group produced the fewest amount of bouts (day 4 < day 7 = day 10, F = 4.52, df = 2, 44, p = 0.0164). The interaction between treatment and age was not significant (F = 1.84, df = 2, 44, p = 0.1714).

Mean bout duration (s). Warm-reared and day 4 chicks maintained longer begging bouts than cold-reared and day 7 chicks, respectively, but these differences were not significant (Fig. 22, main effect of treatment, F = 2.29, df = 1, 42, p = 0.1446, main effect of age, day 10 = day 4 > day 7 = day 10, F = 3.13, df = 2, 42, p = 0.0540, age x treatment interaction was insignificant, F = 0.06, df = 2, 42, p = 0.9442).

Calls per bout. Warm-reared chicks produced significantly more calls per bout than cold-reared chicks (Fig. 23, F = 4.73, df = 1, 44, p = 0.0408). Neither the main effect of age (F = 1.46, df = 2, 44, p = 0.2436) nor the interaction between treatment and age (F = 0.10, df = 2, 44, p = 0.9012) were found to significantly influence the number of begs produced per bout.

Figure 21. Overall number of begging bouts (mean ± SE) produced by warm- and cold-reared chicks during the daytime test period (14 h) at each test age (n = 12 for both treatment groups at each age).

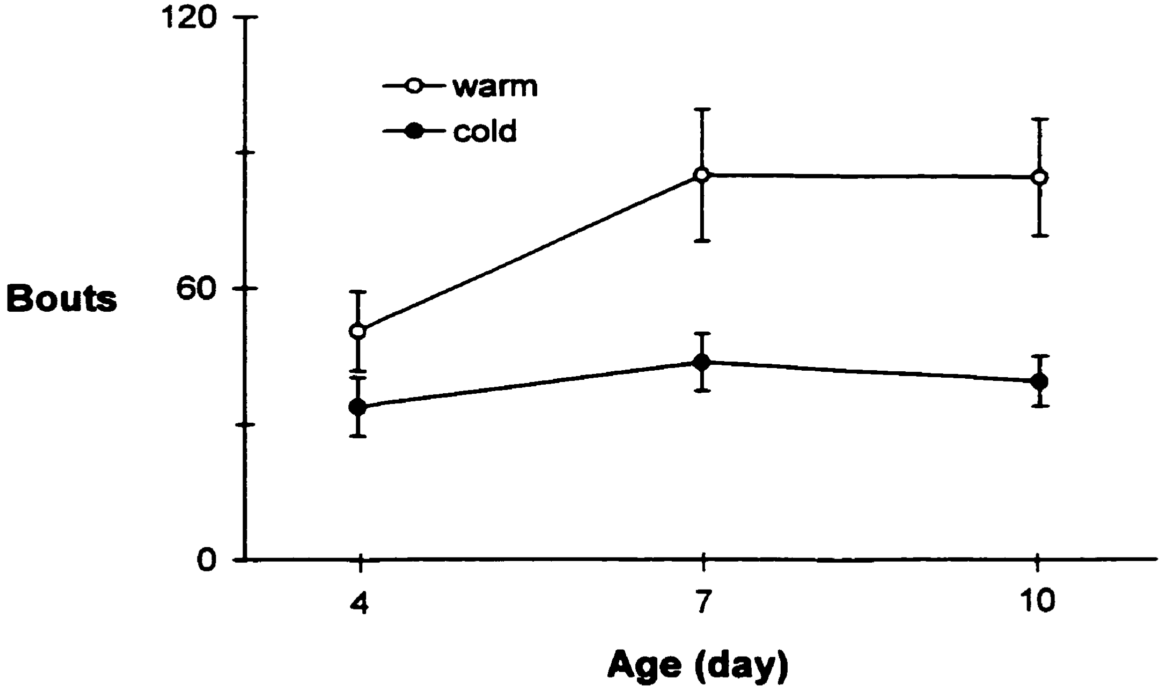

120
60
0
Bouts
warm
cold
4
7
10
Age (day)

Figure 22. Overall mean bout duration (s, mean ± SE) maintained by warm- and cold-reared chicks during the daytime test period (14 h) at each test age. No value for mean bout duration was provided when chicks only produced 1 beg per bout (n = 11 for day 4 and 10 cold-reared chicks, n = 12 for chicks in both treatment groups at all other ages).

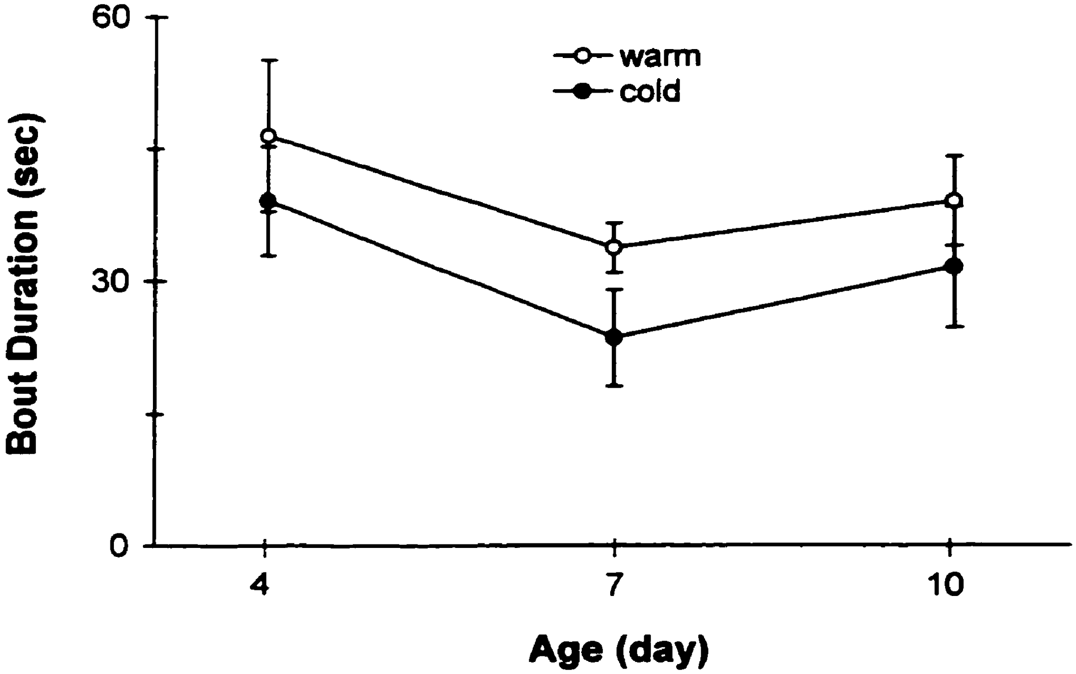
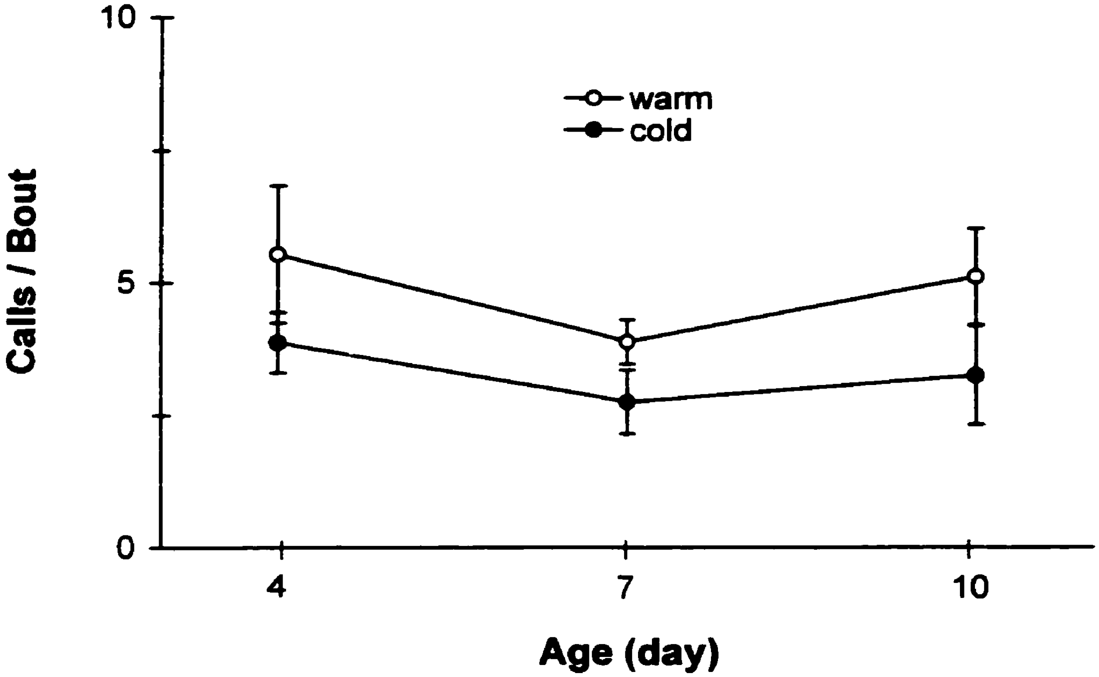
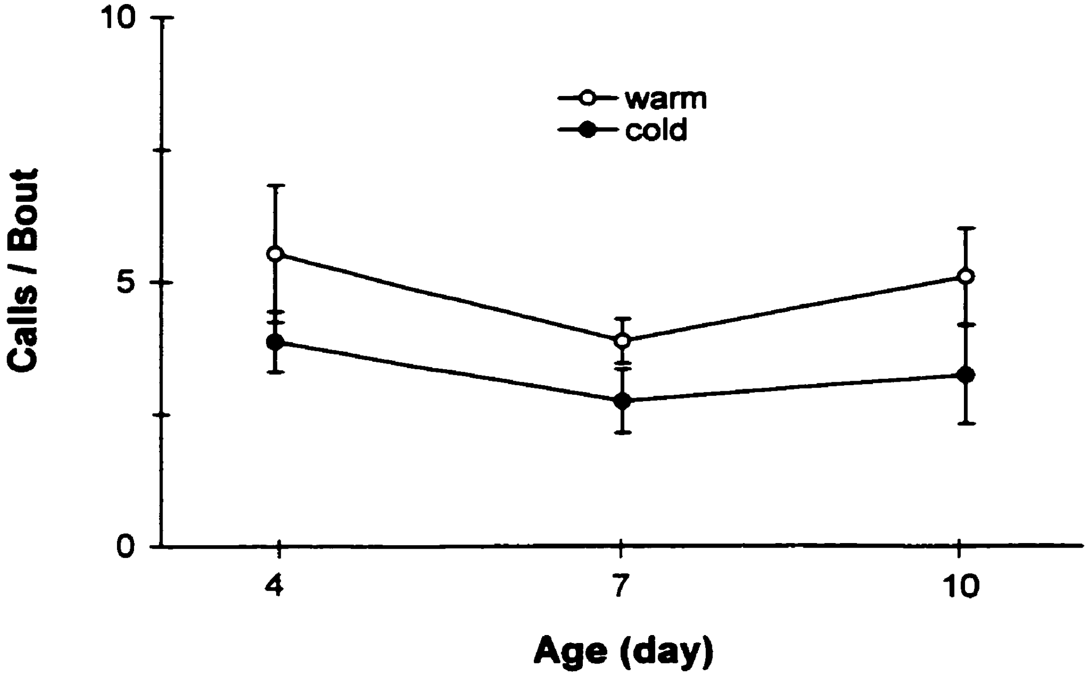

60
30
0
Bout Duration (sec)
warm
cold
4
7
10
Age (day)

Figure 23. Overall number of calls produced per bout (mean ± SE) by warm- and cold-reared chicks during the daytime test period (14 h) at each test age (n = 12 for both treatment groups at each age).


10
5
0
Calls / Bout
warm
cold
4
7
10
Age (day)


10
5
0
Calls / Bout
warm
cold
4
7
10
Age (day)

Calls per minute within bouts. Chicks from both treatment groups (F = 1.00, df = 1, 42, p = 0.3278) and of all ages (F = 1.17, df = 2, 42, p = 0.3195) called at comparable rates (calls/minute, Fig. 24a). This similarity in calling rates was consistent among all ages (F = 1.79, df = 2, 42, p = 0.1790). The conspicuously high calling rate for cold-reared chicks on day 4 was a result of 1 chick that produced two short begging calls in 1 s (yielding a calling rate of 120 calls per min) several times throughout the test day. After this chick's calling rate on day 4 was removed from the analysis, a much more accurate representation of calling rate for this particular group of chicks was determined (Fig. 24b). As expected, the main effects of treatment (F = 0.01, df = 1, 41, p = 0.9083) and age (F = 0.03, df = 2, 41, p = 0.9687) and the interaction between the two (F = 3.06, df = 2, 41, p = 0.0575) remained insignificant.

Mean interbout duration (s). Cold-reared chicks had longer mean interbout durations than warm-reared chicks (Fig. 25, F = 5.54, df = 1, 44, p = 0.0279), a trend which was evident during all test ages (age x treatment interaction, F = 2.97, df = 2, 44, p = 0.0616). Chick age did not significantly influence mean interbout duration (F = 0.19, df = 2, 44, p = 0.8253).

Figure 24a. Overall number of calls produced per minute within bouts (mean ± SE) by warm- and cold-reared chicks during the daytime test period (14 h) at each test age. No value for number of calls per minute was provided when chicks only produced 1 beg per bout (n = 11 for day 4 and 10 cold-reared chicks, n = 12 for chicks in both treatment groups at all other ages).

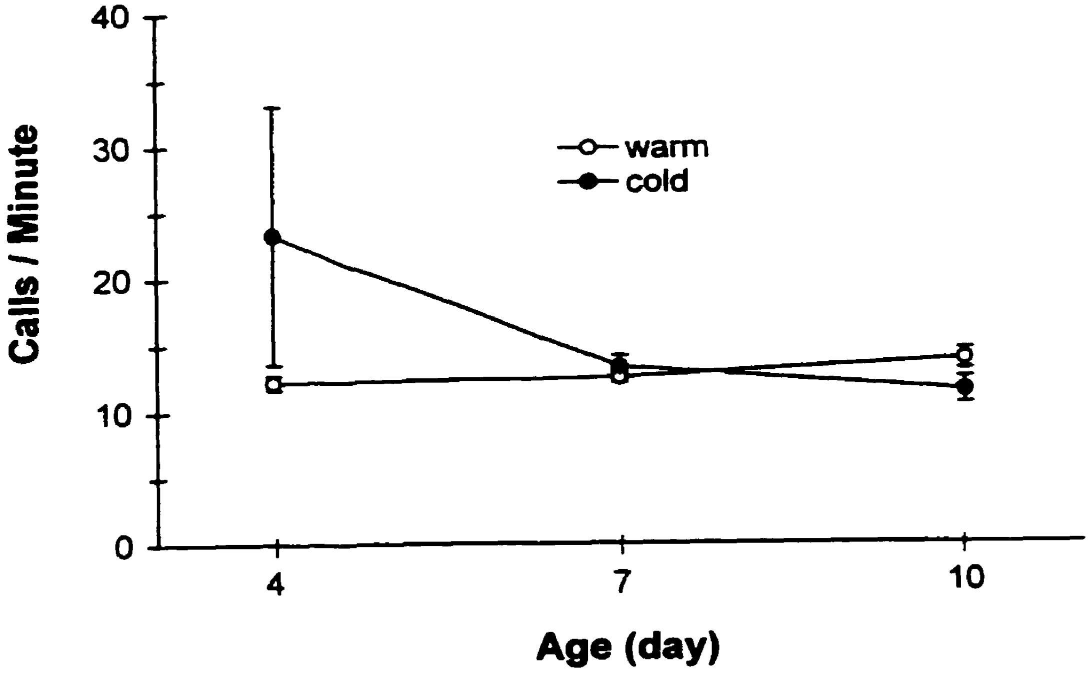

Calls / Minute
40
30
20
10
0
warm
cold
4
7
10
Age (day)

Figure 24b. Overall number of calls produced per minute within bouts (mean ± SE) by warm- and cold-reared chicks during the daytime test period (14 h) at each test age after the day 4 cold-reared chick which produced two short begging calls in 1 s (120 calls per min) was removed from the analysis. No value for number of calls per minute was provided when chicks only produced 1 beg per bout (n = 12 for warm-reared chicks at all ages, n = 10, 12 and 11 for day 4, 7 and 10 cold-reared chicks, respectively).

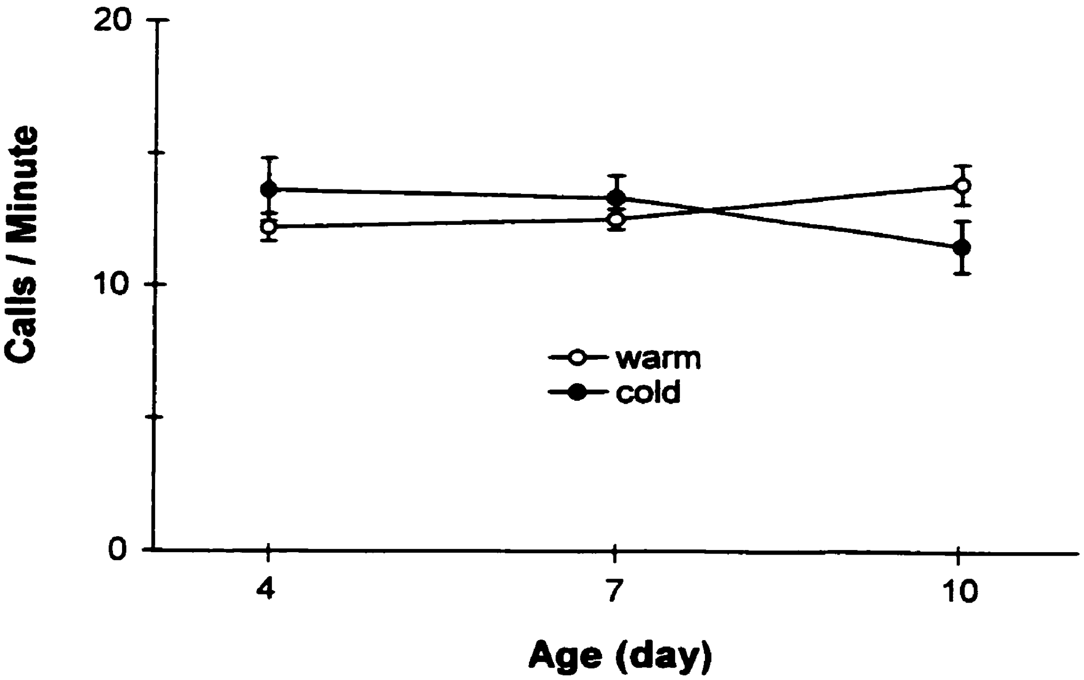
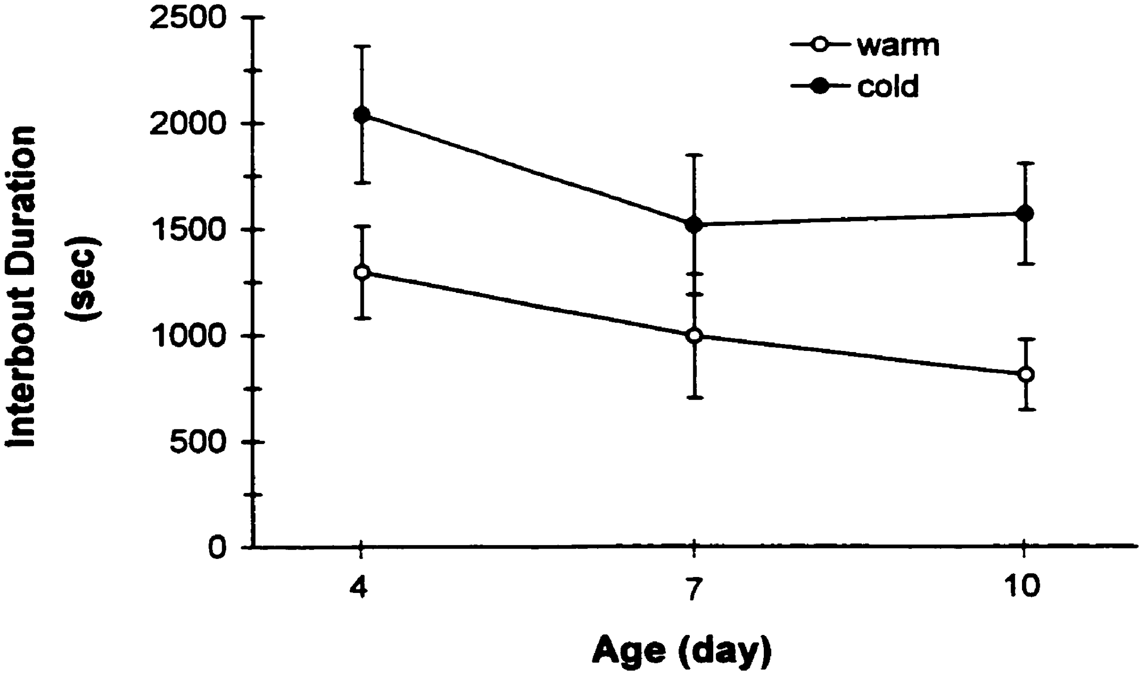

20
10
0
Calls / Minute
4
7
10
Age (day)
warm
cold

Figure 25. Overall mean interbout duration (s, mean ± SE) maintained by warm- and cold-reared chicks during the daytime test period (14 h) at each test age (n = 12 for both treatment groups at each age).



Interbout Duration (sec)
2500
2000
1500
1000
500
0
warm
cold
4
7
10
Age (day)

Mean Amount of Squawks Produced During 1 Hour Sampling Periods

Cold-reared chicks produced a significantly higher mean amount of squawks than warm-reared chicks during their 1 h sampling periods (Fig. 26, $F = 69.22$, $df = 1, 44$, $p < 0.0001$). This trend was evident during all 3 test ages (treatment and age interaction, $F = 0.24$, $df = 2, 44$, $p = 0.7890$), where cold birds squawked approximately 3.2, 2.8 and 3.9 times more often than warm birds on days 4, 7 and 10, respectively. Chick age did not have a significant impact on number of squawks produced ($F = 0.83$, $df = 2, 44$, $p = 0.4449$).

Chick Growth During the Eight-Day Rearing Period (Days 3 to 10)

Mass. Even though daily mass (g) among chicks from the two treatment groups was, overall, not significantly different (Fig. 27, $F = 3.03$, $df = 1, 154$, $p = 0.0959$), it was apparent that warm birds were growing at a relatively faster pace than cold birds once the mid-point of the rearing period had passed (treatment x age interaction, $F = 3.98$, $df = 7, 154$, $p = 0.0006$). As would be expected, chick weight increased with age ($F = 621.68$, $df = 7, 154$, $p < 0.0001$).

Culmen length. Treatment significantly affected daily chick culmen length (mm), as warm-reared chicks developed

Figure 26. Mean amount of squawks (mean ± SE) produced by warm- and cold-reared chicks during 1 h sampling periods before each scheduled feeding at each test age (n = 12 for both treatment groups at each age).

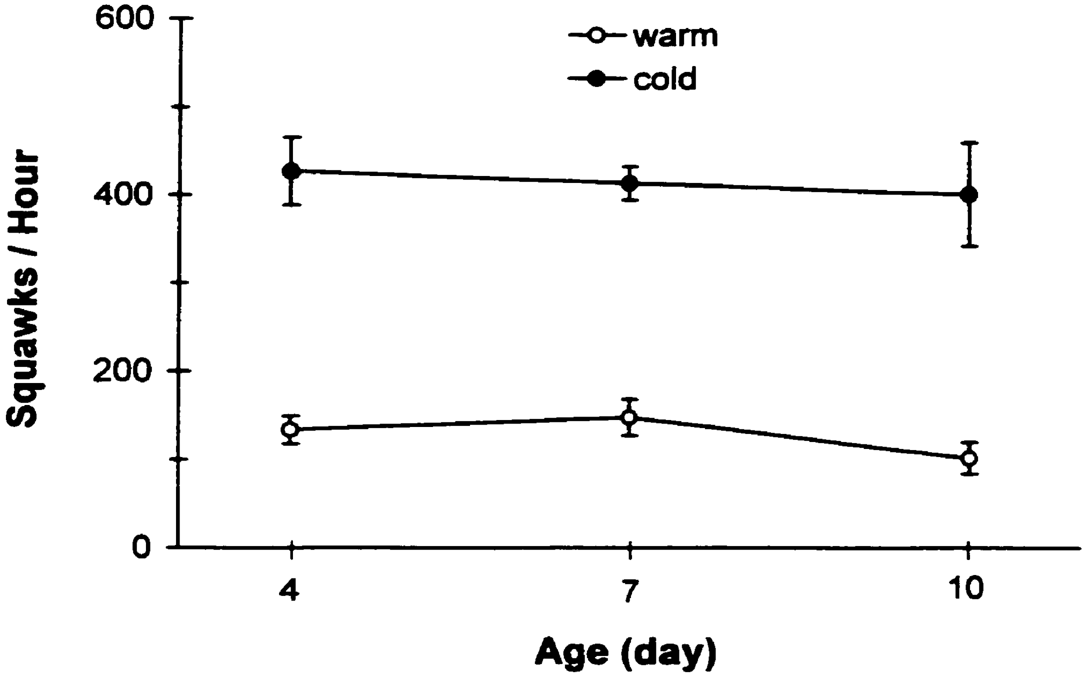
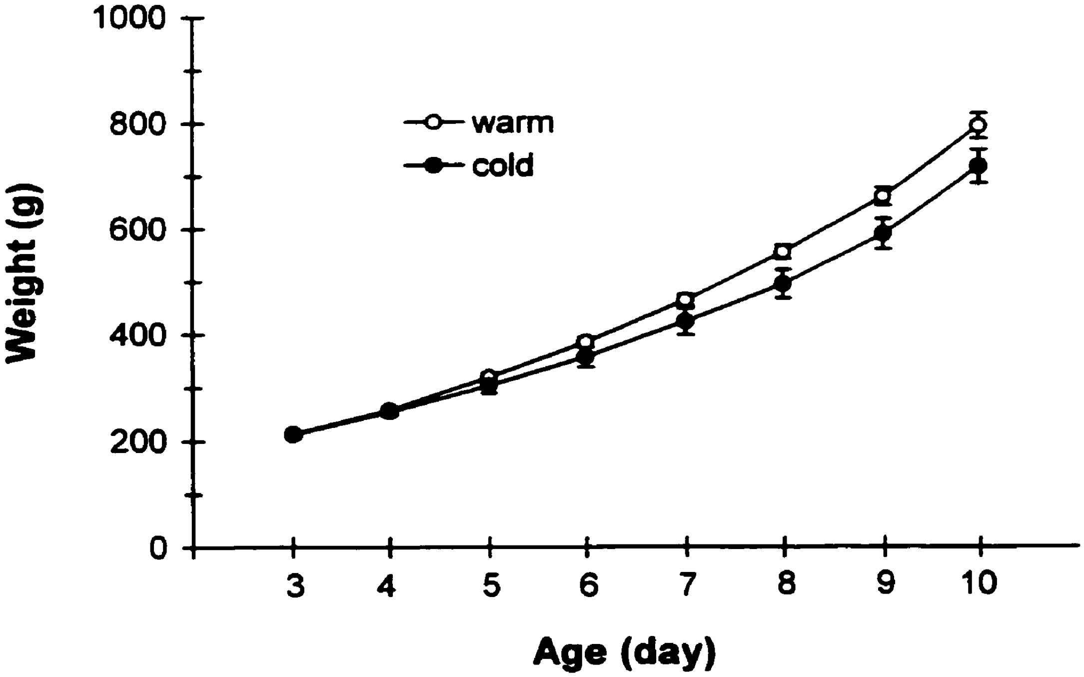

warm
cold
Squawks / Hour
600
400
200
0
4
7
10
Age (day)

Figure 27. Daily weights (g, mean ± SE) of warm- and cold-reared chicks during the eight-day rearing period (days 3 - 10, inclusively, n = 12 for both treatment groups at each age).


1000
800
600
400
200
0
Weight (g)
warm
cold
3
4
5
6
7
8
9
10
Age (day)

significantly longer culmens than cold-reared chicks (Fig. 28, $F = 8.39$, $df = 1, 154$, $p = 0.0084$). The disparity in culmen length between the two treatment groups consistently increased over age (treatment x age interaction, $F = 10.68$, $df = 7, 154$, $p < 0.0001$). Mean daily culmen length in all chicks significantly increased in length with age ($F = 318.93$, $df = 7, 154$, $p < 0.0001$).

Down length. Down length (mm) was significantly influenced by rearing temperature and age, as warm-reared chicks and older chicks developed longer down, respectively (Fig. 29, main effect of treatment, $F = 7.53$, $df = 1, 154$, $p = 0.0118$, main effect of age, $F = 61.39$, $df = 7, 154$, $p < 0.0001$). The difference in down length between treatment groups did not significantly change throughout the test period (interaction between treatment and age, $F = 1.92$, $df = 7, 154$, $p = 0.0699$).

Competitive Tests

Outcomes from competitive tests (with respect to warm-reared chicks) under both warm and cold test temperatures are illustrated in Table 2. In general, more aggressive warm-reared chicks out-competed cold-reared chicks. On day 4, chicks appeared to be fairly evenly matched, however, warm-reared chicks became increasingly successful with age, and by day 10 they were clearly superior competitors. Test

Figure 28. Daily culmen lengths (mm, mean ± SE) of warm- and cold-reared chicks during the eight-day rearing period (days 3 - 10, inclusively, n = 12 for both treatment groups at each age).

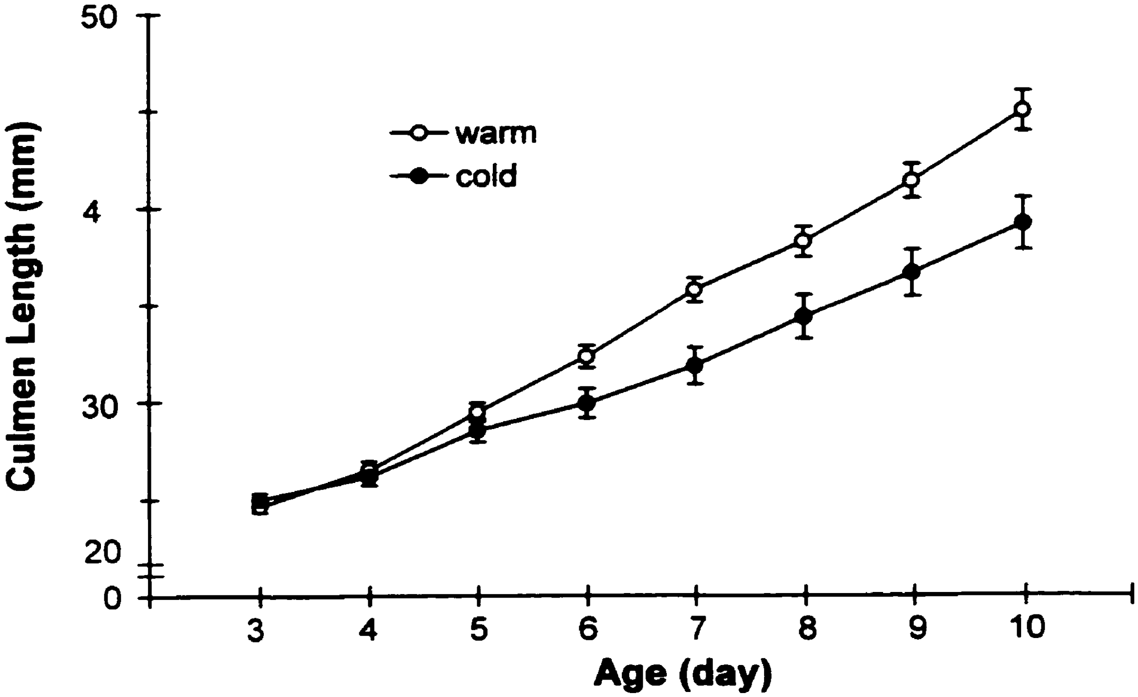
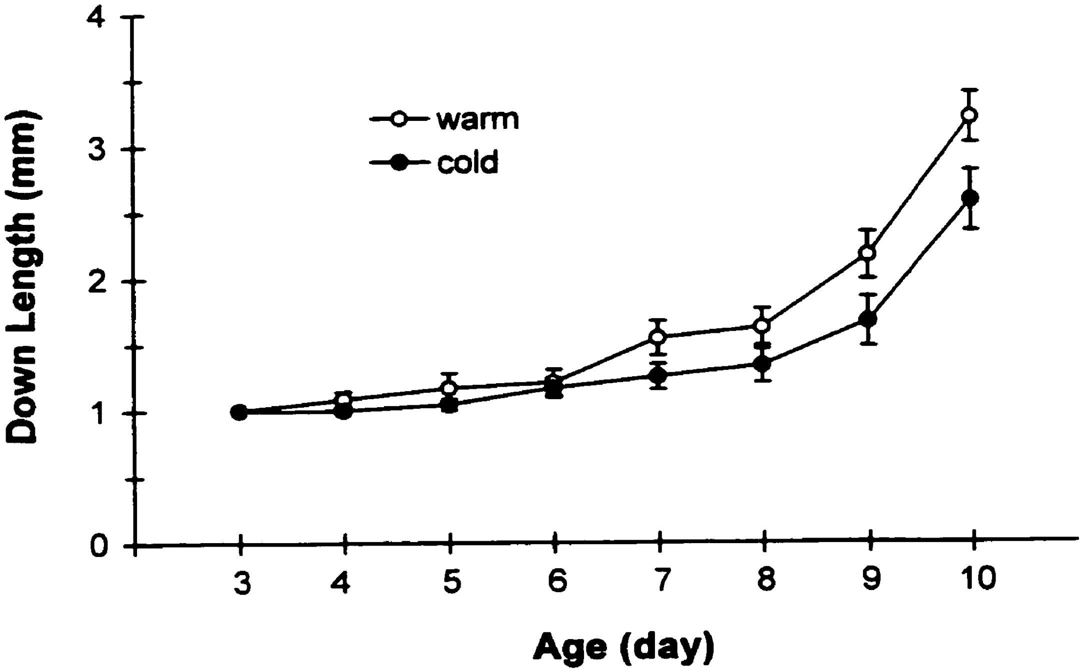

warm
cold
Culmen Length (mm)
50
4
30
20
0
3
4
5
6
7
8
9
10
Age (day)

Figure 29. Daily down lengths (mm, mean ± SE) of warm- and cold-reared chicks during the eight-day rearing period (days 3 - 10, inclusively, n = 12 for both treatment groups at each age).



Down Length (mm)
0
1
2
3
4
warm
cold
3
4
5
6
7
8
9
10
Age (day)

Table 2. Outcomes from competitive tests with respect to warm-reared chicks under both warm and cold test temperatures.

Age	Warm test temperature			Cold test temperature		
	wins	losses	ties	wins	losses	ties
Day 4	3	3	3	4	2	3
Day 7	5	2	2	5	2	2
Day 10	7	1	1	7	0	2

Note: N = 9 for warm- and cold-reared chicks at both test temperatures on each test day. Refer to text for conditions which constitute a win, loss and tie.

temperature had little effect on competitive tests, where warm-reared chicks became slightly better competitors under the cold test temperature (1 more match was won on day 4 and 1 less match was lost on day 10). Participants from both treatment groups had similar weights during contests (weight-matched pairs) on their respective test days (1-way ANOVA, day 4: $F = 0.28$, $df = 1, 17$, $p = 0.6072$, day 7: $F = 2.49$, $df = 1, 17$, $p = 0.1339$, day 10: $F = 2.27$, $df = 1, 17$, $p = 0.1517$).

DISCUSSION

Rearing Temperature and the Development of Chick Vocalizations

Rearing chicks in a moderately chilled environment significantly reduced begging. This was evident throughout the duration of testing as warm-reared chicks begged approximately twice as much as cold-reared chicks (Figs. 20a and b), suggesting that even as chicks grew (prior to the development of endothermy) they were unable to overcome this "dampening" effect of cool ambient temperature on begging. Similar effects of temperature on begging were observed with young gulls and blackbirds (Conover and Miller 1981, Choi and Bakken 1990). Therefore, the interactive effects of nutritional need and warmth is not unique to pelican chicks, and should be incorporated into Godfray's (1991, 1995) honest signalling model (see below).

Warm-reared chicks also elicited a higher number of begging bouts (Fig. 21) and begged more often during bouts (Fig. 23). Although warm-reared chicks consistently produced bouts of longer duration than those of cold-reared chicks, the difference was not statistically significant (Fig. 22). However, cold-reared chicks happened to have longer interbout durations (Fig. 25). Since cold- and warm-reared chicks consumed similar amounts of food (Fig. 19 and Table 1), it can be assumed that they had a similar need for food. In fact, cold-reared chicks may even have had a greater need for nutrition due to their retarded growth and competitive disadvantage (see below). Taken together, these results imply that cold-reared chicks are unable to signal to the parent their true state of nutritional need. Rearing temperature did not influence calling rate (Fig. 24b) as chicks from both treatment groups begged with comparable frequency throughout testing.

There is clearly an inverse relationship between rearing temperature and the number of squawks produced by chicks (Fig. 26). A similar vocal response to moderate chilling has been observed in young rodents (Sewell 1968, 1970, Okon 1970, Allin and Banks 1991, Blake 1992). In this study, a chick's need for warmth seemed to override its need for food. Throughout the duration of testing, cold-reared chicks produced approximately 400 squawks in the 1 h leading up to their scheduled feeding (when hunger level was presumably at its peak) compared to under 200 begs over the entire 14 h daytime testing period.

If cold-induced squawks are considered to be a reliable indicator of a chick's need for heat (see Evans 1994), one may ask why did thermoneutral chicks in this study also produce squawks during the 1 h sampling periods. A plausible explanation for this may be that squawking vocalizations probably act as a general stress signal, where exposure to cold ambient temperatures is the major source of this stress for a young pelican chick at the nest. However, once placed in a laboratory setting, unfamiliar environmental surroundings and social isolation may have contributed to some base-line level of stress experienced by chicks upon removal from the field at such a young age. In addition, the warm-reared chicks appeared to be more curious and active than cold-reared chicks during testing, and were observed to release sporadic squawks whenever they re-adjusted their position in the pen.

Effect of Rearing Temperature on Chick Growth and Competitiveness

Although the difference in chick weight between treatment groups was insignificant, warm-reared birds were heavier than cold-reared birds, and the gap between the two increased as testing proceeded (Fig. 27). If this trend continued, cold birds would most likely have had significantly lower body weights than warm birds by the age of fledging. Similarly, decreased ambient temperature during incubation of pelican (Evans 1990b), gull and domestic chick eggs (Evans 1990c) resulted in the retarded development of embryos as hatching times increased. In addition, cool ambient temperatures cause lower birth mass and growth rates in young Juan Fernandez fur seals (*Arctocephalus philippii*, Trillmich and Limberger 1985) and delayed development in the spotted turtle (*Clemmys guttata*, Litzgus and Brooks 1998).

Hochachka and Smith (1991) reported that when song sparrow nestlings fledged with below average weights their chances of survival were drastically reduced. A similar relationship between mass and survival has been observed in young Northern seal pups (*Callorhinus ursinus*, Boltnev et al. 1998). Therefore, it is quite possible that if young chicks in the field experienced regular or extended periods of exposure to low ambient temperatures (especially if displaced beyond the nestcup), and subsequently suffered a severe retardation in their growth and development, their future survival could be jeopardized after they leave the nest and become independent, if they even survive that long. Three cold-reared chicks died during this study (one on day 6, 7 and 10). Therefore, the adverse effects of moderate chilling are not just restricted to the early nestling period. Young adult pelicans which had experienced decreased growth rates during the early nestling period may not survive the rigorous late-summer migratory trips back to their non-breeding grounds, and if they do, they may do very poorly during the mate-selection periods during the following years.

Culmen development was significantly reduced when chicks were reared under moderately chilled conditions (Fig. 28). A smaller culmen would be a disadvantage because less food could be manipulated at any particular moment in time, which results in either an increase in energy expenditure while feeding or lower amounts of total food ingested during feedings. Also, a smaller culmen would bring about a competitive disadvantage (along with a correspondingly smaller body size) during the brood reduction period (the culmen acts as a chick's main "weapon" during aggressive contests between itself and its sibling).

Colder chicks experienced slower growth of down (Fig. 29, see Grubb et al. 1991 for similar results in Northern cardinals). Less down would lead to less insulation defense against cooler ambient temperatures. Therefore, although chicks are unable to produce heat endothermically, they do expend energy when they shiver, thereby reducing the amount of energy available for growth and development. This may explain the observed lower culmen lengths, and to a certain extent, the lower body weight in colder chicks.

When chicks were younger, rearing temperature did not seem to have much of an effect on chick competitive ability (Table 2), possibly due to their rather undeveloped coordination and motor capabilty at this time. At the older ages, warmer chicks out-competed their cooler competitors under both warm and cold test temperatures. This corresponds to the peak brood reduction period (Cash and Evans 1986), thereby putting cooler chicks at a competitive disadvantage at a very critical point in time, which would in turn elevate a chick's need for food.

To counter the argument that cold-reared chicks may not be in greater need of nourishment than warm-reared chicks because they may simply have lower metabolic rates, and subsequently have lower food requirements to satisfy their energetic demands (i.e. less activity yields lower food requirements and subsequently reduces begging levels), cold-reared chicks could be considered to be in greater need than warm reared chicks because: (1) they require extra energy to offset the energy expenditure during shivering, (2) less energy is available for growth (because chicks squawk more and beg less, lower amounts of food are offered to the chick) and development, (3) they are at a competitive disadvantage when attempting to obtain food, (4) increased exposure to cooler temperatures in and beyond the nestcup boundary due to increased harassment from the larger A-chick may result in the eventual death of the colder B-chick, (5) when a chick is cooled and weakened, it is possible that absolute costs per call (either beg or squawk vocalization) may increase, as it becomes more difficult to call when muscles are tensed during shivering and energy reserves are depleted.

Effects of Heat and Food on Energy and Growth: A Causal Model

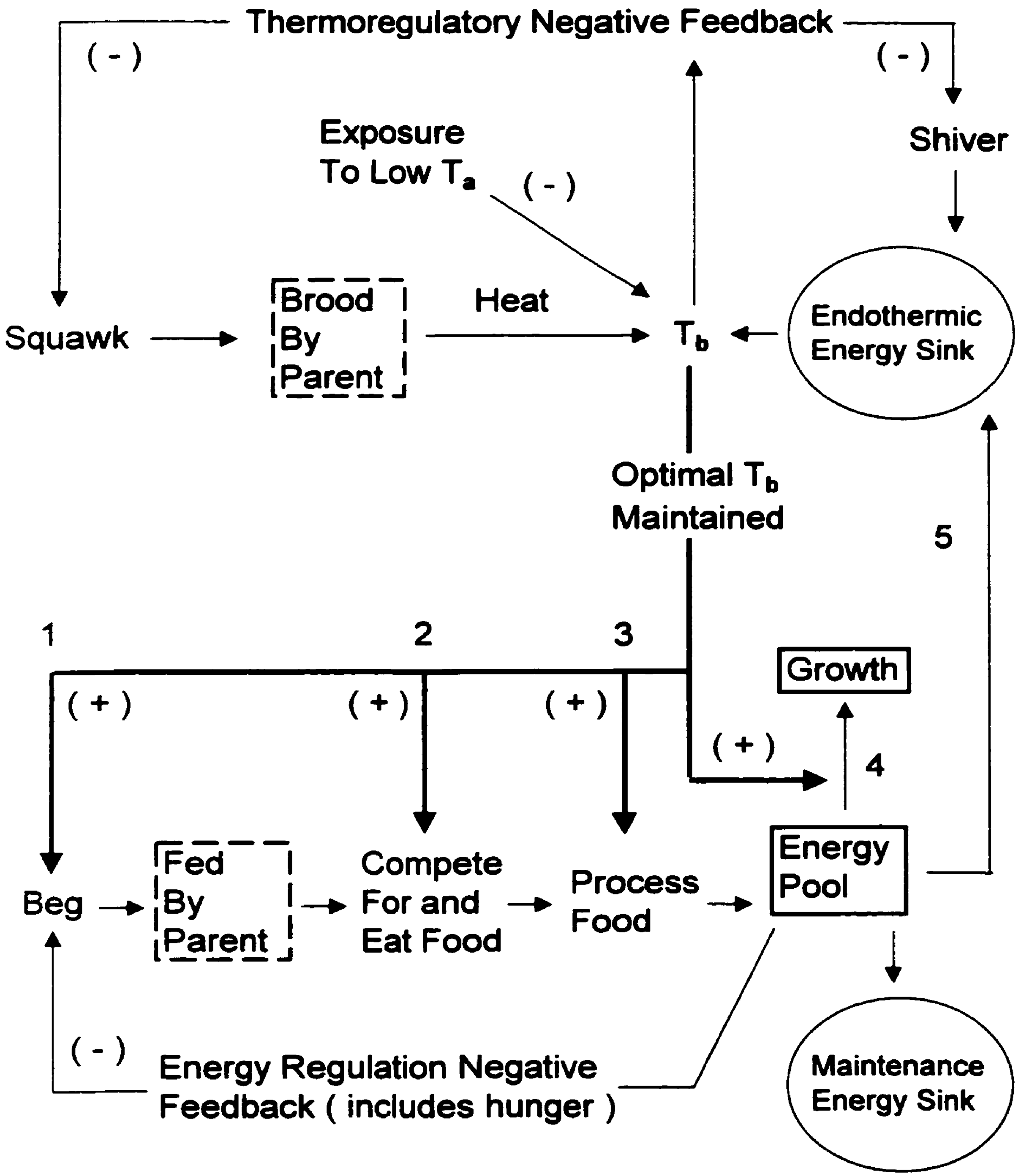
Soliciting heat and food can be usefully conceptualized as components within negative feedback control systems.

This is perhaps most clearly evident for heat, where parental brooding solicited by honest cold-induced squawks act in parallel with shivering to maintain body temperature at a relatively constant level (upper portion of Fig. 30, further details in Evans 1994). Similarly, begging for food (lower portion of Fig. 30) can be conceptualized as a means whereby the offspring regulates its own energy balance by honestly soliciting (see Chapter 1) from a parent when in need of nourishment. In both systems, compensatory regulation is achieved when solicitation increases as a function of the difference between the chick's actual and optimal internal state (temperature, or energy reserves/condition, respectively), in a manner consistent with most models of care soliciting. When the internal state is restored to optimal levels, signalling is expected to cease, as it does, for example, in Godfray's (1991, 1995) honest signalling models.

A fundamental property of regulated body temperature is to facilitate chemical reactions involved in the acquisition and processing of food (Hill and Wyse 1989). An optimally regulated temperature thereby facilitates the optimal functioning and success of the food/energy system. Five of the main ways in which temperature impinges on energy regulation, including feeding, are illustrated by arrows connecting the two control systems in Fig. 30.

Of direct relevance at the behavioural level, begging

Figure 30. Negative feedback control diagram illustrating how chick body temperature (T_b) affects thermoregulatory (upper portion of figure) and energetic (lower portion of figure) needs. A minus sign (-) indicates that a chick's actual internal state is below its optimal internal state (temperature or energy reserves/condition). Dotted boxes refer to parent. Note that upon exposure to low ambient temperatures (T_a) below thermoneutrality, the chick produces honest cold-induced squawk vocalizations to solicit parental brooding. Once an optimal T_b is maintained, we see its positive effects (indicated by heavy lines and plus (+) signs) on a chick's energy pool and growth (represented with solid boxes), here assumed to be the main components of fitness in a young chick. Offspring regulate their own energy balance by producing honest begging vocalizations in order to solicit food form a parent when in need of nourishment. Solid circles represent energy sinks. Refer to text for further discussion of numbers 1 - 5.


Thermoregulatory Negative Feedback
(-)
(-)
Exposure To Low T_a
(-)
Shiver
Squawk
Brood By Parent
Heat
T_b
Endothermic Energy Sink
Optimal T_b Maintained
5
1
2
3
Growth
(+)
(+)
(+)
(+)
4
Beg
Fed By Parent
Compete For and Eat Food
Process Food
Energy Pool
(-)
Energy Regulation Negative Feedback (includes hunger)
Maintenance Energy Sink

for food is inhibited by low temperatures (Conover and Miller 1981, Choi and Bakken 1990, this study). This important relationship (Fig. 30, arrow 1) was observed during this study as young pelicans experienced a 2.3-fold decrease in begging when reared in an environment 4.5°C below thermoneutrality (Fig. 20a,b). During systematic chilling and rewarming done as part of a thermoregulatory study (Evans 1994), chicks only begged when their body temperature was above about 35°C, the temperature at which shivering began. A similar inhibiting effect of moderate chilling on begging has been noted in naturally food-deprived but warm young chicks, which commonly began to beg when first exposed to 30°C, then switched to heat soliciting squawks as body temperature dropped (Evans pers. comm.). It appears that slight chilling, as when a parent first rises above a chick it has been brooding, may activate the chick and simulate it to beg if it is in need of food (pers. obs.). Lower ambient and body temperature then causes thermoregulatory squawks to take precedence over begging for food. The negative effects of moderately low temperature on begging appear to diminish as endothermy develops with age (Daniels 1997).

As a result of thermal action on rates of chemical reactions, heat within normal biological limits acts to facilitate the ability of a chick to compete for food (Fig. 30 arrow 2) and the conversion of food to energy (arrow 3) and growth (arrow 4), the latter two which are assumed to have direct fitness consequences. These facilitating effects occur at several readily identifiable stages within the food processing sequence. Prior to the development of endothermy, heat facilitates the ability of a chick to compete for food, especially starting at 1 week of age when chicks develop functional motor capabilities (competition between cold- and warm-reared chicks in the lab, Table 2). In young pelicans, sustained moderately low temperature equivalent to that commonly occurring overnight within northern breeding colonies causes general slowing of behaviour, which if uncorrected, results in a comatose condition and ultimately death (Evans and Knopf 1993). A similar result of chilling occurs in altricial blackbirds, while short periods of chilling caused a decrease in hunger contractions of the proventriculus (Choi and Bakken 1990). If food is ingested, chilling typically inhibits normal digestion and assimilation. The negative effects of temperature on these physiological reactions has been studied and verified especially in ectothermic reptiles and amphibians (see Chapter 2 introduction for more details). Prior to the development of thermal independence, young pelicans reared in the lab at a mildly cool temperature of 4.5°C below thermoneutrality showed a retardation in weight gain (difference from warm controls approached significance, Fig. 27) and general development (culmen length: Fig. 28, down length: Fig. 29) even when chicks were fed the same amount of food as normally developing controls reared at thermoneutrality.

When endothermic ability begins to develop, temperature also has a direct effect on energy expenditure (Fig. 30, arrow 5). Within limits set by endothermic competence, as temperature drops energy expended on shivering increases (birds lack non-shivering thermogenesis, Marsh and Dawson 1989). Provided the heat generated is translated into elevated body temperature, the energy expended may be in part or completely offset by the positive effects of body temperature on energy acquisition. However, in young chicks, moderate ambient temperature that triggers shivering still brings about a lowering of body temperature (e.g. Evans 1994), although presumably at a slower rate. The net energetic effect of shivering while body temperature lowers in incompletely endothermic young altricial birds appears to represent an energy sink with only limited offsetting benefits. During this study, pelican chicks reared at the cooler temperatures were often seen to shiver, which may well have contributed to their slower growth rates and retarded development.

The above brief overview of some of the effects of temperature on energy balance in young altricial pelicans emphasizes the many energetic consequences of chick temperature, and supports the interpretation that honestly soliciting and obtaining parental heat can be of fundamental benefit to the developing young. Depending on need state, soliciting and obtaining heat appears to be at least as beneficial to a chick as soliciting and obtaining food. To permit a more quantitative ranking of the benefits attained from a bout of parental feeding and brooding, experimental studies of growth under different food intakes done over a range of ambient rearing temperatures would be useful.

Perhaps the most important general conclusion to emerge from this study is that interpretations and predictions about the signalling systems employed in soliciting food and heat must be examined within the overall context and adaptive milieu in which the chicks are reared. For this reason, it may at present be more productive to focus directly on the adaptive, biological aspects of signalling for heat and food as they occur in a particular species. This does not prevent studies being motivated by or related to current theoretical models, but suggests it may be premature to set up studies to directly test substantial predictions derived from Godfray's (1991, 1995) honest signalling models, at least until more information is available on the context in which the behaviour occurs.

A strong theme to emerge from this study is that it should be both possible and highly desirable to develop more detailed and realistic causal models and interpretations when considering adaptive and evolutionary aspects of parent-offspring interactions. The application of a negative feedback regulatory systems approach to care soliciting and parental provisioning of heat and food seems particularly relevant to the development of evolutionary models of honest signalling.

GENERAL DISCUSSION

"Imagine Shoal Lake; a bright, warm sunny day with a slight breeze which causes the water to gently lap up against the rocks that you are sitting on. Without warning, a single pelican catches your attention and flies way up high in the sky. It soars around the sun, this way and that. Your hand tries to shield your eyes from the dazzling brightness as the sun and the pelican dance with each other celebrating the beauty they are creating. Then, as abruptly as it appeared, it flies away."
- Karen Barg Camacho.

The above passage exemplifies both the beauty and vulnerability of the American white pelican. Although American white pelicans are currently maintaining relatively healthy populations numbers in North America, the species remains quite sensitive to human disturbance and habitat degradation, and in fact were considered a threatened species until the early 1970's (Evans and Knopf 1993). Surprisingly very little research in animal behaviour has been geared towards conservation (see Sutherland 1998 for review). A major goal of this thesis was to develop and document viable methodology to rear captive young pelican chicks destined for re-stocking of depleted areas, as well as those used for zoo or research purposes. This research has practical merit in the field of animal welfare assessment, as information about an animal's state and well-being may be understood through the signals it produces (Weary and Fraser 1995, Weary et al. 1996).

This study outlined how to rear healthy young pelicans in a laboratory setting, and results illustrated the biological significance of signals produced by chicks. In addition, the interactive nature of a young chick's most fundamental requirements (i.e. thermal and nutritional needs) were explored. This research also has important implications for evolutionary models, such as Godfray's (1991, 1995) honest signalling model, as it extends his concepts to include interactive effects of need states through the use of a negative feedback control system.

It would be interesting to know whether a difference exists between male and female parental response to elevated begging levels in pelicans. Kolliker et al. (1998) observed that it was more costly for deprived great tit chicks to beg for food when a male parent was feeding, whereas female parents were more responsive to higher begging levels, thereby making them a much more reliable source of food for deprived chicks (see also Stamps 1993 where female budgerigars have been observed to selectively feed their smallest nestling). Therefore, it appears that at least in some species a different signalling system may be operating between the chick and each of its two parents (Kolliker et al. 1998). This phenomenon may manifest itself within pelican parent-offspring relations and has yet to be included in evolutionary models such as Godfray's honest signalling model.

When dealing with conservation of a species it seems important not only to be concerned with simply prolonging the species' existence, but also to maintain the natural behaviour and cultural skills of that species in order to sustain healthy populations (Sutherland 1998). Therefore, it would be interesting to see if feeding chicks on a fixed schedule (i.e. lack of positive reinforcement) influences how they raise their own chicks in the wild. Also, the most efficient method for releasing lab-reared chicks back into the wild should be sought (taking into account both the released animal and wild animals at the respective breeding colony). Success of this type of conservation plan would be best monitored by the reproductive success (fitness) of released animals, which would require constant annual monitoring of previously released lab-reared pelicans.

LITERATURE CITED

Allin, J.T. and E.M. Banks. 1971. Effects of temperature on ultrasound production by infant albino rats. Dev. Psychobiol. 4:149-156.

Bachman, G.C. and M.A. Chappell. 1998. The energetic cost of begging behaviour in nestling house wrens. Anim. Behav. 55:1607-1618.

Bengtsson, H. and O. Ryden. 1983. Parental feeding rate in relation to begging behavior in asynchronously hatched broods of the great tit *Parus major*. Behav. Ecol. Sociobiol. 12:243-251.

Bertram, D.F., C.V.J. Welham and R.C. Ydenberg. 1996. Flexible effort in breeding seabirds: adjustment of provisioning according to nestling age and mass. Can. J. Zool. 74:1876-1881.

Blake, B.H. 1992. Ultrasonic vocalization and body temperature maintenance in infant voles of three species (Rodentia: Arvicolidae. Dev. Psychobiol. 25:581-596.

Blanco, D.E., P. Yorio and P.D. Boersma. 1996. Feeding behavior, size asymmetry, and food distribution in Magellanic penguin (*Spheniscus magellanicus*) chicks. Auk 113:496-498.

Boltnev, A.I., A.E. York and G.A. Antonelis. 1998. Northern fur seal young: interrelationships among birth size, growth, and survival. Can. J. Zool. 76:843-854.

Bolton, M. 1995a. Food delivery to nestling storm petrels: limitation or regulation? Funct. Ecol. 9:161-170.

Bolton, M. 1995b. Experimental evidence for regulation of food delivery to storm petrel, *Hydrobates pelagicus*, nestlings: the role of chick body condition. Anim. Behav. 50:231-236.

Briskie, J.V., C.T. Naugler and S.M. Leech. 1994. Begging intensity of nestling birds varies with sibling relatedness. Proc. R. Soc. London Ser. B. 258:73-78.

Bugden, S.C. and R.M. Evans. 1997. Vocal solicitation of heat as an integral component of the developing thermoregulatory system in young domestic chickens. Can. J. Zool. 75:1949-1954.

Burford, J.E., T.J. Friedrich and K. Yasukawa. 1998. Response to playback of nestling begging in the red-winged blackbird, *Agelaius phoeniceus*. Anim. Behav. 56:555-561.

Cash, K.J. and R.M. Evans. 1986. Brood reduction in the American white pelican (*Pelecanus erythrorhynchos*). Behav. Ecol. Sociobiol. 18:413-418.

Chappell, M.A., M. Zuk, T.H. Kwan and T.S. Johnsen. 1995. Energy cost of an avian vocal display: crowing in red junglefowl. Anim. Behav. 49:255-257.

Chappell, M.A. and G.C. Bachman. 1998. Exercise capacity of house wren nestlings: begging chicks are not working as hard as they can. Auk 115:863-870.

Choi, I. and G.S. Bakken. 1990. Begging response in nestling red-winged blackbirds (*Agelaius phoeniceus*): effect of body temperature. Phys. Zool. 63:965-986.

Christe, P., H. Richner and A. Oppliger. 1996. Begging, food provisioning, and nestling competition in great tit broods infested with ectoparasites. Behav. Ecol. 7:127-131.

Clark, A.B. and W. Lee. 1998. Red-winged blackbird females fail to increase feeding in response to begging call playbacks. Anim. Behav. 56:563-570.

Conover, M.R. and D.E. Miller. 1981. Elicitation of vocalizations and pecking in ring-billed gull chicks. Behaviour 77:268-286.

Cotton, P.A., A. Kacelnik and J. Wright. 1996. Chick begging as a signal: are nestlings honest? Behav. Ecol. 7:178-182.

Daniels, S. 1997. Intergenerational communication and parental care in American white pelicans (*Pelecanus erythrorhynchos*): conflict or honesty? M.Sc. thesis, Univ. of MB.

Davies, N.B. 1978. Parental meanness and offspring independence: an experiment with hand-reared great tits *Parus major*. Ibis 120:509-514.

Dawkins, M.S. and T. Guilford. 1991. The corruption of honest signalling. Anim. Behav. 41:865-873.

Dawson, W.R. and F.C. Evans. 1957. Relation of growth and development of temperature regulation in nestling field and chipping sparrows. Physiol. Zool. 30:315-327.

Dawson, W.R. and F.C. Evans. 1960. Relation of growth and development to temperature regulation in nestling vesper sparrows. Condor 62:329-340.

Dorcas, M.E., C.R. Peterson and M.E.T. Flint. 1997. The thermal biology of digestion in rubber boas (*Charina bottae*): physiology, behavior, and environmental constraints. Physiol. Zool. 70:292-300.

Drummond, H. and C.G. Chavelas. 1989. Food shortage influences sibling aggression in the blue-footed booby. Anim. Behav. 37:806-819.

Drummond, H., E. Gonzalez and J.L. Osorno. 1986. Parent-offspring cooperation in the blue-footed booby (*Sula nebouxii*): social roles in infanticidal brood reduction. Behav. Ecol. Sociobiol. 19:365-372.

Drummond, H. and J.L. Osorno. 1992. Training siblings to be submissive losers: dominanace between booby nestlings. Anim. Behav. 44:881-893.

Dunn, E.H. 1975. The timing of endothermy in the development of altricial birds. Condor 77:288-293.

Espira, A. and R.M. Evans. 1996. Energetic savings from regulation of ambient temperature through vocalizations by three-day old domestic chickens. Can. J. Zool. 74:599-605.

Evans, R.M. 1979. Responsiveness of young herring gulls to stimuli from their own and other species: effects of training with food. Can. J. Zool. 57:1452-1457.

Evans, R.M. 1980. Development of individual call recognition in young ring-billed gulls (*Larus delawarensis*): an effect of feeding. Anim. Behav. 28:60-67.

Evans, R.M. 1984. Development of thermoregulation in young white pelicans. Can. J. Zool. 62:808-813.

Evans, R.M. 1988. Embryonic vocalizations as care-soliciting signals with particular reference to the American white pelican. Proc. Int. Ornith. Congr. 19:1467-1475.

Evans, R.M. 1989. Egg temperatures and parental behavior during the transition from incubation to brooding in the American white pelican. Auk 106:26-33.

Evans, R.M. 1990a. Vocal regulation of temperature by avian embryos: a laboratory study with pipped eggs of the American white pelican. Anim. Behav. 40:969-979.

Evans, R.M. 1990b. Terminal-egg chilling and hatching intervals in the American white pelican. Auk 107:431-434.

Evans, R.M. 1990c. Effects of low incubation temperatures during the pipped egg stage on hatchability and hatching times in domestic chickens and ring-billed gulls. Can. J. Zool. 68:836-840.

Evans, R.M. 1992. Embryonic and neonatal vocal elicitation of parental brooding and feeding responses in American white pelicans. Anim. Behav. 44:667-675.

Evans, R.M. 1994. Cold-induced calling and shivering in young American white pelicans: honest signalling of offspring need for warmth in a functionally integrated thermoregulatory system. Behaviour 120:13-34.

Evans, R.M. 1997. Parental investment and quality of insurance offspring in an obligate brood reducing species, the American white pelican. Behav. Ecol. 8:378-383.

Evans, R.M. and K.J. Cash. 1985. Early spring flights of American white pelicans: timing and functional role in attracting others to the breeding colony. Condor 87:252-255.

Evans R.M. and F.L. Knopf. 1993. American white pelican (*Pelecanus erythrorhynchos*). In The Birds of North America. *Edited by* A. Poole and F. Gill. The Academy of Natural Sciences, Philadelphia; The American Ornithologists Union, Washington D.C. 57:1-24.

Evans, R.M. and B.F. McMahon. 1987. Within-brood variation in growth and condition in relation to brood reduction in the American white pelican. Wilson Bull. 99:190-201.

Evans, R.M., A. Whitaker and M.O. Wiebe. 1994. Development of vocal regulation of temperature by embryos in pipped eggs of ring-billed gulls. Auk 11:596-604.

Evans, R.M., M.O. Wiebe, S.C. Lee and S.C. Bugden. 1995. Embryonic and parental preferences for incubation temperature in herring gulls: implications for parent-offspring conflict. Behav. Ecol. Sociobiol. 36:17-23.

Furlow, B., R.T. Kimball and M.C. Marshall. 1998. Are rooster crows honest signals of fighting ability? Auk 115:763-766.

Godfray, H.C.J. 1991. Signalling of need by offspring to their parents. Nature 352:328-330.

Godfray, H.C.J. 1995. Signalling of need between parents and young: parent-offspring conflict and sibling rivalry. Am. Nat. 146:1-24.

Godfray, H.C.J. and G.A. Parker. 1992. Sibling competition, parent-offspring conflict and clutch size. Anim. Behav. 43:473-490.

Gossling, J., W.J. Loesche and L.D. Ottoni. 1980. Passage of material through the gut of hibernating *Rana pipiens* (Amphibia, Anura, Ranidae). J. Herpetol. 14:407-409.

Gottlander, K. 1987. Parental feeding behaviour and sibling competition in the pied flycatcher *Ficedula hypoleuca*. Ornis Scandinavica 18:269-276.

Grafen, A. 1990. Biological signals as handicaps. J. Theor. Biol. 114:517-546.

Greig-Smith, P. 1985. Weight differences, brood reduction, and sibling competition among nestling stonechats *Saxicola torquata* (Aves: Turdidae). J. Zool. Lond. (A). 205:453-465.

Grubb, T.C., T.A. Waite and A.J. Wiseman. 1991. Ptilochronology: induced feather growth in Northern cardinals varies with age, sex, ambient temperature, and day length. Wilson Bull. 103:435-445.

Hamer, K.C. and J.K. Hill. 1994. The regulation for food delivery to nestling Cory's shearwaters *Calonectris diomedea*: the roles of parents and offspring. J. Avian Biol. 25:198-204.

Hamer, K.C., A.S. Lynnes and J.K. Hill. 1999. Parent-offspring interactions in food provisioning of Manx shearwaters: implications for nestling obesity. Anim. Behav. 57:627-631.

Harper, A.B. 1986. The evolution of begging, sibling competition and parent-offspring conflict. Am. Nat. 128:99-114.

Harris, M.P. 1983. Parent-young communication in the puffin *Fratercula arctica*. Ibis 125:109-114.

Haskell, D. 1994. Experimental evidence that nestling begging behaviour incurs a cost due to nest predation. Proc. R. Soc. Lond. B. 257:161-164.

Henderson, B.A. 1975. Role of the chick's begging behavior in the regulation of parental feeding behavior of *Larus glaucescens*. Condor 77:488-492.

Hill, R.W. and G.A. Wyse. 1989. Animal Physiology. Harper Collins Publishers Inc., New York.

Hochachka, W. and J.N.M. Smith. 1991. Determinants and consequences of nestling condition in song sparrows. J. Anim. Ecol. 60:995-1008.

Horn, A.G., M.L. Leonard and D.M. Weary. 1995. Oxygen consumption during crowing by roosters: talk is cheap. Anim. Behav. 50:1171-1175.

Hussell, D.J.T. 1988. Supply and demand in tree swallow broods: a model of parent-offspring food-provisioning interactions in birds. Am. Nat. 131:175-202.

Iacovides, S. and R.M. Evans. 1998. Begging as graded signals of need for food in young ring-billed gulls. Anim. Behav. 56:79-85.

Jiang, S. and D.L. Claussen. 1993. The effects of temperature on food passage time through the digestive tract in *Notophthalmus viridescens*. J. Herpetol. 27:414-419.

Johnsen, I., K.E. Erikstad and B. Saether. 1994. Regulation of parental investment in a long-lived seabird, the puffin *Fratercula arctica*: an experiment. Oikos 71:273-278.

Johnstone, R.A. and A. Grafen. 1992. The continuous Sir Philip Sidney game: a simple model of biological signalling. J. Theor. Biol. 156:215-234.

Johnstone, R.A. and A. Grafen. 1993. Dishonesty and the handicap principle. Anim. Behav. 46:759-764.

Kacelnik, A., P.A. Cotton, L. Stirling and J. Wright. 1995. Food allocation among nestling starlings: sibling competition and the scope of parental choice. Proc. R. Soc. Lond. B. 259:259-263.

Kaufman, I.C. and R.A. Hinde. 1961. Factors influencing distress calling in chicks, with special reference to temperature changes and social isolation. Anim. Behav. 9:197-204.

Kilner, R. 1995. When do canary parents respond to nestling signals of need? Proc. R. Soc. Lond. Ser. B. 260(1359):343- 348.

Kilner, R. 1997. Mouth colour is a reliable signal of need in begging canary nestlings. Proc. R. Soc. Lond. B. 264:963-968.

Kilner, R. and R.A. Johnstone. 1997. Begging the question: are offspring solicitation behaviours signals of need? Trends Ecol. Evol. 12:11-15.

Kolliker, M., H. Richner, I. Werner and P. Heeb. 1998. Begging signals and biparental care: nestling choice between parental feeding locations. Anim. Behav. 55:215-222.

Lang, J.W. 1979. Thermophilic response of the American alligator and the American crocodile to feeding. Copeia 1:48-59.

Leech, S.M. and M.L. Leonard. 1996. Is there an energetic cost to begging in nestling tree swallows *Tachycineta bicolor*. Proc. R. Soc. Lond. B. 263:983-987.

Leonard, M. and A. Horn. 1996. Provisioning rules in tree swallows. Behav. Ecol. Sociobiol. 38:341-347.

Lipar, J.L., E.D. Ketterson and V. Nolan Jr. 1999. Intraclutch variation in testosterone content of red-winged blackbird eggs. Auk 116:231-235.

Litzgus, J.D. and R.J. Brooks. 1998. Growth in a cold environment: body size and sexual maturity in a northern population of spotted turtles, *Clemmys guttata*. Can. J. Zool. 76:773-782.

Machmer, M.M. and R.C. Ydenberg. 1998. The relative roles of hunger and size asymmetry in sibling aggression between nestling ospreys, *Pandion haliaetus*. Can. J. Zool. 76:181-186.

Marsh, R.L. and W.R. Dawson. 1989. Avian adjustments to cold. *In* advances in comparative and environmental physiology. *Edited by* L.C.H. Wang. Springer-Verlag, New York. pp 205-253.

Maynard Smith, J. 1991. Honest signalling: the Philip Sidney game. Anim. Behav. 42:1034-1035.

Maynard Smith, J. 1994. Must reliable signals always be costly? Anim. Behav. 47:1115-1120.

McBride, G., I.P. Parer and F. Foenander. 1969. The social organization and behaviour of the feral domestic fowl. Anim. Behav. Monog. 2:127-181.

McCarty, J.P. 1996. The energetic cost of begging in nestling passerines. Auk 113:178-188.

McCarty, J.P. 1997. The role of energetic costs in the evolution of begging behavior of nestling passerines. Auk 114:135-137.

Miller, D.E. and M.R. Conover. 1979. Differential effects of chick vocalizations and bill-pecking on parental behavior in the ring-billed gull. Auk 96:284-295.

Mondloch, C.J. 1995. Chick hunger and begging affect parental allocation of feedings in pigeons. Anim. Behav. 49:601- 613.

McRae, S.B., P.J. Weatherhead and R. Montgomerie. 1993. American robin nestlings compete by jockeying for position. Behav. Ecol. Sociobiol. 33:101-106.

Muller, R.E. and D.G. Smith. 1978. Parent-offspring interactions in zebra finches. Auk 95:485-495.

Naulleau, G. 1983. The effects of temperature on digestion in *Vipera aspis*. J. Herpetol. 17:166-170.

Nottebohm, F. and M.E. Nottebohm. 1971. Vocalizations and breeding behaviour of surgically deafened ring doves, *Streptopelia risoria*. Anim. Behav. 19:313-327.

Okon, E.E. 1970. The effect of environmental temperature on the production of ultrasounds by isolated non-handled albino mouse pups. J. Zool. Lond. 162:71-83.

O'Malley, J.B.E. and R.M. Evans. 1980. Variations in measurements among white pelican eggs and their use as a hatch date predictor. Can. J. Zool. 58:603-608.

O'Malley, J.B.E. and R.M. Evans. 1982. Flock formation in white pelicans. Can. J. Zool. 60:1024-1031.

Osbaldiston, G.W. 1966. The response of the immature chicken to ambient temperature. *In* physiology of the domestic fowl. *Edited by* C. Horton-Smith and E.C. Amoroso. Oliver and Boyd, Edinburgh, London. pp. 228-234.

Oyan, H.S. and T. Anker-Nilssen. 1996. Allocation of growth in food-stressed Atlantic puffin chicks. Auk 113:830-841.

Parker, G.A. and M.R. Macnair. 1978. Models of parent-offspring conflict. I. monogamy. Anim. Behav. 26:97-110.

Parmenter, R.R. 1981. Digestive turnover rates in freshwater turtles: the influence of temperature and body size. Comp. Biochem. Physiol. 70A:235-238.

Price, K. 1996. Begging as competition for food in yellow-headed blackbirds. Auk 113:963-967.

Price, K. 1998. Benefits of begging for yellow-headed blackbird nestlings. Anim. Behav. 56:571-577.

Price, K., H. Harvey and R. Ydenberg. 1996. Begging tactics of nestling yellow-headed blackbirds, *Xanthocephalus xanthocephalus*, in relation to need. Anim. Behav. 51:421-435.

Price, K. and R. Ydenberg. 1995. Begging and provisioning in broods of asynchronously-hatched yellow-headed blackbird nestlings. Behav. Ecol. Sociobiol. 37:201-208.

Redondo, T. and L. Arias de Reyna. 1988. Locatability of begging calls in nestling altricial birds. Anim. Behav. 36:653-661.

Redondo, T. and F. Castro. 1992a. The increase in risk of predation with begging activity in broods of magpies *Pica pica*. Ibis 134:180-187.

Redondo, T. and F. Castro. 1992b. Signalling of nutritional need by magpie nestlings. Ethology 92:193-204.

Reed, J.R. 1981. Song sparrow "rules" for feeding nestlings. Auk 98:828-831.

Richter, W. 1984. Nestling survival and growth in the yellow-headed blackbird, *Xanthocephalus xanthocephalus*. Ecology 65: 597-608.

Ricklefs, R.E. 1967. The temporary establishment of dominance between two hand-raised juvenile cactus wrens (*Campylorhynchus brunneicapillus*). Condor 69:528-529.

Ricklefs, R.E. 1987. Response of adult Leach's storm-petrels to increased food demand at the nest. Auk 104:750-756.

Ricklefs, R.E. 1992. The roles of parent and chick in determining feeding rates in Leach's storm-petrel. Anim. Behav. 43:895-906.

Ricklefs, R.E., C.H. Day, C.E. Huntington and J.B. Williams. 1985. Variability in feeding rate and meal size of Leach's storm-petrel at Kent Island, New Brunswick. J. Anim. Ecol. 54:883-898.

Ryan, M.J. 1988. Energy, calling, and selection. Amer. Zool. 28:885-898.

Ryden, O.O. 1982. Selective resistance to approach: a precursor to fear responses to an alarm call in great tit nestlings *Parus major*. Dev. Psychobiol. 15:113-120.

Saether, B., R. Andersen and H.C. Pedersen. 1993. Regulation of parental effort in a long-lived seabird: an experimental manipulation of the cost of reproduction in the antarctic petrel, *Thalassoica antarctica*. Behav. Ecol. Sociobiol. 33:247-150.

Schaller, G.B. 1964. Breeding behavior of the white pelican at Yellowstone Lake, Wyoming. Condor 66:3-23.

Sewell, G.D. 1968. Ultrasound in rodents. Nature 217:682-683.

Sewell, G.D. 1970. Ultrasonic communication in rodents. Nature 227:410.

Silk, J.B., E. Kaldor and R. Boyd. 2000. Cheap talk when interests conflict. Anim. Behav. 59:423-432.

Skoczylas, R. 1970. Influence of temperature on gastric digestion in the grass snake, *Natrix natrix* L. Comp. Biochem. Physiol. 33:793-804.

Smith, H.G. and R. Montgomerie. 1991. Nestling American robins compete with siblings by begging. Behav. Ecol. Sociobiol. 29:307-312.

Stamps, J. 1993. Begging in birds. Etologia 3:69-77.

Stamps, J., A. Clark, P. Arrowood and B. Kus. 1989. Begging behavior in budgerigars. Ethology 81:177-192.

Sullivan, K.A. 1989. Predation and starvation: age-specific mortality in juvenile juncos (*Junco phaenotus*). J. Anim. Ecol. 58:275-286.

Sutherland, W.J. 1998. The importance of behavioural studies in conservation biology. Anim. Behav. 56:801-809.

Teather, K.L. 1992. An experimental study of competition for food between male and female nestlings of the red-winged blackbird. Behav. Ecol. Sociobiol. 31:81-87.

Theberge, J.G. and G.C. West. 1973. Significance of brooding to the energy demands of Alaskan rock ptarmigan chicks. Arctic 26:138-148.

Trillmich, F. and D. Limberger. 1985. Drastic effects of El Nino on Galapagos pinnipeds. Oecologia 67:19-22.

Trivers, R.L. 1974. Parent-offspring conflict. Amer. Zool. 14:249-264.

Verhulst, S. and P. Wiersma. 1997. Is begging cheap? Auk 114:134.

Weary, D.M. and D. Fraser. 1995. Calling by domestic piglets: reliable signals of need? Anim. Behav. 50:1047-1055.

Weary, D.M., G.L. Lawson and B.K. Thompson. 1996. Sows show stronger responses to isolation calls of piglets associated with greater levels of piglet need. Anim. Behav. 52:1247-1253.

Weathers, W.W., P.J. Hodum and D.J. Anderson. 1997. Is the energy cost of begging by nestling passerines surprisingly low? Auk 114:133.

Welham, C.V.J. and D.F. Bertram. 1993. The relationship between previous meal size and begging vocalizations of nestling rhinoceros auklets, *Cerorhinca monocerata*. Anim. Behav. 45:827-829.

Whittingham, L.A. and R.J. Robertson. 1993. Nestling hunger and parental care in red-winged blackbirds. Auk 110:240-246.

Wiebe, M.O. and R.M. Evans. 1994. Development of temperature regulation in young birds: evidence for a vocal regulatory mechanism in two species of gulls (*Laridae*). Can. J. Zool. 72:427-432.

Winer, B.J. 1971. Statistical principles in experimental design. McGraw-Hill Book Co., New York.

Zahavi, A. 1975. Mate selection-a selection for a handicap. J. Theor. Biol. 53:205-214.

Zahavi, A. 1977 Reliability in communication systems and the evolution of altruism. In Evolutionary ecology. *Edited by* B. Stonehouse and C. Perrins. University Park Press, London. 253-259.