HOST SUITABILITY IN THE DIDERIK CUCKOO *CHRYSOCOCCYX CAPRIUS* – PLOCEID BROOD PARASITISM BREEDING SYSTEM

SHARON A. C. LEMOS

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There must always be more fools than knaves, or else the knaves will be deprived of their livelihood.

ABSTRACT

Host suitability is critically important to the success of brood parasitism. Parasites must select a host that not only accepts its egg but also is capable of successfully rearing the parasite to fledging. Nearly all brood-parasites appear to avoid low-quality hosts that are likely to reject their eggs, that are of inappropriate size, or that feed their nestlings nutritionally inadequate or insufficient food. The diderik cuckoo, (*Chrysococcyx caprius*), is an obligate brood parasite known to parasitise a wide spectrum of ploceids, including the yellow weaver (*Ploceus subaureus*) and the southern red bishop (*Euplectes orix*). Theory predicts that brood parasites should exploit insectivorous passerines of similar adult size to themselves that provision large quantities of high protein food to their young. However, the relatively smaller granivorous red bishop is the most heavily parasitised host species of the diderik cuckoo in southern Africa. To investigate why an apparently unsuitable host species was so heavily parasitized several populations of parasitised red bishops and yellow weavers (omnivores) were studied in the Pietermaritzburg region, KwaZulu-Natal, South Africa. Host suitability was assessed by examining diet quality, host-provisioning rates, cuckoo nestling growth and cuckoo fledging success. Diderik cuckoo nestlings were provisioned the same diet as the host nestlings in red bishop and yellow weaver nests. However, cuckoos in bishop nests received a protein-deficient seed diet from as early as six days following hatching. In contrast, weaver-cuckoo faeces contained 1½ times more insect than their bishop counterparts throughout their nestling period. Provisioning rates by bishop females were significantly slower than by yellow weavers, and neither bishop nor weaver hosts showed any 'supernormal' effort when feeding a young cuckoo. Both host species provisioned cuckoo nestlings at a similar rate and with a similar food mass as their own nestlings. Diderik cuckoos in bishop nests grew at a slower rate and fledged in a poorer condition than their yellow weaver counterparts. Red bishops are likely the most exploited host of the diderik cuckoo because i) cuckoo eggs are more readily accepted by the less discriminating bishop and ii) the bishop-breeding season coincides more closely with that of the diderik cuckoo than the yellow weaver. Thus, diderik cuckoos may preferentially exploit bishop hosts because of the low frequency of cuckoo egg rejection, which ultimately results in many cuckoos fledging from bishop nests despite the low-quality diet provisioned and 53% (*n* = 53) fledging success in nests of this species. In the yellow weaver system, the protein-rich diet and the greater probability of cuckoo nestling survival (80%, *n* = 5) may compensate for the high rejection rate of cuckoo eggs by this host. Thus, both host systems seem to represent evolutionary compromises for the diderik cuckoo, with neither red bishops nor yellow weavers being entirely ideal as host species.

PREFACE

The experimental work described in this dissertation was conducted in the School of Botany and Zoology, University of Natal, Pietermaritzburg from December 1998 to March 2000, under the supervision of Prof. M. J. Lawes and the co-supervision of Prof. P. Henzi. The study represents original work by the author and has not been submitted in any form for any degree or diploma to any university. Where use has been made of the work of others, it is duly acknowledged in the text.

The dissertation is compiled as a collection of papers (apart from the Introduction; chapter one) and the chapters are formatted in accordance with the Auk. The chapters depart from this format in the following areas: 1) tables and figures appear in the text and not separately at the end of each chapter, 2) one acknowledgements section, and 3) the study site is outlined in detail only in chapter two, in order to reduce repetition. Nomenclature follows Roberts Birds of southern Africa, 7th ed. Published on the Internet, http://web.uct.ac.za/depts/fitzpatrick/docs.html. Accessed 2 August 2003.

Sharon A.C. Lemos

August 2003

I declare that the above statement is correct

Professor Michael J. Lawes

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CHAPTER ONE

Introduction

HOST SELECTION

AVIAN BROOD PARASITISM is a reproductive strategy in which the parasite lays its eggs in the nests of other genetically unrelated bird species that then incubate the parasite's eggs and take care of the unrelated chicks (Payne and Payne 1967; Davies and Brooke 1989a, b; Brooker and Brooker 1990; Rothstein 1990; Marchetti 1992; Payne 1998; Takasu 1998; Soler 1999; Krüger and Davies 2002). In most cuckoo-host systems the parasite removes one host egg from the nest and the parasite nestling evicts and/or kills all the host young in the nest (Payne 1977, 1998; Rothstein 1990; Øien et al. 1995). With the exception of one study (Brooker and Brooker 1996), such exploitation by the parasite significantly compromises the reproductive success of the host (Davies and Brooke 1989a, b; Rothstein 1990; Redondo 1993; Soler 1999). Why host species accept the parasite's egg or nestling when this is a potentially maladaptive host decision, is a central theme in brood parasitism research (Smith 1968; Jensen and Vernon 1970; Davies and Brooke 1989a; Rothstein 1990; Lotem et al. 1995; Marchetti 1992; Redondo 1993; Soler et al. 1995; Brooker and Brooker 1996; Payne 1998; Winfree 1999).

There are two general explanations for the lack of egg and chick rejection behaviour in hosts: (1) the "evolutionary lag" or "continuing arms race" hypothesis in which it is argued that rejection behaviour has not had sufficient time to evolve in the host population (Dawkins and Krebs 1979; Brooke and Davies 1989; Davies and Brooke 1989b; Rothstein 1990; Payne 1997; Takasu 1998; Davies 1999; Winfree 1999), and (2) the "evolutionary equilibrium" hypothesis, which suggests that although there has been sufficient time for evolution to occur, the costs associated with egg rejection (e.g., rejecting or breaking one's own eggs, or misidentifying an own egg) outweigh the benefits, thereby preventing the evolution of rejection behaviour in hosts (Davies and Brooke 1989a; Jervis and Kidd 1995; Lotem et al. 1995; Marchetti 1992; Payne 1997; Takasu 1998; Winfree 1999). Irrespective of which hypothesis applies, brood parasite nestlings survive to manipulate the host parents into caring for them, and a 'naive' host has the fitness-reducing task of raising genetically unrelated young.

Hosts however, have evolved some defences against brood parasites (Davies and Brooke 1989a; Brooker and Brooker 1990; Rothstein 1990; Marchetti 1992; Øien et al. 1995; Takasu 1998; Winfree 1999). A number of pre-egg laying behaviours combine to reduce the likelihood of parasitism of host species (e.g., aggression toward the parasite, nest abandonment at high parasite densities; Davies 2000). In addition, egg recognition is more likely when the parasite does not coincide its egg-laying within the egg-laying period of the host. However, even if the parasite manages to penetrate these defences the host must be suitable for the subsequent rearing and care of the parasites' young if the host-parasite system is to succeed (Kozlovic et al. 1996). Thus, the parasite must select a host that not only accepts its egg but also is capable of successfully rearing the parasite nestling. It is this last, largely unexplored aspect of brood parasitism systems that is investigated in this thesis.

Host species exploited by brood parasites tend to be altricial, locally common passerines, thereby providing an abundance of nests to parasitise. The criteria defining a suitable host species are summarised as follows:

- Nests must be accessible, comprising an open cup or possessing an entrance hole big enough for the laying parasite female to enter and deposit her egg (Wiley 1988; Johnsgard 1997; Davies 2000).
- Hosts must have a laying season that spans the period when the parasite is able to breed (Wiley 1988; Soler et al. 1999).
- Hosts must also be of a suitable size for efficient incubation (Davies 2000). If host parents are too small parasite eggs may be relatively too large to receive adequate incubation. Conversely, parasite eggs may receive insufficient contact with the brood patch of relatively large hosts.
- Hosts must be sufficiently large to provide adequate food to support the nestling parasite in its later growth stages where parasite mass may exceed that of the host adult (Wiley 1988).
- Suitable nestling diets, comprising invertebrates (high protein; Jones and Ward 1976; Turner 1982; Klasing 1998), must be provisioned to parasite nestlings (Payne 1977, 1998; Davies and Brooke 1989a; Marchetti 1992; Johnsgard 1997; Davies 2000). Furthermore, the diet of the host and parasite should be similar (Wiley 1988).

Seed and fruit-eating passerines are generally avoided by parasites unless the hosts feed some insect to their young (Payne 1977; Payne and Payne 1967; Wiley 1988). These latter species are considered unsuitable hosts (Øien et al. 1995; Davies and Brooke 1989a; Johnsgard 1997; Davies 1999, 2000) and where they are parasitised, is probably the consequence of opportunistic behaviour on the part of the brood parasite (Kozlovic et al. 1996; Payne 1998). Such opportunistic behaviour predisposes the parasite to use other potential host species should the current host become extinct or if the parasite were to disperse to a new area (Payne 1998).

Host selection is of critical importance in determining the success of brood parasitism. For successful parasite rearing and thus parasitism, the adult host and parasite should be of similar size (Wiley 1988; Johnsgard 1997). Furthermore, parasite incubation and nestling periods should be similar in duration (Johnsgard 1997). Surprisingly, these requirements are seldom met (Jensen and Clinning 1974; Gill 1983; Brooker and Brooker 1989; Davies 2000).

Among the parasitic host-evicting African cuckoos, the mean adult mass of the host species ranges from 28-133% of the adult parasite's mass, averaging 89% (Reed 1968; Rowan 1983; Maclean 1993). In addition, the incubation period for parasites is typically a day or two shorter than the host's (ranging from 11-15 days). This may be because the female parasite carries a ready-to-lay egg in her cloaca for up to a day, or sometimes more, allowing for initial embryonic development to occur before egg deposition (Johnsgard 1997; Davies 2000). This developmental edge gives the early hatching parasite sufficient time and strength to eject the smaller host eggs and/or chicks that hatch after it (Davies 2000).

Parasite nestlings have substantially longer nestling periods (18-26 days) than their hosts, because of their larger size, greater food requirements and the relatively greater foraging efforts required of the much smaller foster parent (Johnsgard 1997). However, another possible explanation is that parasite nestlings delay leaving the nest, because once they do so host parents are able to distinguish the parasite from their own fledglings and refrain from providing post-fledging care to the parasite fledgling.

The diderik cuckoo-ploceid brood parasitism system.–This study investigates the brood parasitism system of the diderik cuckoo, *Chrysococcyx caprius*, and its ploceid hosts. The diderik cuckoo parasitises a wide spectrum of passerines throughout southern Africa (Reed 1968, Rowan 1983). Of the 24 authenticated host species in southern Africa only a few are intensively exploited namely the Cape sparrow (*Passer melanurus*), Cape weaver (*Ploceus capensis*), southern masked weaver (*P. velatus*), spotted-backed weaver (*P. cucullatus*), yellow weaver (*P. subaureus*), and the southern red bishop (*Euplectes orix*) (Payne and Payne 1967; Reed 1968; Jensen and Vernon 1970; Rowan 1983). Almost all diderik cuckoo hosts are locally common and breed communally in reed beds and build closed hanging nests, with the exception of Cape sparrows (breed in trees, bushes and crevices) and red bishops, which build semi-closed upright nests (Johnsgard 1997).

The diderik cuckoo is larger in size (length: 18-20 cm) and 15-50% heavier (mass ~32 g) than its primary hosts (Table 1.1; Rowan 1983; Maclean 1993; Johnsgard 1997; Davies 2000). Of its favoured southern African hosts, the red bishop is the most commonly used (Payne and Payne 1967; Jensen and Jensen 1969). The red bishop breeding season coincides most closely with that of the diderik cuckoo (Craig 1982; Ferguson 1994), which may explain the frequent parasitism of this species. In contrast, weaver and sparrow hosts commence breeding several weeks before the migratory diderik cuckoo arrives in southern Africa (Reed 1968; Rowan 1983; Maclean 1993).

TABLE 1.1. Percentage host adult mass of parasite and comparative breeding traits of the diderik cuckoo's primary host species.

Host species	Mean adult mass (g)	Incubation period (days)	Nestling period (days)	% Adult mass of parasite
Diderik cuckoo (mean mass 32.4g; incubation period 10-12 days; nestling period 20-21 days)				
Red bishop (*Euplectes orix*)	23.1	12-13	12-16	71
Cape sparrow (*Passer melanurus*)	25.7	12-14	16-25	79
Spotted-backed weaver (*Ploceus cucullatus*)	39.8	12	17-21	123
Cape weaver (*Ploceus capensis*)	44.1	13.5	17	136
Southern masked weaver (*Ploceus velatus*)	26.7	unrecorded	unrecorded	82
Yellow weaver (*Ploceus subaureus*)	27.4	13.8	unrecorded	85
Spectacled weaver (*Ploceus ocularis*)	29	13.5	18-19	89

The red bishop cuckoo gens (a term used for a race of female cuckoos which specialises on a particular host species, and lays distinctive eggs that tend to match its host's eggs; plural = gentes; Davies 2000) also shows close egg colour mimicry (Reed 1968; Jensen and Vernon 1970; Ferguson 1994) and there is a low rate of rejection of the cuckoo egg (11.1%) by red bishops (Lawes and Kirkman 1996). However, red bishops are also the most granivorous species among the hosts used by the cuckoo (Reed 1953; Skead 1956; Lindholm 1997). Young cuckoos are rarely successfully reared to fledging when provisioned predominantly seed diets (Wyllie 1981; Davies 2000). For this reason granivorous species are considered unsuitable cuckoo hosts. Unlike red bishops, weavers and Cape sparrows feed their young insects and, at least from the perspective of the diet they provide to their nestlings, are potentially more suitable host species (Øien et al. 1995; Davies and Brooke 1989a; Davies 1999, 2000).

The use of the red bishop by the diderik cuckoo, seemingly in preference to theoretically more suitable insectivorous host species, poses an intriguing evolutionary enigma that is the central theme of this thesis.

NESTLING DIET QUALITY

Of the three major dietary requirements (protein, carbohydrates and fat), protein is considered the most important for successful growth and development of nestlings (Stevens 1996). A diversity of essential nutrients is required for nestling growth (Klasing 1998). For example, nestling Japanese quail (*Coturnix japonica*) require a diet comprising several nutrients, including 28% protein (amino acids), 1.0% linoleic acid, 0.8% calcium; but only 0.0000003% of vitamin B12 (Ricklefs et al. 1998; Klasing 1998). Similar essential nutrients in comparable proportions are reported for chickens and turkeys (National Research Council 1994).

The nutritional status of a nestling is ultimately regulated by the nestling's ability to metabolise and assimilate the food provisioned to it by its parents (Ricklefs 1984). These processes are influenced by the energy and nutrient composition of the diet fed to nestlings emphasising the importance of adequate nutrition (O'Connor 1984; Richner et al. 1989; Johnston 1993; Rovee-Collier et al. 1993; Stevens 1996; Schew and Ricklefs 1998).

The greatest nutritional demands during a bird's life occur during the rapid growth period occurring immediately after hatching (Klasing 1998; Konarzewski et al. 1998).

During this nutritionally demanding period, amino acids, water and energy are essential nutrients for proper growth and development (Bryant and Gardiner 1979; Klasing 1998). Dietary deficiencies at this critical time retard growth in many animals (Klasing 1998; Ricklefs et al. 1998). The effects of dietary deficiencies have been frequently demonstrated in chickens, quails, ducks, pheasants and turkeys (Marks and Lepore 1968; Scott 1973; Street 1978; Magladery et al. 1979; Ricklefs 1983; Boag 1987; Rovee- Collier et al. 1993; Stevens 1996). Rovee-Collier et al. (1993) showed that diets containing above (45% or more) or below (8%) optimal 22% protein content depressed the growth rates of nestling white cockerels (*Gallus gallus*), while Stevens (1996) and Magladery et al. (1979) report optimum protein levels for white leghorn chicks (*G. domesticus*) as 28% (whole diet). In mallard ducklings (*Anus platyrhynchos*; Street 1978) and Japanese quail (Marks and Lepore 1968; Ricklefs et al. 1998) optimal dietary protein levels are 22-28% of the whole diet.

There is also circumstantial evidence of an effect of diet quality on nestling growth in altricial passerine species (Roudybush and Grau 1986; Boag 1987; Johnston 1993; Ricklefs et al. 1998; Schew and Ricklefs 1998; McCarty 2001). Johnston (1993) found that house martin (*Delichon urbica*) nestlings fed on reduced quality diets (low protein; high fat diets) grew at slower rates and were smaller at fledging than control (high protein; low fat diets) nestlings. Johnston (1993) further found that optimal nestling growth rates occurred at dietary protein levels of 65%. A study by Roudybush and Grau (1986) demonstrated negative nestling growth rates in cockatiels (*Nymphicus hollandicus*) at protein levels above (30%) or below (10%) an optimum 20% dietary protein. Diet composition was also shown to have a clear effect on zebra finch *(Poephila guttata*) nestling growth rates, with high quality diets (38% protein) resulting in significantly faster growth rates (Boag 1987).

Nestlings are invariably reared on protein-rich diets, even if this means they have to be provisioned diets that are very different from that of the adult (Rovee-Collier et al. 1982; O'Connor 1984). For example, granivorous house sparrows (*Passer domesticus*) average 96.6% vegetable matter and 3.4% animal matter as adults, but 31.2% vegetable matter and 68.1% animal matter as nestlings (O'Connor 1984).

Adult insects are high in protein (50-75%) and relative to plant protein approach the amino acid balance required by birds more closely (Jones and Ward 1976; Turner 1982; Klasing 1998). Although the chitinous exoskeleton of insects is relatively indigestible, the efficiency of digestion of the nonchitin components by birds is very high, approaching 100% in some cases (Klasing 1998). In contrast, grain and seeds, which have the highest nutrient density of any plant part, are very rich in starch but have low to moderate levels of protein (Earl and Jones 1962; O'Connor 1984). In addition, the poorly developed gizzard of young birds is usually too weak to crack hard seeds and low enzyme levels limit the digestion of lipid and raw starch (Klasing 1998), thereby negatively affecting the digestibility of seeds and grain. Thus most granivorous, frugivorous, nectarivorous and herbivorous birds augment their nestling diets with insects, spiders and other invertebrates that are rich in protein (Ricklefs 1983; O'Connor 1984; Johnston 1993; Klasing 1998).

Diet quality plays a fundamental role in determining the nutritional status of nestlings and therefore is an integral factor in determining host suitability in brood parasitism. Failure of brown-headed cowbird (*Molothrus ater*) parasitism of the house finch (*Carpodacus mexicanus*) has been attributed to the poor diet quality provisioned to the demanding cowbird nestling (Kozlovic et al. 1996). House finches feed their young a diet comprising seed (limited in protein; Jones and Ward 1976; Turner 1982; Klasing

1998) and very little or no animal material. Nestling body mass of cowbirds raised by this host failed to follow a sigmoidal (logistic function) growth pattern typical of normal growth (Ricklefs 1968) and never attained the fledging mass of cowbirds reared by 'suitable' hosts (Kozlovic et al. 1996). Only one of 78 cowbird nestlings in the study survived to fledging, but even this fledgling was found dead the following day (Kozlovic et al.1996).

In this study, the red bishop is predominantly granivorous and past studies have shown that the faeces of diderik cuckoo chicks raised in red bishop nests contain large numbers of grass seeds (Reed 1953, 1968; Skead 1956; Lindholm 1997). Some diderik cuckoo hosts provision insects throughout the cuckoo's nestling period (days 1-23) (e.g., Cape sparrow, yellow weaver) but the red bishop begins feeding a granivorous diet to young cuckoos from an early age (Benson and Serventy 1957; Reed 1953, 1968; Rowan 1983). Thus diderik cuckoos parasitising red bishops are faced with a compromise or energetic trade-off between the quality of the diet provisioned to them and the constraints on digestion and assimilation of low quality foods by their comparatively simple digestive system (Klasing 1998). Superficially, red bishops appear to provision cuckoos with an inadequate diet and are unsuitable hosts. This should result in selection pressure against parasitism of red bishops by the diderik cuckoo, yet as noted above, red bishops are the most frequently parasitised host species. In this thesis I compare the diets, particularly the potential protein content (invertebrates), provisioned to cuckoos by the red bishop and a predominantly insectivorous host, the yellow weaver, (chapter two). I further examine whether or not poor nestling diet results in extended nestling periods and higher than normal rates of nestling mortality.

HOST PROVISIONING RATES

The young of altricial birds are entirely dependent on their parents to feed them from hatching to fledging (Ricklefs 1968, 1984; O'Connor 1984; Cotton et al. 1996). Provisioning rates and mean load size increase gradually throughout the nestling period for most avian species as the energy requirements of the young increase with age and the young can cope with larger food items (Royama 1966; O'Connor 1984).

Provisioning rates differ significantly as a function of brood size (Royama 1966; O'Connor 1984; Wright et al. 1998). Experimentally enlarged brood sizes of European starlings (*Sturnus vulgaris*) and house martins showed that parents feeding larger broods visited the nest more frequently per day (Bryant and Gardiner 1979; Wright et al. 1998). However, nestlings in large broods received fewer individual visits and the extra provisioning demands on starling parents resulted in them provisioning greater proportions of smaller prey, which were of inferior nutritional quality, but of greater availability (Bryant and Gardiner 1979; Wright et al. 1998). In addition, the amount of food provisioned to individual nestlings is reported as being inversely related to brood size (Royama 1966).

Food intake also differs significantly as a function of diet quality (Rovee-Collier et al. 1993). Nestlings provisioned with low-protein diets consume large quantities of food thereby increasing the absolute amount of protein intake and facilitating growth (Rovee-Collier et al. 1993). In high-protein diets, however, the limiting factor for growth is energy. Nestlings that are provisioned high-protein diets consume small quantities of food and should experience slower provisioning rates (Rovee-Collier et al. 1993).

There are very few direct quantitative studies on provisioning rates in altricial birds. Available research includes the effect of different mating systems on provisioning rates and most studies address begging behaviour effects on parental provisioning rates. Little data exists regarding species involved in host-evicting parasitic systems. Consequently, we are reliant on the extensive studies on the European cuckoo (*Cuculus canorus*) (Brooke and Davies 1989; Davies et al. 1998; Kilner and Davies 1999; Kilner et al. 1999; Davies 2000; Grim and Honza 2001).

Young cuckoos are very successful in eliciting food from their foster parents. Studies have shown that although hosts discriminate at the egg stage, they typically show blind acceptance of cuckoo nestlings (Redondo 1993; Davies 2000). Therefore, at the nestling stage, cuckoos rely on host manipulation rather than deception (Dawkins and Krebs 1979; Davies 2000). However, a recent study by Langmore et al. (2003) provides contradictory evidence, in which fairy wren hosts (*Malurus cyaneus*) abandoned nests containing Horsefield's bronze-cuckoo (*Chrysococcyx basalis*) and shining bronze-cuckoo (*Chrysococcyx lucidus*) nestlings. Studies of the European cuckoo have shown that nestlings persuade and trick foster parents into provisioning them (Davies 1999, 2000; Davies et al. 1998; Kilner et al. 1999; Soler and Soler 1999). The extraordinary brood-mimicking vocalisations of the European cuckoo result in adequate provisioning by its reed warbler (*Acrocephalus scirpaceus*) host (Davies et al. 1998). In fact, a single European cuckoo chick receives food at a rate equivalent to that of an average brood of host young (Brooke and Davies 1989; Davies et al. 1998; Kilner et al. 1999) and its growth rate has been shown to be similar to that of the entire host brood (Soler and Soler 1999). The begging European cuckoo nestling provides a supernormal stimulus to host parents and exploits its host by eliciting a higher level of parental care relative to the host young

(Davies et al. 1998). Theoretically, the cuckoo should demand a much faster provisioning rate than an average brood of host nestlings due to its lack of kinship with the host (Kilner et al. 1999). However, several factors may limit a cuckoo's selfishness. The cuckoo nestling may have to match its demands to that of an average brood of host young because it is unable to provide signals that would get the hosts to increase their provisioning rate (Kilner and Davies 1999; Davies 2000; Grim and Honza 2001). Alternatively, cuckoo nestling survival may be compromised if foster parents are provoked into feeding cuckoos at a rate that they are incapable of sustaining throughout the cuckoo's period of dependence, which is already several days longer than the host's own young (Brooke and Davies 1989; Davies 2000). In addition, the increased begging by a cuckoo nestling may increase the risk of predation, thus counteracting any benefits of faster growth (Brooke and Davies 1989).

While I do not examine begging behaviour *per se* (largely because diderik cuckoo nestlings in this study did not display obvious vocal begging – but see Reed 1968, Rowan 1983), I do investigate provisioning rates by the host to the cuckoo and its own nestlings.

Chapter three investigates whether or not the diderik cuckoo exploits the parental care of its hosts by comparing host provisioning rates to nestling cuckoos and to their own brood. Provisioning rates of yellow weaver hosts, which are similar in size to diderik cuckoos, are compared to those of smaller red bishops, to determine the effect of host size on provisioning rates to cuckoo nestlings. In addition, I determine whether a single cuckoo nestling differs in mass from broods of two or three bishop and weaver nestlings. The influence of diet quality on red bishop and yellow weaver provisioning rates is also compared between the two host species. Furthermore, feeding rates to bishop, weaver and cuckoo nestlings throughout the nestling period are compared to determine the influence of extended cuckoo nestling periods on host provisioning rates.

NESTLING GROWTH AND DEVELOPMENT

Avian growth is conventionally described in the form of mass versus age curves and is summarised by the parameters of growth equations that approximate the form, magnitude, and rate of growth (O'Connor 1984). Most bird species show some form of sigmoidal growth, in which hatchling mass increases in a logistic fashion and reaches an asymptote at fledging (Ricklefs 1968; O'Connor 1984). In some species fledging mass approaches or is equal to the adult mass (e.g., starlings, *Lamprotornis* spp.), while in others the fledging mass is substantially below that of the adult mass (e.g., wood pigeon, *Columba palumbas*, American robin, *Turdus migratorius*; O'Connor 1984). More rarely, the nestling mass of other species, particularly those of swifts and oceanic species, increases to a maximum above adult mass and then declines before fledging (O'Connor 1984). These species generally forage on the wing, thus the flight muscles of these fledglings must be fully matured to allow them to feed themselves (Ricklefs 1968).

The rate of nestling development is characterised by the growth rate constant (*K*) of the sigmoid equations fitted to the body mass versus age relationship (Ricklefs 1968). Of the five sigmoid equations outlined by Starck and Ricklefs (1998) the logistic growth function, which has the form:

$$y = \frac{A}{1 + e^{(-K*(t-t_i))}}$$

is used in chapter four to describe nestling growth. Variations in different aspects of growth including the shape of the growth curve, the asymptote, *K*, and the maximum growth rate, have been demonstrated for several avian species (reviewed in Gebhardt-Henrich and Richner 1998). However, because *K* is independent of developmental time (Starck and Ricklefs 1998), it is the parameter most frequently reported in comparative analyses of nestling growth variation.

Altricial birds grow at a fast rate and are fed and cared for intensively by their parents (Ricklefs 1984; Starck and Ricklefs 1998). Typically, altricial young complete their growth before leaving the nest (Ricklefs 1969) with small passerines attaining full adult mass within 10-20 days of hatching (Case 1978; McCarty 2001). Despite the prevalence of altriciality among birds, available growth data are restricted to few altricial and even fewer passerine species (reviewed in Starck and Ricklefs 1998).

Intraspecific variation in growth rates of altricial nestlings is attributed to a variety of factors, including habitat (Richner et al. 1989), weather (Ross 1980; McCarty 2001), predation intensity on nestlings (Ricklefs 1984), diet quality (O'Connor 1984, Ricklefs 1983; Boag 1987; Johnston 1993; Ricklefs et al. 1998; Schew and Ricklefs 1998; McCarty 2001) and the amount of food available to parents to feed their young (Lack 1968; Price 1985; Quinney et al. 1986; Gard and Bird 1992). In particular, the quantity and quality of food provisioned to nestlings have been identified as the major sources of variation in growth rates (reviewed in Gebhardt-Henrich and Richner 1998). Manipulation of these factors in altricial birds have often resulted in significantly elevated nestling growth rates when i) food supply is abundant for parents to feed their young and provisioning rates to nestlings are subsequently faster (reviewed in Martin 1987) and/or ii) when nestlings are provisioned diets containing optimum levels of dietary protein (Roudybush and Grau 1986; Boag 1987; Johnston 1993; Ricklefs et al. 1998).

Lack (1968) proposed that optimum nestling growth rates represent a compromise between mortality rates and the limits set by the availability of food. Higher risk of nestling mortality favours faster growth because the length of time the nestlings are exposed to risk is reduced. However, the greater food demands created by faster growth rates limit the number of young per brood that parents can rear (Lack 1968; Ricklefs 1984; Martin 1987). In addition, Ricklefs (1969) suggests that growth rates are further determined by physiological constraints such as the rate at which food is digested and assimilated or the rate at which tissues proliferate and grow. Thus, nestling growth rates and brood size are determined by the capability of parents to feed their young, which is ultimately dependent on food availability and may be further influenced by adult body size (Ricklefs 1969), parental age and nesting experience (Richner et al. 1989).

Nestling growth rates influence the duration of the nestling period, which ultimately affects the probability of fledging success (Nice 1957; Ricklefs 1979; Richner 1989; Johnston 1993; Pereyra and Morton 2001). Furthermore, fledgling mass is positively correlated with post-fledging survival (Perrins 1965; Davies 1986; Magrath 1991; McCarty 2001). Perrins (1965) attributed this relationship to the higher energy reserves available to heavier young birds, whilst Garnett (1981) proposed social dominance for juvenile success. Fledgling body mass can therefore influence reproductive fitness by decreasing a juvenile's ability to obtain a breeding territory, a mate or by lowering subsequent fecundity (Martin 1987; Gebhardt-Henrich and Richner 1998). Adequate fledging mass is therefore imperative to the post-fledging survival of parasite nestlings, particularly as host parental care to fledged parasites is limited (Wiley 1986; Redondo 1993). Parasite fledglings that are highly developed in terms of adult size are expected to cope better with the critical period of independence from their foster parents, and are thus more likely to survive as juveniles (Wiley 1986). In shining-bronze cuckoos (*Chrysococcyx lucidus*) extended nestling periods resulted in heavier fledglings (Gill 1983), suggesting that parasite nestlings remain in the nest as long as possible so as to reach adult body size before fledging.

Although several early studies document the development of cuckoo nestlings from hatching to fledging (Skead 1952; Jensen and Clinning 1974; Rowan 1983; Brooker and Brooker 1989; Chalton 1991; Soler and Soler 1991), growth parameter data for cuckoo nestlings is minimal (Table 1.2). Moreover, only one study has compared the growth rates of cuckoo nestlings raised by different host species, in which European cuckoos raised by larger great reed warbler (*Acrocephalus arundinaceus*) hosts grew faster and were significantly larger at fledging than those raised by smaller reed warbler hosts (Kleven et al. 1999). Chapter four documents the growth rates of diderik cuckoo nestlings in red bishop nests and compares these growth rates to those of cuckoo nestlings in yellow weaver nests. By comparing growth rates of diderik cuckoos raised by hosts that differ in the quality of food provisioned to the cuckoo chick and the rate at which diet is provisioned to cuckoo chicks, I aim to determine whether cuckoo growth in bishop nests is indeed constrained by diet quality and/or host provisioning rates. In addition, the mass of diderik cuckoo fledglings is compared to those of adult cuckoos to determine whether cuckoos approach adult mass before leaving the nests of bishop and weaver hosts.

TABLE 1.2. Asymptote body mass and growth rate constant (*K*) for cuckoo nestlings as determined by the logistic growth function. The sample size (*n*) and reference have been included.

Species	Asymptote body mass (g)	*K*	*n*	Reference
Great spotted cuckoo (*Clamator glandarius*)	132.5	0.318	1-11	Soler and Soler 1991
Horsefield's bronze-cuckoo	20.9	0.410	11	Brooker and Brooker 1986
(*Chrysococcyx basalis*)	22.8	0.410	-	Brooker and Brooker 1989
Diderik cuckoo (*Chrysococcyx caprius*)	36.2	0.375	1	Chalton 1991
Shining bronze-cuckoo	21.6	0.350	-	Brooker and Brooker 1989
(*Chrysococcyx lucidus*)	22.9	0.350	-	Gill 1983

Adapted from Starck and Ricklefs 1998

GENERAL AIMS AND OBJECTIVES

Host suitability, including diet quality, host-provisioning rates and parasite nestling survival, is examined. With few exceptions (Kattan 1996; Kozlovic et al. 1996; Kleven et al. 1999), the effect of host quality on parasite nestling growth and development has not been determined. However, more pertinent is the lack of contemporary diderik cuckoo studies that encompass the above issues. This research therefore aims to assess the suitability of the red bishop as a host of the diderik cuckoo, by determining the following:

i. Nestling diet and the differences between host species and host specific cuckoo nestlings. Do poor quality diets result in prolonged fledging and higher than normal rates of nestling mortality?

ii. How much parental effort, measured as provisioning rates, does a cuckoo demand from its foster parents? Does one cuckoo nestling demand as much feeding effort as a brood of bishops or weavers? Are red bishop and yellow weaver provisioning rates influenced by diet quality? Do extended cuckoo nestling periods affect host-provisioning rates?

iii. Is the growth and development of cuckoo nestlings raised by bishop hosts constrained by the poor quality diet and/or host provisioning rates?

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CHAPTER TWO

Diet quality and the successful fledging of diderik cuckoo nestlings: A granivorous-omnivorous host species comparison

ABSTRACT.–Host species that provision predominantly seed diets to cuckoo nestlings are rarely successful in rearing parasite nestlings to fledging and are considered unsuitable hosts. This study compares the faecal content of diderik cuckoo (*Chrysococcyx caprius*) nestlings raised by southern red bishop (*Euplectes orix*) and yellow weaver (*Ploceus subaureus*) hosts and determines whether insect rich diets are essential for the successful rearing of cuckoo nestlings. Red bishops provisioned large quantities of grain to cuckoo nestlings from an early age compared to yellow weaver hosts. Cuckoo nestling mortality in bishop nests was correlated with the protein deficient diet provisioned to cuckoos by this host. Nevertheless, red bishops are the most exploited host of the diderik cuckoo in southern Africa. We propose that this is because i) cuckoo eggs are more likely to be accepted by the less discriminating bishop and ii) the bishop-breeding season coincides more closely with that of the diderik cuckoo than the yellow weaver. Ultimately, both host systems represent evolutionary compromises for the diderik cuckoo, with neither red bishops nor yellow weavers being entirely ideal as host species.

SEVERAL STUDIES highlight the importance of high protein diets for nestling growth and development, and ultimately nestling survival (Storer 1971; Scott 1973; Street 1978; Magladery et al. 1979; Ricklefs 1983; Roudybush and Grau 1986; Boag 1987; Johnston 1993; Rovee-Collier et al. 1993; Stevens 1996; Klasing 1998; Ricklefs et al. 1998). In passerine birds high protein diets are commonly derived from invertebrates, particularly insects (Moir 1994; Klasing 1998). Insects contain high proportions of protein (50-75%; Jones and Ward 1976; Turner 1982; Klasing 1998) and the digestion efficiency of their non-chitin components by birds is very high (Klasing 1998). In contrast, grain and seeds have a high nutrient density and are very rich in starch, but have low to moderate levels of protein (Earl and Jones 1962; Morton 1973; O'Connor 1984; Kozlovic et al. 1996). Furthermore, the immature gizzard of young nestlings is too weak to crack hard seeds and the digestion of the lipid, protein and raw starch components of seeds is limited by the low enzyme levels of nestlings (Klasing 1998). Thus most granivorous, frugivorous, nectarivorous and herbivorous birds supplement their nestlings' diets with protein-rich insects, albeit a diet that is very different from that of the adult (Rovee-Collier et al. 1982; Ricklefs 1983; O'Connor 1984; Mason 1986; Johnston 1993; Klasing 1998; Schew and Ricklefs 1998).

Few studies have directly investigated the effect of diet quality on the growth of passerine nestlings (Krebs and Avery 1984; Boag 1987; Johnston 1993; McCarty 2001). Only one study has addressed the influence of a nutrient deficient diet on parasite nestling development and the subsequent failure of brood parasitism (Kozlovic et al. 1996). For parasitism to be successful, hosts must not only accept and incubate parasite eggs, but they also must provide the nestling parasite with a protein-rich diet to ensure proper growth and development (Kozlovic et al. 1996). Diets comprising invertebrates, particularly insects, are considered suitable for all nestlings, including parasites (Ricklefs 1983; O'Connor 1984; Mason 1986; Roudybush and Grau 1986; Boag 1987; Johnston 1993; Klasing 1998; Davies 2000). No frequent hosts of the European cuckoo (*Cuculus canorus*), or of any of the Australian shiny cuckoos (*Chrysococcyx* spp.), raise their young primarily on seeds (Davies 2000). Host species that provision predominantly seed diets to cuckoo nestlings are rarely successful in rearing parasite nestlings to fledging and are usually considered unsuitable hosts (Kozlovic et al. 1996; Davies 2000).

The diderik cuckoo (*Chrysococcyx caprius*) parasitises several species that provision diets comprising varying proportions of insect and plant material (Rowan 1983; Johnsgard 1997; Davies 2000). Insectivorous species such as the Cape wagtail (*Motacilla capensis*) feed their own young and presumably diderik cuckoo nestlings, on invertebrates and occasionally small fish (Berry 1973; Rowan 1983). Similarly, sparrow and weaver hosts provision invertebrates, particularly insects, throughout the cuckoo's nestling period (days 1-23) (e.g., Cape sparrow (*Passer melanurus*), yellow weaver (*Ploceus subaureus*; Reed 1968; Rowan 1983; Lindholm 1997). However, the southern red bishop (*Euplectes orix*), a common host of the diderik cuckoo, is predominantly granivorous and reputed to provision large quantities of grass seed and grain to cuckoo nestlings from an early age (Skead 1956; Benson and Serventy 1957; Reed 1953, 1968; Rowan 1983). Similar diets provisioned by granivorous hosts to other cuckoo species rarely result in the parasite nestling surviving to fledging and successful parasitism of these host species is rare (Wyllie 1981; Davies 2000).

This study investigates the proposition that insect rich diets are essential for the successful rearing of parasite nestlings. The diet provisioned to cuckoo nestlings by red bishop and yellow weaver hosts is compared, with the latter species chosen as a representative, predominantly insectivorous host. Foster parents are expected to provision host and parasite nestlings with similar diets. However, red bishop hosts are expected to provision relatively low proportions of insect to nestlings compared to yellow weaver hosts. Consequently, extended nestling periods (Magladery et al. 1979; Boag 1987; Richner et al. 1989; Johnston 1993) coupled with the subsequent increased vulnerability to nest predation (Lack 1968) are expected to decrease the fledging success of diderik cuckoo nestlings from red bishop nests. Furthermore, the prolonged fledging period of cuckoos in bishop nests may result in reduced parental care due to the tiring of bishop foster parents, thereby further compromising the success of cuckoo fledging.

STUDY AREA AND METHODS

Study site.–The study was conducted in and around Pietermaritzburg, KwaZulu-Natal Province, South Africa, during the summer months (November to February) of 1996-1997 (year 1); 1998-1999 (year 2) and 1999-2000 (year 3), coinciding with red bishop, yellow weaver and diderik cuckoo breeding. Small, low-density colonies, prone to parasitism by diderik cuckoos (Ferguson 1994; Lawes and Kirkman 1996), were selected for observation (Table 2.1) and monitored daily between 05h00 and 10h00.

Yellow weaver nests were observed during the 2nd and 3rd years (1998-2000) only and parasitism of yellow weavers by diderik cuckoos was observed only in the 2nd year (1998-1999). During 1999-2000, sampling was conducted in Pietermaritzburg colonies and in two colonies situated at Cedara in the mist-belt region of the KwaZulu-Natal midlands. Preliminary analysis of these data revealed similar nestling diet trends for both regions, thus these data were combined for further analyses.

TABLE 2.1. A list of red bishop and yellow weaver colonies in Pietermaritzburg and Cedara, which were designated as study sites. The latitude and longitude co-ordinates are given, along with the number of active nests in each colony.

Colony name	Latitude	Longitude	No. of active nests
Pietermaritzburg			
Alex	29°37'00"	30°23'35"	35
Bisley Bottom Dam*	29°30'15"	30°24'30"	57
Bisley Top Dam*	29°39'45"	30°23'35"	19
Bridge	29°38'15"	30°25'06"	1
Cabbage Patch	29°37'00"	30°23'35"	1
Cleland	29°38'20"	30°25'30"	1
Hayfields	29°38'15"	30°25'06"	21
Jesmond	29°37'55"	30°24'55"	41
Oribi New	29°39'15"	30°24'20"	10
Oribi Old	29°39'15"	30°24'20"	5
Railway	29°30'15"	30°24'30"	8
Sakabula A	29°32'30"	30°13'00"	12
Sakabula B	29°32'30"	30°13'00"	10
Cedara			
Cedara Right Fork	29°30'00"	30°16'00"	39
Cedara Sewerage	29°30'00"	30°16'00"	10

* denotes yellow weaver colonies

Red bishop and yellow weaver nests were predominantly located in reed beds dominated by *Phragmites australis*, with the exception of Jesmond Park (Jesmond), where nests were built in a dense stand of *Sesbania punicea* bushes, and the surrounding tall grass. At Railway bishop nests were built in *Typha capensis* and *Kniphofia spp.* Yellow weaver nests at both Bisley colonies were found in either *Typha capensis* or *Cypress* spp. Active nests were marked with a coded tag inconspicuously placed on the lower parts of the reed, and plotted on field maps.

Nestling faecal content.–Faecal samples were collected from cuckoo, bishop and weaver nestlings at each visit to the nest during all three years of the study period (i.e. almost every day), except when faecal sacs were not visible in the cloaca. However, the absence of visible faecal sacs was infrequent. An initial analysis revealed that the faeces of one-day-old nestlings did not contain insect and grain fragments, only calcium deposits, consistent with the findings of Klasing (1998). Thus only samples from nestlings that were older than one-day were included in the analysis. Samples were stored separately in 98% ethanol. For examination the faecal samples were moistened with 98% ethanol, teased apart with dissecting needles and placed on a 50mm x 50mm grid comprising 100 equally sized grid cells. The number of insect and seed fragments in each grid cell was counted using a Leica Zoom 2000 dissecting microscope. In order to minimise bias towards small items, particularly when the samples from older young contained progressively more digested food, and for comparative purposes, samples were analysed at a constant magnifying power (magnification 12X). The percent proportion of insect and seed material in the diet was calculated for each sample and the relative increase in proportions in nestling faeces was taken as an increase of that item in the diet (Rosenberg and Cooper 1990).

Cross-fostering experiments were carried out during the 3rd year of study, where two red bishop and eight yellow weaver nestlings of the same age were placed in other yellow weaver and red bishop nests, respectively. In all cases, nestlings died within fours days of being cross-fostered. As a result this experiment was discontinued.

Nestling mortality.–The number of dead young present on each visit was recorded, including nestlings that were absent from nests. The cause of death was assigned to either extrinsic ecological factors (climate and predation) or non-ecological factors (parental care, diet quality, provisioning rates, clutch size and parasites) (Lack 1968; O'Connor 1984; Ricklefs 1984; Martin 1987; Kozlovic et al. 1996). Nestling mortality was calculated as a percentage of the total number of nestlings that hatched.

Statistical models.–The aim of these analyses was to model the proportion of insect in the diet of host and parasite nestlings as a function of age, species, brood size, year, rainfall and temperature. The proportion was estimated from the ratio of a count of insect fragments relative to the total number of fragments in the sample (see above). A generalised linear model (GLM) was constructed for data with the proportion of insects as the response variable (McCullach and Nelder 1989; Dobson 1991). Given that only insect and grain fragments were counted, the proportion was modelled using the binomial distribution and a logit link function (McCullach and Nelder 1989; Dobson 1991). The variables discussed below were entered into the model in linear combinations. The GLMs were fitted using Genstat (Genstat 5 committee 1987). The goodness of fit of a model was assessed using the X^2 statistic in which the actual insect proportion in nestling diet was compared with predicted insect proportion; X^2 has the useful property that it is asymptotically distributed as χ^2 (Dobson 1991). For model selection and parameter estimation a set of candidate models was formulated *a priori* and fitted (as opposed to analysing all possible combinations of variables and models). This approach is recommended by Anderson and Burnham (2001).

The following independent variables were defined:

Age – the age of each nestling recorded from hatching (day = 1) to fledging.

Age^2 – the square of age was used to determine if a quadratic relationship existed between age and insect proportion in nestling faeces.

Year – the 3 different field seasons during which data was collected (see above).

Species – Host nestlings: red bishops (sp. 1) and yellow weavers (sp. 2); parasite nestlings: diderik cuckoos in red bishop nests (sp. 3) and diderik cuckoos in yellow weaver nests (sp. 4).

Brood – The number of nestlings occupying the nest: one red bishop (1), two red bishops (2), three red bishops (3), diderik cuckoo in a red bishop nest (4), one diderik cuckoo and two red bishops (5), one diderik cuckoo and one red bishop (6), one yellow weaver (7), two yellow weavers (8), three yellow weavers (9), diderik cuckoo in a yellow weaver nest (10).

Bird – each individual nestling was modelled separately, thereby removing the effect of pseudoreplication.

In anticipation of annual differences in the amount of a food item provisioned to nestlings, and in the absence of data for invertebrate abundance in each season, I included rainfall and temperature in the model as surrogate measures of environmental conditions and potential invertebrate availability (Romoser 1981).

Rainfall – the amount of rain recorded daily, (mm). Rainfall recorded on the previous day (Last Rain) and rainfall averaged over the previous 10-day period (10-day running mean) were also included in the model. The 10-day period of the running mean represents the time period over which short-term environmental response to rainfall takes place. Warm, wet conditions promote vegetation growth, which in turn is correlated to increased arthropod abundance (Romoser 1981).

Temperature – the minimum and maximum daily temperatures, (°C). Previous-and present-day temperatures were also included.

The response variable, proportion of insect in the sample, p, is defined as follows:

n_I = number of insect fragments in faecal sample;

n_G = number of grain fragments in faecal sample;

p = proportion of insect in faecal sample; and therefore

$p = n_I/(n_I + n_G)$.

The logit is defined as:

$\text{Logit}(p) = \text{Ln}(p/(1-p))$.

The GLM is:

$\text{Logit}(p) = a_0 + a_1x_1 + a_2x_2 \ldots$,

where $x_1, x_2, \ldots$ are the independent variables, e.g., age, species . . ., a_0 is the constant term and a_i are the model coefficients for the predictor or independent variables (x_i).

Writing the linear models as

$L = a_0 + a_1x_1 + a_2x_2 \ldots$

The reverse transform or predicted probability of insect in the faeces of nestlings is given as:

$p = \exp(L)/(1 + \exp(L))$.

The Akaike information criterion (AIC) (Burnham and Anderson 1998) and Akaike weights were computed for all the candidate *a priori* models. The models were compared and the model with the lowest AIC value (and a difference of at least two AIC values from the other models) was accepted as the best-fit model (Anderson and Burnham 2001). The Akaike information criterion (AIC) was computed using the method described by Anderson and Burnham (2001).

RESULTS

During the study period (1996-2000) diderik cuckoos parasitised 53 (37.3%) of 142 red bishop nests and five (10.4%) of 48 yellow weaver nests, with the frequency of parasitism of red bishops peaking during 1996-1997 (year 1; 53.9%). A total of 79 (43.9%) red bishop and 28 (52.8%) diderik cuckoo nestlings fledged during the study period. Red bishops fledged from as early as 8 days to 14 days old (mean age = 13 days), whereas diderik cuckoos fledged, on average, nine days later than bishop nestlings (mean age = 22 days).

Of the five diderik cuckoo nestlings that parasitised yellow weavers during the study period, four (80%) fledged successfully. The remaining diderik cuckoo died in a flood (January 1999). Yellow weaver fledging success was 43.7% (n = 87), with a mean fledging age of 17 days (range = 14-19 days old). Although not statistically significant, diderik cuckoos raised by weaver hosts fledged on average two days later than host fledglings (mean age = 19 days) and three days earlier than their red bishop counterparts.

Nestling faecal content.–The overall mean proportion of insect in the faeces of hatchlings (age = 2 days) exceeded 60% for all species investigated (Table 2.2). At fledging the insect content in faeces reached mean proportions of 37.9% and 49.3% for red bishop host and parasite nestlings, respectively (Table 2.2). In contrast, insect proportions in the faeces of diderik cuckoos raised by weaver hosts remained high and relatively constant with increasing age, reaching a minimum of 74.1% at fledging (Table 2.2). Similarly, relatively stable insect proportions were recorded in the faeces of yellow weaver fledglings (Table 2.2).

TABLE 2.2. The mean percentage of insect in nestling faeces at hatching and fledging during the study period. Data are represented by the mean ± SD, with the range and sample size in parentheses.

	Mean percentage of insect in nestling faeces	
Species	Hatching	Fledging
Red Bishop	71.5 ± 17 (0.0-93.0, 30)	37.9 ± 20 (2.7-92.9, 41)
Diderik Cuckoo $_{RB}$	60.5 ± 19 (43.5-88.0, 5)	49.3 ± 18 (16.9-80.0, 16)
Yellow Weaver	65.0 ± 18 (27.3-100.0, 21)	65.3 ± 19 (45.1-81.7, 3)
Diderik Cuckoo $_{YW}$	84.4 (1)	74.1 ± 10 (66.7-81.5, 2)

Data were subjected to generalised linear models (GLM) to quantify these preliminary discrepancies in nestling diet. The GLM that best fit the data included the variables - age, age^2, rainfall and temperature and the factors - year, species, brood size and bird (AIC = 3404, and a weight of 99.3%). There was significant variation between years in the proportion of insect in nestling faeces (Fig. 2.1). The GLM coefficient for the proportion of insect in nestling faeces was significantly larger for years one and three relative to year two (Fig. 2.1), suggesting greater insect abundance in the 1st and 3rd year.

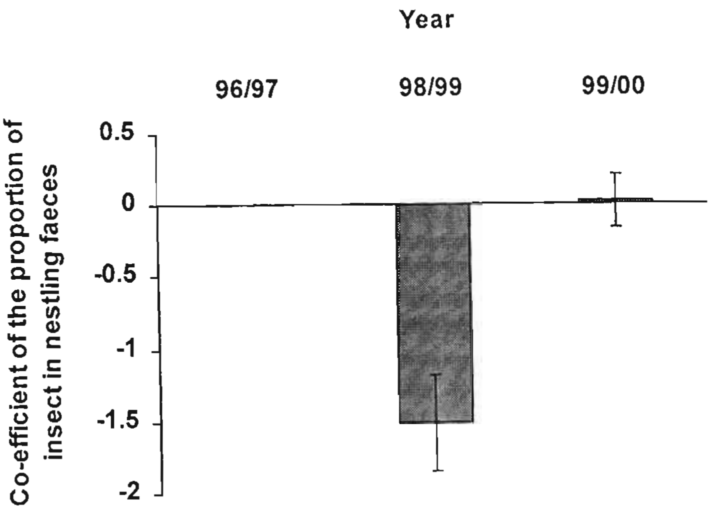


FIG. 2.1. Annual variation in the proportion of insect in nestling faeces during the study period. Insect proportions in nestling faeces are represented by the GLM coefficients. The effect of each year is plotted relative to the constant (96/97), so that negative values indicate comparatively lower proportions of insect. Error bars represent ± 2 SE.

Single or compound omissions of rainfall- and temperature-related variables from the GLM, resulted in weaker AIC and weighting values of the models. Thus data could not be combined across years and therefore were analysed independently (Fig. 2.2). Consequently, the faecal content of red bishop and diderik cuckoo nestlings was compared for each year. Yellow weaver nestling diet comparisons were made using data collected during 1998-2000. Yellow weaver-brood parasite comparisons were restricted to year two. As a result, inter-host comparisons were made only where data were available for all species.

The proportion of insect in nestling faeces decreased quadratically with increasing nestling age in all years (Fig. 2.2). However, this trend was less prominent during 1998-1999, which correlated with the potentially lower insect abundance in this season. Although not statistically significant, diderik cuckoo faeces contained lower insect proportions than red bishops for the duration of the nestling period and throughout the study period (Fig. 2.2). In contrast, the faeces of cuckoo nestlings in weaver nests contained higher insect proportions than weaver nestlings throughout the nestling period (Fig 2.2). During the early phase of the nestling period (2-4 days) the proportions of insects did not differ significantly between species ($F_{154} = 2.278$, $P > 0.05$). Although not statistically significant, proportions were highest in the faeces of weaver-cuckoos (84.2 ± 3%; range = 81.6-88.2%, $n = 4$). With the exception of diderik cuckoos in red bishop nests during year two, insect proportions in excess of 60% were recorded in the faeces of the remaining species across all years (Table 2.3 and 2.4). At fledging (mean age = 13 days) red bishop faeces contained less than 41% insect during all three years (Table 2.3). Faeces collected from bishop-cuckoos at fledging (mean fledging age = 22 days; 9 days following bishop fledging) comprised low insect proportions, averaging between 42.9% and 52.0% during the three years (Table 2.3). With the exception of year three, a further comparison of cuckoo faeces at 13 days (bishop fledging age) yielded similar proportions to those of cuckoo fledglings. Thus the proportion of insect in cuckoo faeces remained relatively constant during the last nine days of the cuckoo's nestling period (Table 2.3). During year three the faeces of cuckoo fledglings contained almost twice as much insect as found in the faeces of 13-day old cuckoos (Table 2.3). In the yellow weaver system the faeces of host and parasite fledglings contained in excess of 70% insect during the second year (Table 2.4).

FIG. 2.2. The proportion of insect in nestling faeces plotted as a function of nestling age. Each year has been represented independently illustrating varying insect proportions in nestling faeces during the study period. The percentage insect in the nestling faeces of red bishops (solid circle), yellow weavers (solid square) and diderik cuckoos in bishop (open circle) and weaver (open square) nests is compared, data permitting. The fitted GLM models are included for comparison. Insect proportions were calculated as logits from the coefficients of the best fit GLM [insect proportion = e (coeff.)/(1+e (coeff.))].

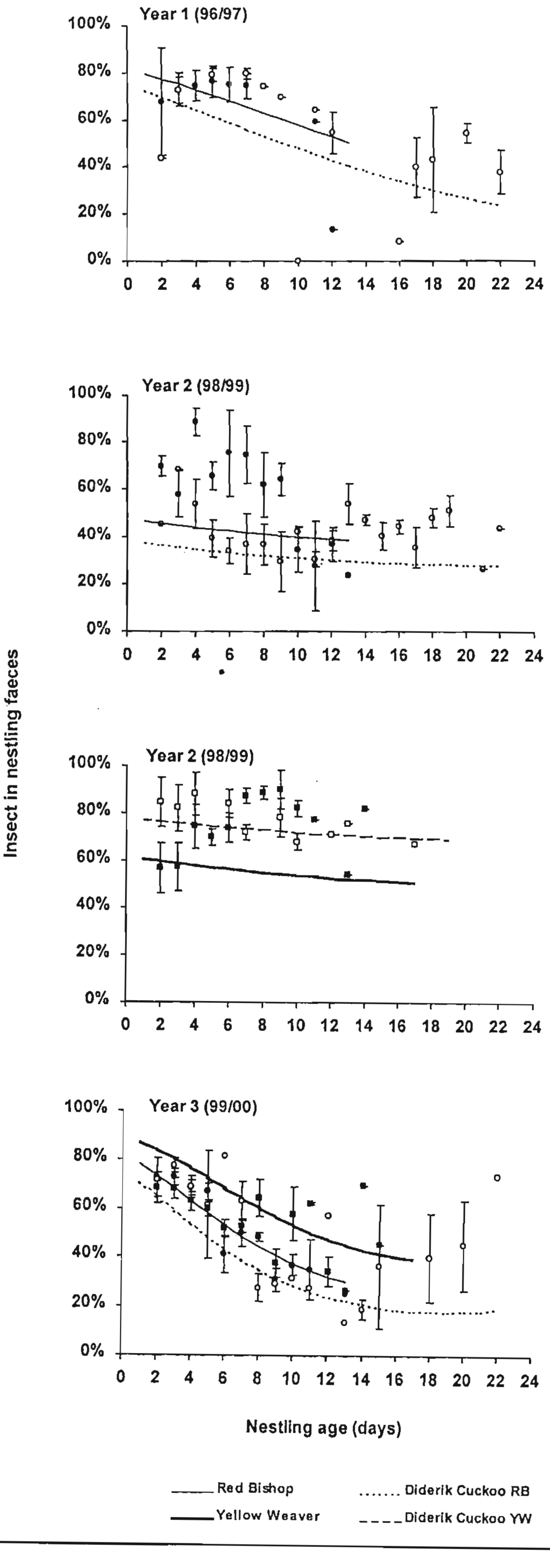

Year 1 (96/97)
Year 2 (98/99)
Year 2 (98/99)
Year 3 (99/00)
100%
80%
60%
40%
20%
0%
0
2
4
6
8
10
12
14
16
18
20
22
24
Insect in nestling faeces
Nestling age (days)
Red Bishop
Yellow Weaver
Diderik Cuckoo RB
Diderik Cuckoo YW

TABLE 2.3. An annual comparison of the mean percentage of insect in nestling faeces at post-hatching and fledging within the red bishop-diderik cuckoo system. Data are represented by the mean ± SD, with range and sample size in parentheses.

		Mean percentage of insect in nestling faeces		
Year	Species	2-4 days	13 days (Bishop fledging)	22 days (Cuckoo fledging)
(96/97)	Red bishop	71.7 ± 26 (0.0-93.0, 12)	36.0 ± 32.0 (36.0-59.0, 2)	
	Diderik cuckoo	65.4 ± 16 (43.5-82.4, 4)	52.8 ± 28 (0.0-74.2, 6)	51.2 ± 16 (20.8-72.6, 8)
(98/99)	Red bishop	69.6 ± 19 (20.0-100.0, 13)	40.6 ± 24 (2.7-92.9, 22)	
	Diderik cuckoo	55.4 ± 13 (43.5-68.4, 4)	42.0 ± 13 (16.7-85.9, 27)	42.9 ± 13 (26.1-57.3, 4)
(99/00)	Red bishop	71.0 ± 11 (25.0-88.3, 55)	34.7 ± 11 (16.3-50.3, 17)	
	Diderik cuckoo	71.1 ± 12 (47.5-88.0, 14)	27.8 ± 13 (13.3-57.3, 9)	52.0 ± 30 (16.9-80.0, 4)

TABLE 2.4. An annual comparison of the mean percentage of insect in nestling faeces at post-hatching and fledging within the yellow weaver-diderik cuckoo system. Data are represented by the mean ± SD, with range and sample size in parentheses.

		Mean percentage of insect in nestling faeces		
Year	Species	2-4 days	17 days (Weaver fledging)	19 days (Cuckoo fledging)
(98/99)	Yellow weaver	61.1 ± 22 (27.3-90.9, 12)	81.7 (1)	
	Diderik cuckoo	84.2 ± 3 (81.6-88.2, 4)	66.7 (1)	74.1 ± 10 (66.7-81.5, 2)
(99/00)	Yellow weaver	68.0 ± 15 (31.6-100.0, 40)	57.1 ± 17 (45.1-69.2, 2)	
	Diderik cuckoo	No active parasitised nests in study area		

The above trends were supported by the GLM, with the coefficients for the proportion of insect revealing a lack of significant host-parasite difference within the individual brood parasite systems (Fig. 2.3). In contrast, significant variation existed in the insect content of faeces between brood parasite systems (Fig. 2.3). Faeces of cuckoo nestlings reared by yellow weaver hosts comprised 30% more insect at fledging than their red bishop counterparts and approximately twice as much at 13 days (bishop modal fledging age). Similarly, proportional insect content in yellow weaver nestling faeces was between 10% and 40% larger relative to that in red bishop nestling faeces.

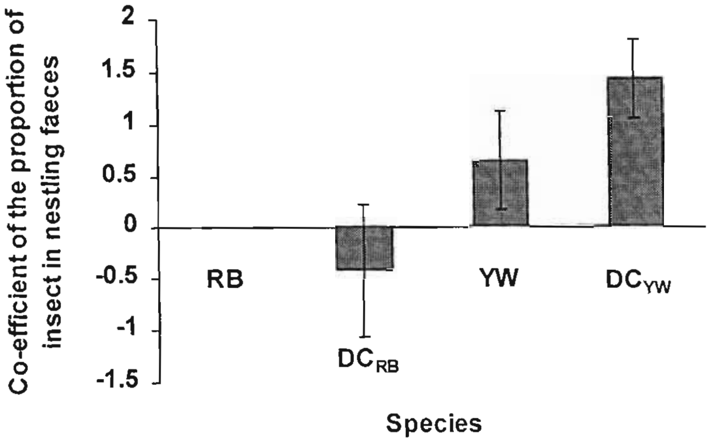


FIG. 2.3. Variation in the proportion of insect in nestling faeces between host and parasite nestlings within the red bishop and yellow weaver brood parasite systems. Insect proportions in nestling faeces are represented by the GLM coefficients. The effect of each species is plotted relative to the constant (RB), so that negative values indicate comparatively lower proportions of insect. Red bishops, bishop-cukoos, yellow weavers and weaver-cuckoos are represented by RB, DC_{RB}, YW and DC_{YW}, respectively. Error bars represent ± 2 SE.

The GLM residuals (variation in the proportion of insect in nestling faeces) for red bishop nestlings increased with increasing nestling age ($F_{1,168} = 18.318$; $P < 0.0001$), suggesting low variability in an insect-dominated (> 60%) diet among 2-4 day old nestlings (Fig. 2.4A). A small increase in the residual proportion of insect in nestling faeces across the nestling ages was evident for yellow weaver nestlings (Fig. 2.4C), however this increase was not significant ($F_{1,137} = 3.579$; $P = 0.061$), and variation in the proportion of insect in weaver nestling faeces was independent of nestling age. Similarly, variation in insect content in the faeces of bishop-cuckoo nestlings and weaver-cuckoo nestlings was constant throughout the nestling period indicating an independent relationship between the variation of insect in nestling faeces and nestling age (Fig. 2.4B and D).

Diet switching from predominantly insect to grain was particularly pronounced in red bishop nestlings. The diet switch occurred when nestlings of this species were eight days old, only five days before fledging (Fig. 2.5A). A less prominent and unexpectedly early switch (age = 6 days) from insect to grain was observed in diderik cuckoo nestlings raised by bishop hosts (Fig. 2.5B). Thus, in red bishop nests seed-rich faeces were evident for more than half of the cuckoo's nestling period (Fig. 2.5B). However, the proportion of seed in cuckoo faeces decreased towards 50% as cuckoos approached fledging (Fig. 2.5B). In contrast, insects were significantly more abundant in the diet of host and parasite nestlings in yellow weaver nests throughout the nestling period and there was no diet switch in this system (Fig. 2.5C and D). Grain proportions above 50% were observed in the faeces of only one yellow weaver nestling, only two days before fledging (Fig. 2.5C).

FIG. 2.4. GLM residuals plotted as a function of nestling age. The significant regression computed for (A) red bishop nestlings indicates increasing variation in the proportion of insect in the diet with increasing nestling age. Non-significant regressions plotted for (B) diderik cuckoos in bishop nests, (C) yellow weavers and (D) diderik cuckoos in weaver nests indicate no correlation between nestling age and insect variation in nestling diet. The linear regression equation and the significance of the regression are included.

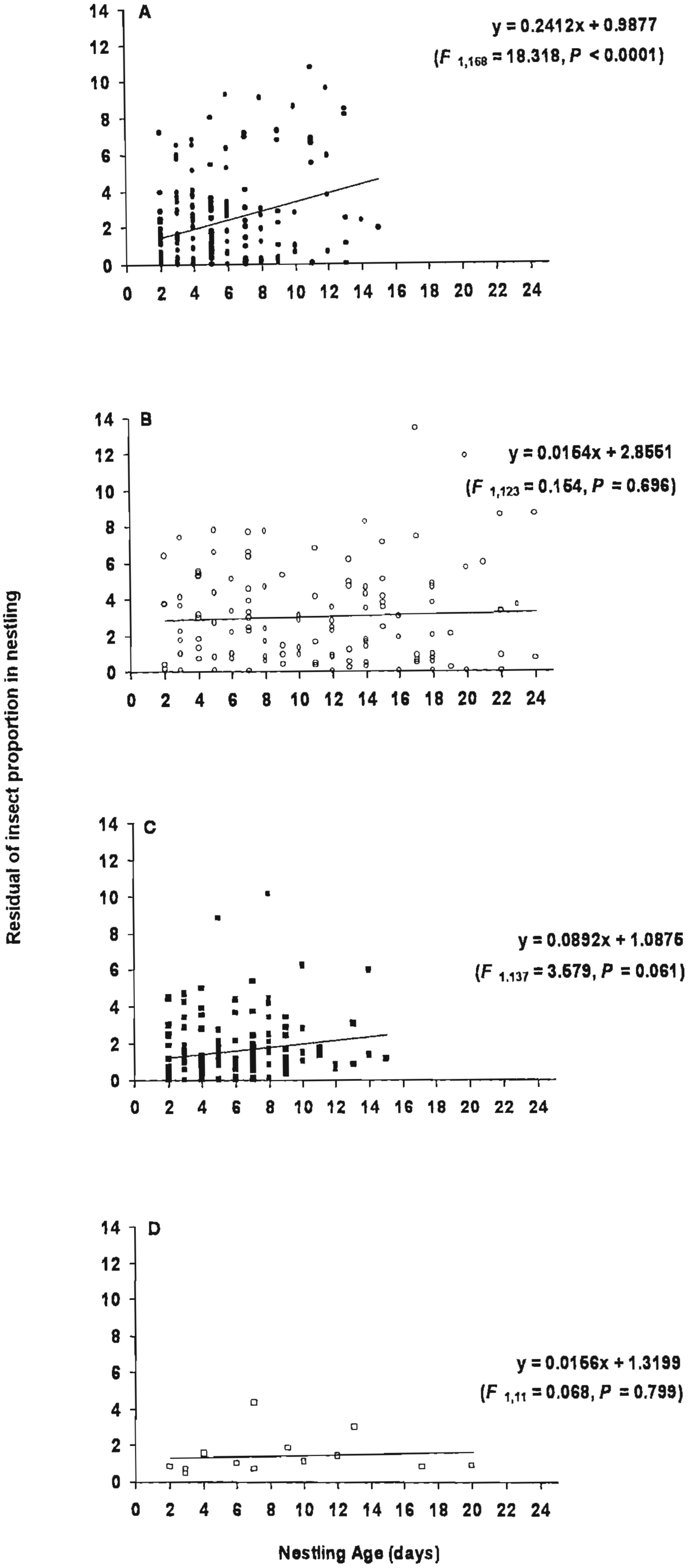
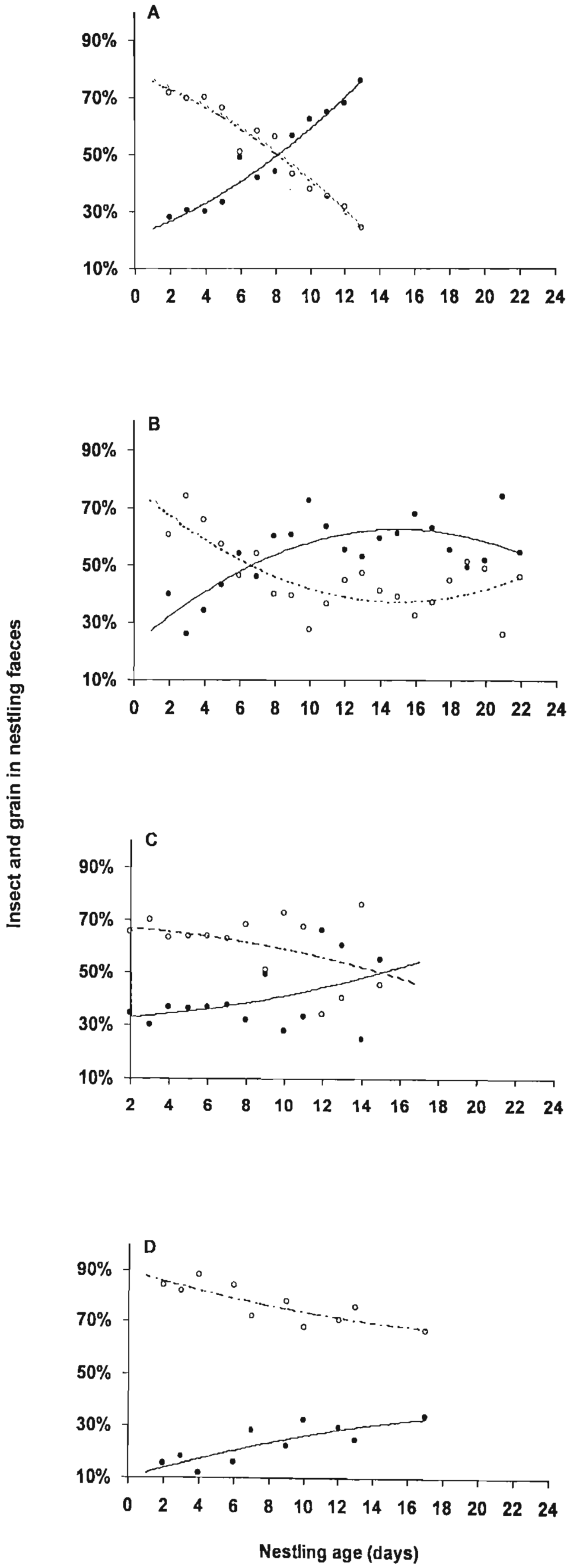

A
y = 0.2412x + 0.9877
(F 1,168 = 18.318, P < 0.0001)
B
y = 0.0164x + 2.8551
(F 1,123 = 0.164, P = 0.696)
C
y = 0.0892x + 1.0875
(F 1,137 = 3.579, P = 0.061)
D
y = 0.0156x + 1.3199
(F 1,11 = 0.068, P = 0.799)
14
12
10
8
6
4
2
0
0 2 4 6 8 10 12 14 16 18 20 22 24
Residual of insect proportion in nestling
Nestling Age (days)

FIG. 2.5. The proportion of insect (open circle) and grain (solid circle) in nestling faeces plotted as a function of nestling age, illustrating the switch in diet from predominantly insect to grain in (A) red bishop and (C) yellow weaver host nestlings. An early switch from insect to grain in the diet of (B) diderik cuckoos in red bishop nests is evident. In contrast there is no diet switch in (D) diderik cuckoos raised by yellow weaver hosts. Regression lines are included for comparison.


A
90%
70%
50%
30%
10%
0 2 4 6 8 10 12 14 16 18 20 22 24
B
90%
70%
50%
30%
10%
0 2 4 6 8 10 12 14 16 18 20 22 24
Insect and grain in nestling faeces
C
90%
70%
50%
30%
10%
2 4 6 8 10 12 14 16 18 20 22 24
D
90%
70%
50%
30%
10%
0 2 4 6 8 10 12 14 16 18 20 22 24
Nestling age (days)

An analysis of diet content in relation to brood size further showed no significant differences in insect proportions between one cuckoo and the three brood size classes of bishop nestlings (Fig. 2.6). Increased insect content of individual red bishop nestling faeces was observed when two and three nestlings occupied the nest, relative to a single bishop nestling (Fig. 2.6). Insect proportions did not differ between the brood size classes of yellow weaver nestlings (Fig. 2.6). Data for three weaver nestlings and diderik cuckoos in weaver nests could not be analysed due to small sample sizes.

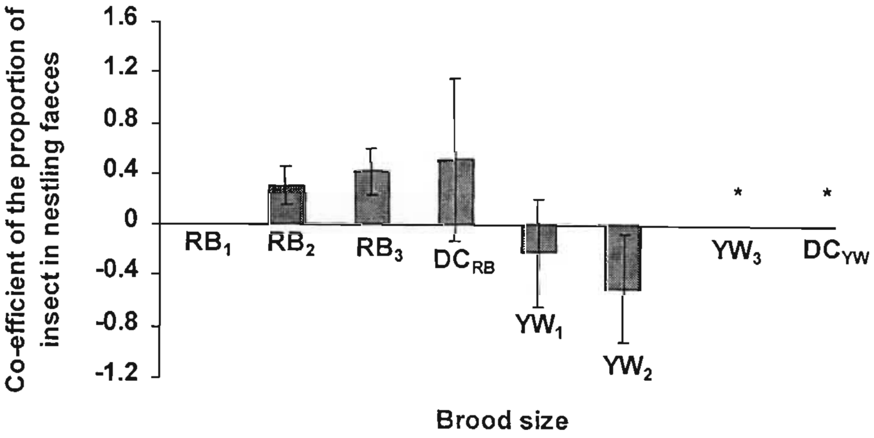


FIG. 2.6. Variation in the proportion of insect in nestling faeces between different brood sizes. Insect proportions in nestling faeces are represented by the GLM coefficients. The effect of each brood size is plotted relative to the constant (RB_1), so that negative values indicate comparatively lower proportions of insect. Red bishops, bishop-cuckoos, yellow weavers and weaver-cuckoos are represented by RB, DC_{RB}, YW and DC_{YW}, respectively. Brood size is indicated in subscript, except for cuckoos where brood size always equaled 1. Error bars represent ± 2 SE. Asterisks (*) represent data that were not analysed by GLM due to small sample sizes.

Diderik cuckoos raised by red bishop hosts therefore had significantly less insect in their faeces, from as early as day six, relative to their yellow weaver counterparts. Similar significant differences were observed between the nestlings of the host species, with fewer insects observed in bishop faeces relative to weavers. In summary these data illustrate significant differences in insect content in the diets of granivorous and omnivorous brood parasite systems. However, there was no significant difference within systems (i.e. between host and parasite nestlings). These findings suggest that foster parents do not discriminate against cuckoo nestlings and that parasite and host nestlings are provisioned similar diets.

Nestling mortality.–In red bishop nests 47% (n = 53) of diderik cuckoo nestlings died during the study period (Table 2.5), with over 40% mortality recorded each year. More than half of these deaths (56%) occurred within 13 days after hatching (modal age of mortality = 9 days). Interestingly, high mortality was also recorded for bishop nestlings (56%, n = 180) and the modal age of mortality was eight days following hatching.

Approximately 9% of bishop nestlings died as a result of strong winds and rain that characterised summer thunderstorms during the study period (Table 2.5). Twice as many cuckoos in bishop nests (19%) died as a result of these adverse conditions. The tall vegetation (*Phragmites australis*) in which bishops nested was often broken during thunderstorms and nests were found abandoned on the ground. Only fully feathered nestlings in unaffected nests survived such storms.

Of the five diderik cuckoos that parasitised yellow weavers, only one (20%) nestling died due to flooding in year two. In contrast, 56% (n = 87) of yellow weaver nestlings died during the study period (51% and 74% in years 2 and 3 respectively), with most weavers dying 13 days after hatching. Weaver colonies were subjected to severe extrinsic ecological conditions, such as flooding (1998-1999) and high predation rates (1999-2000), during which a resident water mongoose (*Atilax paludinosus*) or a Burchell's coucal (*Centropus bruchellii*) destroyed 6 of the 19 active nests in the colony. Flooding and predation accounted for 24% of yellow weaver nestling mortalities (Table 2.5).

A chi-square test revealed that cuckoo nestling mortality was not significantly higher in bishop nests than weaver nests (Yates corrected $\chi^2 = 0.49$, d.f. = 1, $P = 0.49$). The lack of statistical significance between bishop- and weaver-cuckoo nestling mortality is likely due to the small sample size of weaver-cuckoos ($n = 5$) and hence the power of this test is questioned. In subsequent chapters I therefore refer to the percent cuckoo mortality in bishop and weaver nests as these provide biologically meaningful, if not statistically significant, results.

TABLE 2.5. Mean percentage nestling mortality during the study period. Mortalities due to non-ecological factors (parental care, provisioning, nestling diet, clutch size and nest parasites) and extrinsic ecological factors (predation and climate) are tabulated separately. Total percentage mortality and sample size are included.

	Mean nestling mortality (%)			
	Non-ecological	Ecological	Total	*n*
Red bishop	47	9	56	180
Diderik cuckoo $_{\mathrm{RB}}$	28	19	47	53
Yellow weaver	32	24	56	87
Diderik cuckoo $_{\mathrm{YW}}$	0	20	20	5

Although predation, thunderstorms, cold weather and flooding contributed to nestling mortalities, almost 30% of nestlings died as a result of (excluding weaver-cuckoo nestlings) non-ecological factors, including parental care, diet quality, provisioning rates, clutch size and nest parasites (Table 2.5). Red bishop nestlings were most vulnerable with 47% dying due to these non-ecological factors (Table 2.5). The removal of runt (last-hatched nestlings) bishop nestlings from the data set had no significant effect on overall nestling mortality.

In conclusion, most nestling mortalities were due to factors relating to parental care, diet quality and provisioning rather than climate and predation. High mortality of diderik cuckoos prior to the 13 day-old threshold casts some doubt on whether or not extended nestling periods beyond that of the host's result in elevated mortality due to reduced parental care and to increased predation risk. Furthermore, higher mortality rates were recorded for host nestlings relative to parasite nestlings in both red bishop and yellow weaver brood parasite systems.

DISCUSSION

Previous studies report that individual host species provision nestling cuckoos with the same food as they would their own young (Wyllie 1981). Subsequent work by Brooke and Davies (1989) in their study of the European cuckoo and its reed warbler (*Acrocephalus scirpaceus*) host, confirm that cuckoo and host nestlings are provisioned similar diets. This study corroborates these findings in diderik cuckoo nestlings and broods of host young, despite differences between the feeding guilds of red bishop and yellow weaver hosts.

Bishop and weaver hosts provisioned young nestlings (2-4 day old) with an insect-rich diet, which correlated with the critical stage of nestling growth during which dietary protein and amino acid requirements are highest (Bryant and Gardiner 1979; Robbins 1993; Klasing 1998). During this period the diet provided by bishop and weaver hosts most likely approximated optimal protein levels. In the weaver-system insect-rich nestling diets were maintained through to fledging with no diet switch observed in this brood-parasite system. In contrast, diet switching was evident in the bishop system and female hosts provisioned significantly less insect material to host and parasite nestlings relative to yellow weavers. This relatively insect-poor diet was anticipated for this granivorous host, although diet switching so early in the nestling period was unexpected. For bishop-cuckoos the diet switch occurred as early as day six, confirming previous reports of large quantities of seed and grain provisioned to bishop-cuckoos from an early age (Skead 1956; Benson and Serventy 1957; Reed 1968; Rowan 1983). More importantly, this means that bishop-cuckoos were reared on a seed-rich diet for 15 days, more than half of their nestling phase. Bishop nestlings only experienced a seed-dominated diet five days prior to fledging (13 days).

Nestling diets comprising primarily seed and/or grain contain limited levels of dietary protein and often lack one or several of the essential amino acids that cannot be synthesized by the nestlings themselves (Earl and Jones 1962; Morton 1973; O'Connor 1984; Klasing 1998). The effects of such low-protein diets have been described for several altricial passerine species, including cockatiels (*Nymphicus hollandicus*), zebra finches (*Poephila guttata*) and house martins (*Delichon urbica*) (Roudybush and Grau 1986; Boag 1987; Johnston 1993). These studies showed that low-quality diets reduce growth rates, which subsequently result in prolonged fledging periods and lowered fledging success. The influence of low-quality diets on parasite nestling development and success of brood parasitism has only been addressed in one prior study (Kozlovic et al. 1996). Kozlovic et al. (1996) showed that despite high hatching success, no brown-headed cowbird (*Molothrus ater*) nestling was reared to fledging by the granivorous house finch (*Carpodacus mexicanus*). No cuckoo studies directly address this issue, but ninety percent of all recorded hosts of the European cuckoo are insectivorous, and none of the remaining 10% are known to have successfully reared a young cuckoo (Wyllie 1981; Davies 2000). Similarly, there are no reports of hosts successfully raising Australian shiny cuckoos primarily on seed (Brooker and Brooker 1989; Gill 1998). However, there is one record of red bishops rearing diderik cuckoos on a seed-rich diet with some level of success (Lindholm 1997). Although based on a small sample size ($n = 3$), Lindholm's (1997) study suggests that bishop-cuckoos are able to adapt their digestive tract to a diet containing a high proportion of seeds. If this is so, bishop-cuckoos may be potentially disadvantaged immediately post-fledging when they revert back to an exclusively insect diet, which is their natural adult diet. However, the response of gut size to changes in diet is remarkable in birds. A study of adult Japanese quail (*Coturnix japonica*) illustrated the considerable gut size plasticity of the avian intestine, with the turnover time of intestinal cells being in the order of days (Ricklefs et al. 1998). This suggests that the transition from primarily seed to exclusively insect is likely to be unproblematic and that the fledging success of cuckoos from bishop nests will be unaffected by the seed-rich diet.

Parasitic cuckoos often have substantially longer nestling periods than their hosts, presumably because they frequently exploit hosts that are much smaller than they are (Jensen and Clinning 1974; Rowan 1983; Brooker and Brooker 1989; Johnsgard 1997; Davies 2000). Fledging estimates for diderik cuckoos range from as early as 19 days (southern masked weaver host, *Ploceus velatus*; Reed 1968) to as late as 22 days (Cape weaver host, *P. capensis*; Skead 1952), with an average fledging age of between 20 and 21 days (Rowan 1983; Johnsgard 1997). Our results confirm these estimates, with cuckoos fledging from yellow weaver nests within 19 days, two days later than weaver fledglings. However, in bishop nests parasite nestlings fledged three days later than their weaver counterparts (22 days), extending the period of bishop parental care by an additional nine days. The nestling period reported in this study for bishop-cuckoos was two days longer than that recorded by Lindholm (1997). There is no comparative data for cuckoo fledging ages from other granivorous hosts, mainly because these host species are rarely exploited by cuckoos (Brooker and Brooker 1989; Gill 1998; Davies 2000). However, other cuckoo species that parasitise insectivorous hosts fledge between 19 and 22 days (Jensen and Clinning 1974; Brooker and Brooker 1989; Gill 1998), indicating that the nestling period for bishop-cuckoos is not abnormally long. Fledging records for the larger *Cuculus* cuckoos are consistent with these nestling periods, ranging between 17 and 23 days (Jensen and Clinning 1974; Brooker and Brooker 1989; Maclean 1993; Davies 2000).

Prolonged nestling periods are associated with increased nest predation (Lack 1968) and therefore negatively affect fledging success. Furthermore, reduced parental care from exhausted foster parents may limit cuckoo fledging success. However, more than half (56%, $n = 25$) of cuckoo nestling mortality in bishop nests occurred within 13-days of hatching and only four cuckoo nestlings died following the 19-day weaver-cuckoo fledging age. The high rate of mortality prior to these critical periods provides indirect evidence that prolonged nestling periods with associated reduced parental care and nest predation do not affect cuckoo nestling success in the red bishop system. Despite occasional adverse climatic conditions experienced during the study period, lower fledging success was attributable to factors other than climate and predation, including a combination of diet quality and provisioning with parental care, clutch size and nest parasites. The latter three factors were not addressed in this study.

The common occurrence of cuckoo deaths at day nine, three days following the diet switch, suggests cuckoo nestling mortality in bishop nests was due to the protein deficient diet provisioned to cuckoos. Support for this argument is found from the mortality of cowbirds in nests of the house finch due to the inappropriate granivorous diet provisioned by this host (Kozlovic et al. 1996). Furthermore, the infrequent parasitism of granivorous hosts by other cuckoo species has highlights the potential role of diet quality in brood parasitism (Brooker and Brooker 1989; Davies 2000). However, the similar modal age of mortality (at 8 days) recorded for bishops does suggest that other factors, independent of diet (e.g. parasitic infection), may also affect both host and parasite nestling survival. Nevertheless, red bishops remain the most highly parasitised host species in South Africa, even though the larger, omnivorous weaver is a more suitable cuckoo host species. One possible explanation for the frequent parasitism of red bishops in this study is that their breeding season coincided more closely with that of the diderik cuckoo than the yellow weaver. Similar breeding times have been previously reported (Reed 1968; Rowan 1983; Maclean 1993). Furthermore, red bishop hosts are less discriminating of the cuckoo's egg (Lawes and Kirkman 1996) because of the close mimicry of the immaculate red bishop egg by diderik cuckoos (Fig. 2.7). Therefore, it may benefit diderik cuckoos to exploit this low level of egg rejection, despite the low-quality diet and 53% (*n* = 53) fledging success in bishop nests (Fig. 2.7). In weaver nests cuckoo egg rejection rates are higher due to the large variability in weaver egg colouration (Lindholm 1997). However, the protein-rich diet (Fig. 2.7) and the greater probability of cuckoo nestling survival (80%, $n = 5$) in weaver nests may compensate for the high rejection rate of cuckoo eggs (Fig. 2.7).

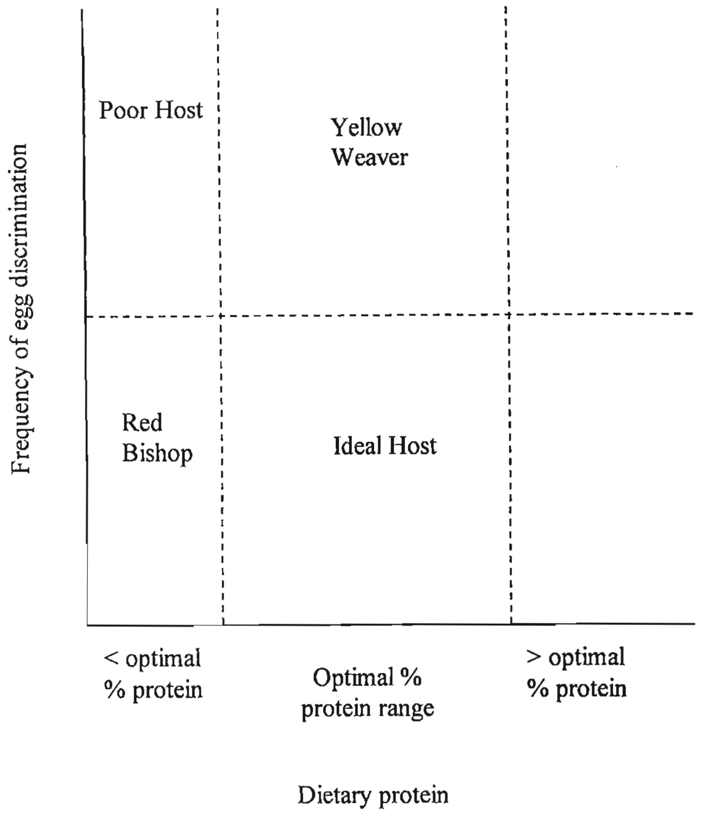


FIG. 2.7. Model showing host suitability as a function of diet quality and the frequency of egg discrimination. Higher fledging success of cuckoos would be expected in nests of ideal hosts than those of poor hosts.

Thus, both host systems seem to represent evolutionary compromises for the diderik cuckoo, with neither red bishops nor yellow weavers being entirely ideal as host species (Fig. 2.7). Therefore, it is conceivable that diderik cuckoos preferentially exploit bishop hosts because parasite eggs are more likely to be accepted than in weaver nests, which ultimately result in more cuckoos fledging from bishop nests in spite of the low quality of the diet provisioned to nestlings by this species.

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CHAPTER THREE

Provisioning of diderik cuckoo nestlings by red bishops and yellow weavers: Do diderik cuckoos exploit host parental care?

ABSTRACT.–Cuckoos are very successful in eliciting food from their foster parents, yet they rarely exploit the full feeding capacity of their hosts. Provisioning of diderik cuckoo (*Chrysococcyx caprius*) nestlings was examined in two host systems; the small, granivorous southern red bishop (*Euplectes orix*) and the omnivorous yellow weaver (*Ploceus subaureus*), which is similar in size to the diderik cuckoo. Provisioning rates and food mass delivered to cuckoo nestlings was compared to host nestlings and between hosts. Red bishops provisioned host and parasite nestlings at a slower rate than yellow weavers given that unlike bishops, both male and female weavers provisioned nestlings. Cuckoo nestlings displayed neither an elaborately coloured gape nor enhanced vocal begging behaviour and each received the same amount of food as single host nestlings, irrespective of their host. To reach fledging mass bishop-cuckoos remained in the nest nine days longer than bishops, while weaver-cuckoos fledged two days later than weavers. Although there was no evidence of exhaustion of bishop hosts, the shorter nestling period of weaver-cuckoos suggests weavers may be the better host. Neither provisioning rates nor food loads to nestlings provided evidence of 'supernormal' effort by host species and except for the duration of the nestling stage, cuckoo nestlings do not appear to exploit the full extent of their host's brooding capabilities.

THE SIGHT of a small passerine host feeding a nestling cuckoo several times its size has raised several questions about the host's ability to provision it and the parasite's ability to reach adequate fledging mass (Brooke and Davies 1989; Davies 2000; Davies and Brooke 1989a, b). However, recent studies have shown that the task of feeding a young cuckoo is not especially demanding on the host parents (Gill 1982; Brooke and Davies 1989; Sealy and Lorenzana 1997; Davies et al. 1998; Payne and Payne 1998; Kilner and Davies 1999; Kilner et al. 1999; Soler and Soler 1999). By evicting competing host young cuckoos monopolise host parental care, receiving the food that would otherwise be provisioned to the host brood (Payne and Payne 1998). Studies of the European cuckoo (*Cuculus canorus*) have shown that nestlings receive adequate provisioning from their much smaller reed warbler (*Acrocephalus scirpaceus*) hosts by providing a 'supernormal' stimulus in which foster parents are deceived by the cuckoo's extraordinary brood-mimicking vocalisations (Davies and Brooke 1988; Brooke and Davies 1989; Davies et al. 1998; Kilner et al. 1999). In this system the cuckoo's supernormal stimulus results in 'supernormal' parental effort and a single European cuckoo chick is provisioned at the same rate as an average brood of four reed warblers (Brooke and Davies 1989; Davies et al. 1998; Payne and Payne 1998; Kilner et al. 1999) and has been shown to grow at the same rate as an average host brood (Soler and Soler 1999). Similar results have been reported for the shining bronze-cuckoo (*Chrysococcyx lucidus*), where a single cuckoo never weighed more than a maximum brood of four grey warbler (*Gerygone igata*) host nestlings and the provisioning rate to shining bronze-cuckoos was slower than to broods of three and four grey warblers (Gill 1982). However, in the latter system the supernormal begging stimulus of the cuckoo did not result in supernormal effort on the part of the host parent and host provisioning rates were not as high as expected. This may be because if a cuckoo stimulates its foster parents to provision above their normal rate, its chance of surviving until independence is substantially reduced (Gill 1982; Wiley 1986; Brooke and Davies 1989; Davies 2000). In many instances, cuckoos exploit their hosts by forcing them to provide parental care for a period several days longer than would be afforded to their own young (Brooke and Davies 1989; Kilner et al. 1999; Davies 2000). For example the European cuckoo is dependent on its reed warbler host for 17 days post-hatching with an additional 16 days post-fledging, compared with 11 days in the nest plus 12 days post-fledging for host young (Davies 2000). Similarly, diderik cuckoos (*Chrysococcyx caprius*) remain in southern red bishop (*Euplectes orix*) nests for 22 days (chapter two) with a post-fledging period ranging between 17 and 25 days (Reed 1968; Rowan 1983; Maclean 1993) although the latter was not observed in this study (chapter two). In yellow weaver (*Ploceus subaureus*) nests diderik cuckoos fledged at 19 days, two days later than weaver nestlings (chapter two). There are no reports on the post-fledging care of diderik cuckoos by yellow weaver hosts, however southern masked weavers (*Ploceus velatus*) have been observed feeding cuckoos 25 days after fledging (Reed 1968; Rowan 1983).

This study investigates whether the diderik cuckoo exploits the parental care of its red bishop and yellow weaver hosts. If diderik cuckoo nestlings are indeed manipulating their host parents we expect the host to provision a single cuckoo nestling at the same rate as an average brood of their own young (Dawkins and Krebs 1979). Furthermore, by evicting the host young from the nest the cuckoo gains the benefit of receiving all the food brought to the nest and thus, the amount of food provisioned to a manipulative cuckoo chick is expected to be the same as that provisioned to an average sized brood of host young (Kilner et al. 1999; Soler and Soler 1999). The influence of diet quality on red bishop and yellow weaver provisioning rates is also compared between the two host species.

It has been suggested that the smaller the difference between host and parasite mass, the more similar the needs of a cuckoo chick and a single host nestling will be (Kilner et al. 1999). Assuming that the optimal growth rate of a cuckoo is the same regardless of host size, a cuckoo should solicit a large host to provision at a rate similar to one or two host nestlings as opposed to a rate equivalent to a brood of maximum size (Kilner and Davies 1999; Soler and Soler 1999), as would be necessary in nests of small hosts. Furthermore, the larger provisioning capacity (i.e. in terms of amount of food brought per visit) of large hosts (Wiley 1986; Soler and Soler 1999) leads to the prediction that the provisioning rates by yellow weavers, which are similar in size to diderik cuckoos, will be slower than those of the smaller red bishop. In addition, slower provisioning rates are expected in yellow weaver nests because nestlings fed high-protein diets should consume smaller quantities of food (Rovee-Collier et al. 1993). Alternatively, if cuckoo nestlings display exaggerated begging behaviours, regardless of host size, I predict similar provisioning behaviours for both host species (Soler and Soler 1999). I further examine whether a single diderik cuckoo nestling weighs the same as broods of single, two or three host nestlings of the same age.

STUDY AREA AND METHODS

Study site.–For details refer to chapter 2, page 33.

Feeding observations.–Food provisioning was monitored during the 2nd (1998-1999) and 3rd year (1999 – 2000) study periods at 62 nests using video cameras when nestlings were between the age of 2-4 days, 6-8 days, 10-12 days and in the case of yellow weavers and diderik cuckoos, 16-18 days (hatching day = day 1). The camera was mounted on a tripod 1-2 m from the nest. Video recordings lasted one hour or until the battery ran out (minimum duration = 55min) and were made between 06h30 and 08h30. The number of host nestlings or cuckoo nestlings in a nest was recorded and each nestling was weighed immediately before and on completion of the experiment to within 0.01g using a Sartorius (PT 600) portable digital scale.

Videotapes were later analysed in the laboratory. Observations commenced only 10 minutes after the start of recording to allow adult birds to become habituated to the camera at the nest. For each nest, the number of feeding visits made by the female, in the case of the red bishop, but by either the male or female in yellow weavers, was recorded. Male and female yellow weaver feeding visits were not differentiated in this study due to the silhouetted appearance of adult birds at the nest entrance on the video footage, making positive sexual identity between male and female weavers difficult. Visits to the nest were recorded as feeding visits only if the adult perched at the nest opening and was seen regurgitating food or delivering insects to the nestlings. Brooding and general upkeep of the nest (such as removal of a faecal sac) were not recorded as feeding visits. The provisioning rate (number of times food was brought to the nest per hour) was calculated from the video recordings. Provisioning rate per nestling was not measured directly in this study as it was not possible to film individual nestlings with the available equipment.

Yellow weaver adults primarily feed their young insects, which they bring to nestlings in their bill (Maclean 1993). However, red bishops mostly regurgitate food loads to their chicks from the crop making it difficult to record the type and quantity of prey brought to nestlings by females. Direct methods of measuring the amount of food delivered at each visit, such as the 'neck-collar', and 'artificial gape' method were not used in this study because these methods have the potential to change the begging behaviour of nestlings and thereby reduce the provisioning efforts of parents (Royama 1966; Wright, et al. 1998). In the absence of such direct data the mass of food provisioned was inferred from nestling mass gain after each provisioning bout. These data were independent of time (grams/hr) and were calculated per nestling and per nest. Due to asynchronous hatching, host nestlings in broods of several young were easily distinguished from each other on the basis of size. At the start of each provisioning session defecation was induced when faecal sacs were visible in the cloaca. The mass of food provisioned by hosts to nestlings was compared between cuckoos and different sized broods of host young. In addition, the mass of a single cuckoo nestling was compared to the total mass of broods of one, two or three host nestlings of the same age.

Statistical analyses.–Of the 169 provisioning periods recorded, records were excluded from the analyses if there was no evidence of provisioning behaviour by the parents (i.e. either the visit was very brief or the host parent did not enter the nest) and/or if the total change in nestling mass was negative. Consequently, a total 111 records (62 nests) were used in the analyses (red bishops $n = 28$, cuckoos in red bishop nests $n = 36$, yellow weavers $n = 40$, cuckoos in yellow weaver nests $n = 7$). Data were combined into two relative age classes - young and old, according to nestling age. This was done in order to address how provisioning rates and the mass of food provisioned by hosts changed with nestling age. The 'young' age-class comprised records from 2-8 days for red bishop nestlings and 2-12 days for yellow weaver nestlings. Red bishops, older than 10 days and yellow weavers older than 16 days were included in the 'old' age-class. Cuckoo nestlings were categorised into 'young' and 'old' age classes according to the classes assigned to yellow weaver nestlings, because of the similarity in duration of the nestling periods.

The data were analysed using a two factor repeated measures ANOVA design where the fixed factors were host species (bishop or weaver) and nestling species (host or cuckoo) and the relative age of the nestlings was the repeated measure (young or old). Brood size was included in the model as a covariate. Three ANOVA's were run for the different response variables – provisioning rate (logarithmic transformation), mass of food delivered to the nest (reciprocal transformation) and mass of food provided to individual nestlings (reciprocal transformation) (Zar 1996). Data were plotted independently of the repeated measure because relative nestling age had no significant effect on any of the response variables.

The effect of brood size on the rate of provisioning and amount of food provided to host and parasite nestlings were compared using an ANOVA with a crossed design, where the fixed factors were host species (bishop or weaver) and brood size (number of host or cuckoo nestlings in the nest). The data from each age class were combined because no significant differences were recorded between broods of different ages. A total of 36 red bishop and 31 yellow weaver nests were used in the analysis. Data from the two years were pooled in order to minimise fragmentation of the data. All analyses were performed using Statistica (Statsoft Inc. 1998).

RESULTS

There was no significant effect of relative age (young or old) of host and parasite nestlings on i) overall red bishop and yellow weaver provisioning rates ($F_{1,15} = 0.15$, $P = 0.71$), ii) the amount of food provisioned per hour to the nest ($F_{1,15} = 0.23$, $P = 0.64$) and

iii) the amount of food provisioned per hour to individual nestlings ($F_{1,\,15} = 0.43$, $P = 0.52$).

Red bishops provisioned host and parasite nestlings at a significantly slower rate than yellow weavers ($F_{1,\,14} = 9.19$, $P < 0.05$; Fig. 3.1). Within the red bishop and yellow weaver systems there was no significant difference between the provisioning rate to cuckoo nestlings and host broods of different sizes ($F_{3,\,103} = 1.73$, $P = 0.17$), although there was a trend for broods of three weaver nestlings to be fed at a faster rate than broods of smaller size (Fig. 3.1B). In red bishop nests the mean provisioning rate to a single cuckoo nestling was most similar to the provisioning rate to a single host nestling (Fig. 3.1A), whilst weaver hosts provisioned a cuckoo nestling at a rate most comparable to broods of two host nestlings (Fig. 3.1B).

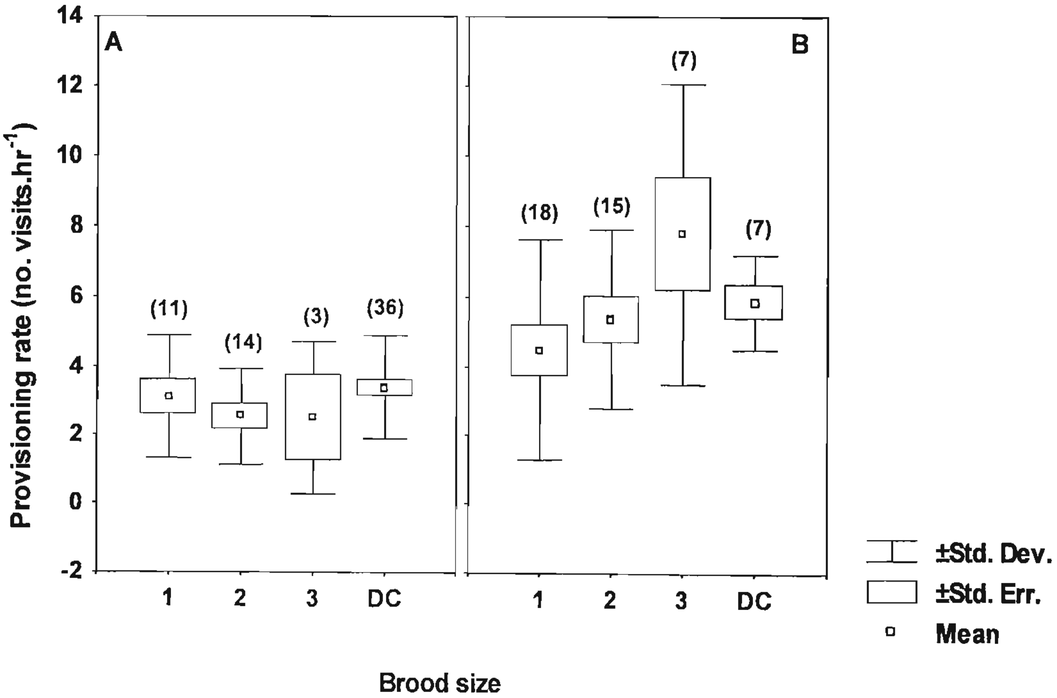

FIG. 3.1. Box and whisker plot of mean provisioning rates by (A) red bishop and (B) yellow weaver hosts. Data for increasing broods of host young and cuckoo nestlings (DC) are presented, with sample size indicated in parentheses.

Within the bishop system, bishop females provisioned nests containing cuckoos with a similar mass of food as nests of their own nestlings, regardless of brood size ($F_{3,\,103} = 3.16$, $P < 0.05$; Tukey HSD test for unequal n: $P = 1.00$; Fig. 3.2A). Bishop nestlings in larger broods each received less food than nestlings in smaller broods however this result was not statistically significant (Fig. 3.3A). Bishop hosts fed cuckoo nestlings (0.49 ± 0.46g.hr^{-1}, $n = 36$) with the same mass of food per hour as they did a single nestling of their own (0.37 ± 0.34g.hr^{-1}, $n = 11$; $F_{3,\,103} = 2.41$, $P = 0.07$), this in turn was more than individual bishops in broods of two or three nestlings received (Fig. 3.3A). Nests containing broods of three bishops were infrequently observed possibly because of constraints of large broods on red bishop provisioning. Thus, as the provisioning rate and mass of food appears to remain constant independent of brood size cuckoos may be receiving an amount of food that approximates the maximum mass of food that can be provisioned by bishop females.

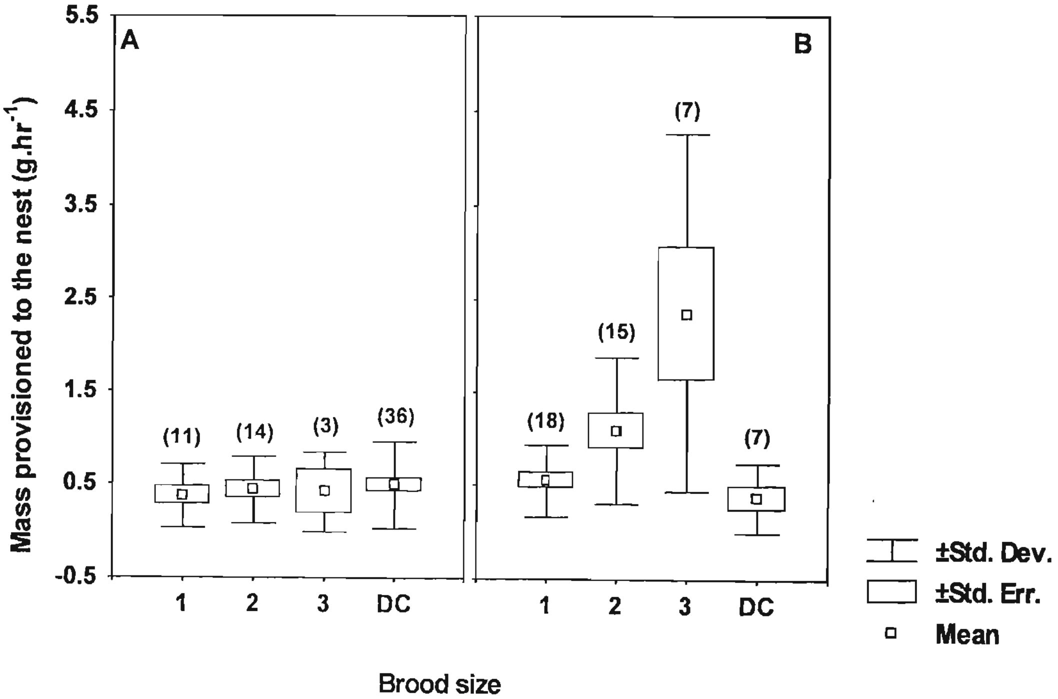

FIG. 3.2. Box and whisker plot of the mean mass provisioned per hour to nests by (A) red bishop and (B) yellow weaver hosts. Data for increasing broods of host young and cuckoo nestlings (DC) are presented, with sample size indicated in parentheses.

In contrast, yellow weavers provisioned more food to the nest as weaver brood size increased and although this was a clear increasing trend it was not statistically significant (Fig. 3.2B). The removal of cuckoo nestlings from the analysis yielded a similar non-significant result. As a result weaver nestlings in different sized broods each received a similar quantity of food ($F_{3,\,103} = 2.41$, $P = 0.07$; Fig. 3.3B).

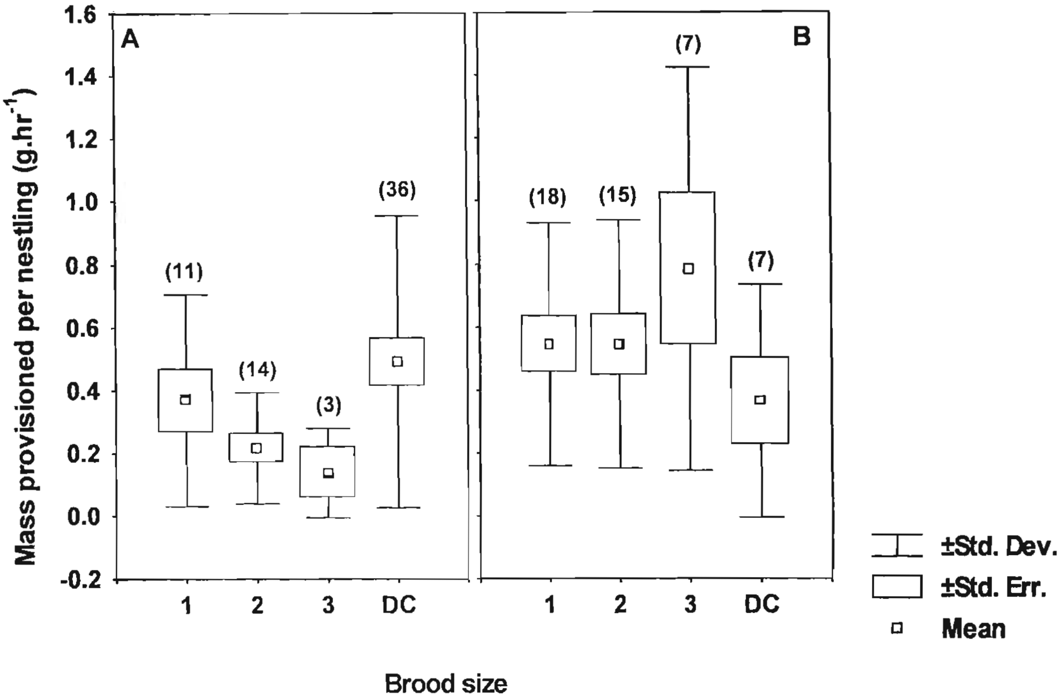

FIG. 3.3. Box and whisker plot of mean mass provisioned per hour to individual nestlings by (A) red bishop and (B) yellow weaver hosts. Data for increasing broods of host young and cuckoo nestlings (DC) are presented, with sample size indicated in parentheses.

Although yellow weavers were clearly capable of providing more food to nests of increasing brood size, weaver hosts provisioned significantly less food to nests containing a cuckoo nestling than to nests of three weaver nestlings ($F_{3,\,103} = 3.16$, $P < 0.05$; Tukey HSD test for unequal n: $P < 0.01$; Fig. 3.2B). In addition, weavers provisioned cuckoo nestlings (0.36 ± 0.37g.hr^{-1}, $n = 7$) with the same mass of food per hour as a single nestling of their own (0.54 ± 0.38g hr^{-1}, $n = 18$; $F_{3, 103} = 2.41$, $P = 0.07$; Fig. 3.3B).

A comparison between bishop and weaver systems showed that due to the slower provisioning rate by bishop females, the mass of food provisioned per hour to nests containing bishop nestlings was significantly less than that provisioned to nests containing weaver nestlings ($F_{1, 103} = 9.90$, $P < 0.05$; Fig. 3.2). However, cuckoo nestlings in bishop nests (0.49 ± 0.46g.hr^{-1}, $n = 36$) received equivalent amounts of food to their weaver counterparts (0.36 ± 0.37g.hr^{-1}, $n = 7$; $F_{1, 14} = 3.25$, $P = 0.09$; Fig. 3.3).

In bishop and weaver systems the mass of the cuckoo nestling never exceeded that of a maximum brood of host nestlings (Fig. 3.4). In bishop nests cuckoo nestling mass was equivalent to between one and two bishop nestlings for most of the nestling period (Fig. 3.4A). However, from an age of 15 days until fledging cuckoo mass more closely approximated that of two bishop nestlings (Fig. 3.4A). Similarly, single weaver nestlings and weaver-cuckoos weighed approximately the same until day five, after which cuckoos weighed the equivalent of between one and two weaver nestlings (Fig. 3.4B). Comparative growth rates of cuckoo nestlings are investigated and discussed in detail in chapter four.

Thus slower provisioning rates were evident in the bishop-cuckoo system relative to the weaver-system. However, host provisioning rates and the mass of food delivered to cuckoo nestlings was not significantly different and did not exceed that delivered to the modal brood sizes of their bishop and weaver hosts (two and one nestling, respectively). In addition, cuckoo nestling mass did not exceed that of a modal brood of red bishop nestlings. In contrast, weaver-cuckoos were heavier than a single weaver nestling (modal brood size), but never exceeded that of a brood of two or three weaver nestlings.

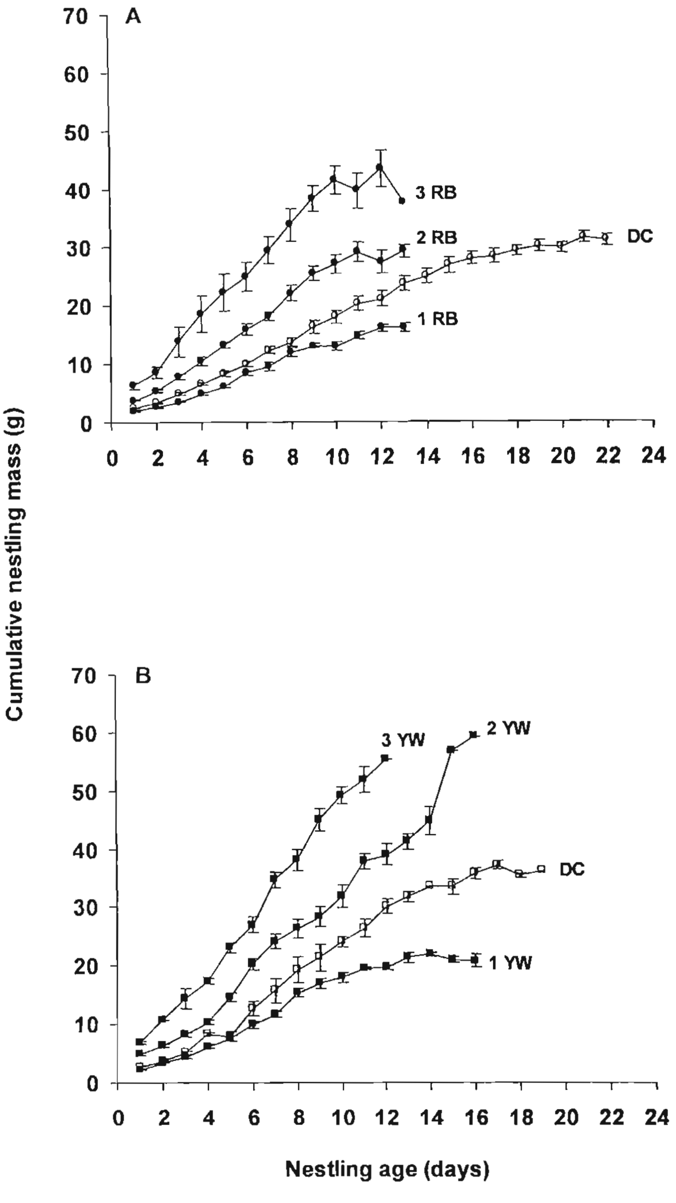

FIG. 3.4. Mean daily mass (mean ± SE) of single cuckoo nestlings and broods of 1-3 (A) red bishops and (B) yellow weavers as a function of nestling age. Species and brood size are indicated.

DISCUSSION

Red bishop and yellow weaver hosts did not provision cuckoo nestlings at a supernormal rate nor did they provision an abnormally large amount of food to cuckoos compared to the amounts provisioned to their own nestlings. Thus bishop and weaver hosts showed no sign of 'supernormal' effort when feeding a young cuckoo. This apparent lack of exploitation of the host parents by diderik cuckoos is similar to findings from studies of the European cuckoo, where i) provisioning rates to a cuckoo did not exceed those to an average brood of host young (Davies and Brooke 1988; Kilner et al. 1999) and ii) food was delivered to host and parasite young in loads of similar size (Kilner et al. 1999). Gill (1982) in a study of the shining-bronze cuckoo also found no evidence of cuckoos eliciting 'supernormal' effort in terms of provisioning rates from their grey warbler hosts. This study confirms that bishop and weaver hosts do not provision diderik cuckoos at a faster rate or with more food than the modal brood size of their own young.

Foster parents are capable of provisioning experimentally enlarged broods of their own young at an elevated rate (Brooke and Davies 1989). This has been demonstrated in red bishops where females adjusted their provisioning rate to compensate for an additional nestling (Slotow and Lawes unpubl. data). An increase in provisioning rate should result in an increase in the amount of food female bishops deliver to the nest because females are predicted to return to the nest with a full beak and crop at each feeding visit (Slotow and Lawes unpubl. data). However, in this study bishop nests containing broods of different size were all provisioned at a similar rate. Consequently nestlings in larger broods each received less food than nestlings in smaller broods. Therefore, bishop-cuckoo nestlings appeared to receive an amount of food that approximated the maximum mass of food that could be provisioned by bishop females during the study period. In contrast, weavers provisioned more food to nests containing broods of three weavers than smaller broods of their own young and weaver-cuckoos. However, the mass of food provisioned to each weaver nestling was similar regardless of brood size and weaver hosts provisioned cuckoo nestlings with the same amount of food a single nestling of their own. This supports the notion that the requirements of a cuckoo nestling that parasitises a large host species will match those of one or two host nestlings rather than an entire brood (Kilner and Davies 1999).

Several studies, including this one, have established that cuckoos do not exploit the 'extra' feeding capacity of their host, even though cuckoos have no genetic investment in the future breeding success of their host species and therefore may be expected to do so (Gill 1982; Brooke and Davies 1989; Davies et al. 1998; Kilner, et al. 1999). Cuckoos may 'choose' to not over work their host if this means relying on a provisioning rate that the hosts are unable to sustain to fledging (Davies et al. 1998). Alternatively, constrained by the visual signal of a single gape, cuckoo nestlings may be unable to solicit a faster rate of provisioning without other stimuli such as vocal begging behaviours being involved. However, there may be an upper limit to the rate at which begging calls can be produced by the cuckoo or perceived by the host, and louder or more persistent begging by the cuckoo nestling may increase the risk of predation (Brooke and Davies 1989). The latter considerations are not likely to be applicable in the case of the diderik cuckoo because there was neither audible vocal begging by diderik cuckoo nestlings nor evidence of exaggerated gape colour compared to bishop and weaver nestlings. This suggests that there is very little active manipulation of host parents by diderik cuckoos to provide larger or more frequent meals. Such passive behaviour may be expected for bishop-cuckoos that are at an early stage in the coevolutionary arms race. However, passive behaviour of weaver-cuckoo nestlings is surprising because weaver parents appeared to respond positively to the vocal begging of their own nestlings by increasing the amount of food they provision to broods of increasing size. As weaver-cuckoos are at a more advanced stage in the arms race, it is therefore puzzling that more vocal begging has not evolved in this cuckoo gens.

It is possible that instead of monopolising a higher provisioning effort, cuckoo nestlings exploit their hosts by forcing them to provide parental care for several days longer than they would for broods of their own young (Kilner et al. 1999). Such additional parenting includes prolonged dependency in the nest and extended post-fledging care. In this study diderik cuckoos remained in the nest nine days longer than bishop nestlings, while weaver-cuckoos fledged two days later than weaver fledglings. The shorter nestling period of weaver-cuckoos (19 days) relative to bishop-cuckoos (22 days) further suggests weavers are the better host. Although not observed during this study, post-fledging care of between 17 and 25 days has been previously recorded for bishop-cuckoos (Reed 1968; Rowan 1983; Maclean 1993; Johnsgard 1997). There are no records for the post-fledging care of red bishop and yellow weaver nestlings, or for the post-fledging care of diderik cuckoos in yellow weaver nests.

Cuckoo begging rates are hypothesised to be dependent on the cuckoo nestling's level of need and/or the feeding capacity of the foster parents (Soler and Soler 1999). Thus, provisioning rates to cuckoo nestlings should be slower by host species of larger size because of their greater capacity to provision food (Soler and Soler 1999). Furthermore, nestlings fed high-protein diets should consume smaller quantities of food and thus provisioning rates by yellow weaver hosts should be slower (Rovee-Collier et al. 1993).

However, yellow weaver hosts provisioned both host and parasite nestlings at a significantly faster rate than the smaller red bishop hosts. This may be because of differences between the provisioning behaviours of the two host species. Unlike the red bishop, where only the female provisions the nestlings, both male and female yellow weaver parents provision nestlings as do most others members of the genus *Ploceus* (Maclean 1993). In addition, the faster provisioning rate observed for yellow weavers may be a consequence of the insect-rich diet that they provision. A large proportion of the diet provisioned to host and parasite nestlings by yellow weavers consists of insect material, which they bring in their bill. Consequently, weaver adults may visit the nest more often to deliver individual prey items to nestlings. In contrast, red bishops regurgitate food loads from their crop and provision predominantly seed to both host and parasite nestlings (chapter two). Ecological factors such as differences in food availability between study sites and annual variation at a site must also be considered as possible factors influencing the provisioning rates by bishop and weaver parents.

In conclusion, diderik cuckoos raised in yellow weaver nests were provisioned the same amount of food as their red bishop counterparts, despite slower provisioning rates by red bishop parents. In addition, bishop and weaver hosts did not provision cuckoo nestlings at a supernormal rate nor with an abnormally large amount of food relative to their own nestlings. Remarkably, the cuckoo was able to achieve a maintenance diet without stimulating 'supernormal' effort from either bishop or weaver hosts. To compensate for the potentially slow growth rate that results from the latter, the diderik cuckoo exploited its hosts by extending the nestling period and the duration of parental care it received (chapter two). In addition, 47% (*n* = 53) cuckoo mortality was recorded in bishop nests relative to 20% (*n* = 5) in weaver nests (chapter two). These results further suggest that yellow weavers are more suitable as a host for the diderik cuckoo and that cuckoos should parasitise species that are of similar adult size to them and that have similar diets.

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CHAPTER FOUR

Comparative growth of diderik cuckoo nestlings raised by different hosts

ABSTRACT.–Previous studies have identified differences in the quantity and/or quality of food provisioned as major sources of variation in nestling growth rates, making these significant determining factors of host quality in brood parasitism. This study compares the growth rates of diderik cuckoos (*Chrysococcyx caprius*) raised by two different host species, the granivorous southern red bishop (*Euplectes orix*) and the omnivorous yellow weaver (*Ploceus subaureus*). Growth rate of diderik cuckoo nestlings was primarily influenced by diet quality and not by host size (i.e. diet quantity). Cuckoo nestlings grew faster, fledged three days earlier and were in better condition when raised by yellow weaver hosts than by red bishops. Although postfledging survival was not addressed in this study, weaver-cuckoos are more likely to survive after fledging than bishop-cuckoos, because of their relatively faster growth rates and higher fledging mass. Thus, of the two species investigated, the yellow weaver appears to be a more suitable host of the diderik cuckoo and would therefore be expected to be parasitised more frequently than red bishops. However, red bishops are parasitised more often than yellow weavers, implicating factors other than diet in determining host suitability and ultimately host selection.

INTERSPECIFIC BROOD PARASITES lay their eggs in the nests of other bird species, which incubate the parasitic egg and rear the young. Brood parasites frequently exploit several host species, which can differ in the quality of food they deliver to the nest and in their ability to adequately provision young (Wiley 1986). Several studies on non-cuckoo species have shown large intraspecific variation in growth rate among nestlings, mainly as a consequence of differences in the quantity or quality of food delivered to the young (Roudybush and Grau 1986; reviewed by Gebhardt-Henrich and Richner 1998). Nestling growth rate is positively correlated with post-fledging survival (Perrins 1965; Richner et al. 1989; Magrath 1991) and ultimately juvenile reproductive success (Martin 1987; Gebhardt-Henrich and Richner 1998; McCarty 2001). The quantity and/or quality of food provisioned by the host species is therefore crucial for young parasites, making these significant determining factors of host quality in brood parasite systems.

The diderik cuckoo (*Chrysococcyx caprius*) is an obligate interspecific brood parasite, exploiting six primary hosts in southern Africa, viz. the Cape sparrow (*Passer melanurus*), Cape weaver (*Ploceus capensis*), southern masked weaver (*P. velatus*), spotted-backed weaver (*P. cucullatus*), yellow weaver (*P. subaureus*), and the southern red bishop (*Euplectes orix*) (Reed 1968; Jensen and Vernon 1970; Rowan 1983; Maclean 1993). Growth rates of diderik cuckoo nestlings are expected to vary among hosts according to i) diet quality, as cuckoo hosts provision diets comprising varying proportions of insect and plant material (Rowan 1983), and ii) host size because of the variation among host species in provisioning rates and the amounts of food delivered (Wiley 1986).

If host quality is critical for the parasite nestling, natural selection will favour individuals parasitising high-quality host species. This study investigates whether the growth of diderik cuckoos is affected by host size and the quality of diet provisioned by different host species. This was done by comparing the growth rates of cuckoo nestlings reared by relatively small red bishop hosts to those reared by yellow weavers, which are of similar adult size to diderik cuckoos (Maclean 1993). As female diderik cuckoos have evolved to specialise on different hosts, laying eggs that closely mimic those of their host, differences in cuckoo nestling growth rates may be a result of genetic differences between gentes. However, for the purposes of this study cuckoo nestling growth rates are assumed to be independent of inherited genetic differences.

The red bishop, a predominantly granivorous species, provisions large quantities of seed to cuckoos from an early age (chapter two). In contrast, yellow weavers feed an insect-rich diet throughout the cuckoo's dependency period and are therefore theoretically more suitable hosts than red bishops. Due to the low-protein diet provisioned by red bishops (chapter two), I predict that the growth rate of cuckoo nestlings will be slower when raised by red bishops than yellow weavers. In addition, slower provisioning rates by red bishop females as a consequence of their small size and single parent provisioning (chapter three) are expected to further lower the growth rate of cuckoo nestlings. Bishop-cuckoos are predicted to take longer to approach a fledging mass similar to that of adult cuckoos.

There is little data on growth rates of cuckoo nestlings (Gill 1983; Soler and Soler 1991; Kleven et al. 1999) and the effect of host quality on nestling growth rate has been addressed in only one study on the European cuckoo (*Cuculus canorus*; Kleven et al. 1999). The development of a single diderik cuckoo nestling has been reported in an earlier study, but this study did not quantify host quality (Chalton 1991). Lindholm (1997) reported comparative fledgling morphometrics for cuckoos raised by two different host species (lesser-masked weaver, *Ploceus intermedius*, and red bishop). However, no data exists on the ratio of fledgling to adult body mass for various diderik cuckoo gentes. By comparing growth rates of diderik cuckoos raised by hosts of different quality, I aim to determine whether cuckoo growth in bishop nests is indeed constrained by diet quality and/or host provisioning rates.

STUDY AREA AND METHODS

Study site.–For details refer to chapter 2, page 33.

Morphometric data.–Host and parasite nestlings from red bishop and yellow weaver nests were observed daily from hatching (day = 1) to fledging during all three years of the study period. Host and cuckoo nestlings that were found after hatching were aged on the basis of growth curves and included in the analysis. At each visit the number of nestlings was recorded and nestlings were weighed using 5g, 10g and 50g Pesola spring balances depending on their size and age. A total of 161 red bishops, 95 yellow weavers, 51 bishop-cuckoos and 5 weaver-cuckoos were weighed and measured. Due to asynchronous hatching, host nestlings in broods of several young were easily distinguished from each other on the basis of size. Measurements were made to the nearest 0.1g (young bishops and cuckoos) or 0.25g (bishops and cuckoos above 10g). Defecation was induced before weighing nestlings, when faecal sacs were visible in the cloaca. Nestling morphometrics were also measured each day to the nearest 0.01mm using electronic callipers. Morphometrics included measurements of tarsus (length of tarso-metatarsus, measured by bending the foot at the intertarsal joint and toes and measuring the distance between the extreme bending points), culmen-notch (bill length from notch where bill joins skull to bill tip), nares-tip (distance from posterior of nares to bill tip) and gape (from the back of the flanges to bill tip). The measure of tarsus employed in this study is greater than the true tarsus but is subject to a lower measurement error, especially in young nestlings (Richner 1989). Measurements of wing (length of the chord of the longest flattened primary wing feather) and tail-feather lengths were included and were measured using a steel ruler with a "stop" at zero (accuracy 0.5mm). Older nestlings (from age 12 onwards) were ringed using aluminium rings.

Statistical analyses.–Principal component analysis (PCA) was performed on all measured morphometrics, with the exception of body mass, to detect co-linearity among the variables. Nestling body mass was excluded from PCA because it is subject to greater seasonal and diet-related variability than the other measurements (Ricklefs 1968; Richner 1989; Rising and Somers 1989) and therefore skews the results by accounting for the majority of the variation. PCA was carried out separately for red bishops, bishop-cuckoos and yellow weavers after the methods of Johnston and Fleischer (1981) and Rising and Somers (1989). PCA was not performed on weaver-cuckoo data because the sample size was too small. The ordination program, CANOCO was used for PCA (Ter Braak and Smilauer 1999). Nestling morphometric data for all three years were pooled because similar trends in the data were observed from each year.

Nestling growth was modelled using the logistic growth function, which has the form:

$$y = \frac{A}{1 + e^{(-K*(t-t_i))}}$$

where

y = body measurement at age t

A = the approximate asymptote of the body measurement,

K = the growth rate constant, and

t_i = the inflection point of the growth curve, which occurs at one half the asymptote on a logistic curve (Starck and Ricklefs 1998).

The instantaneous growth rate at age t is given by differentiation of the original equation:

$$\frac{dy}{dt} = \frac{A * K * e^{-K*(t-t_i)}}{(1+e^{-K*(t-t_i)})^2}$$

The parameters of the logistic equation were determined using the Quasi-Newton, least-square iterative fitting method (Statsoft Inc. 1998). The maximum pre-fledging body mass was used as the start value for the asymptote, A (Starck and Ricklefs 1998). Fitted curves were accepted when the sum of the squared deviations about the predicted values, from iteration to iteration, was less than 0.0001 (Statsoft Inc. 1998). The logistic function was fitted to selected nestling morphometrics determined from the PCA.

RESULTS

The first (PC1) and second (PC2) principal components for red bishops accounted for 84% of the variation in the morphometric data. Similarly, PC1 together with PC2 explained 96% of the variation in both bishop-cuckoos and yellow weavers. In all three species, PCA revealed a co-linear relationship between wing, tarsus, gape, nares-tip and culmen-notch. Co-linearity between these variables and tail length was not observed. From these co-linear variables tarsus length was selected for comparison as it is less susceptible to environmental variation (Gard and Bird 1992; Rodway 1997) and is reportedly the most accurate measure of overall body size in birds (Richner 1989; Rising and Somers 1989;

Freeman and Jackson 1990). Although wing length is considered a poor measure of overall body size (Rising and Somers 1989; Freeman and Jackson 1990; Gard and Bird 1992), it is a good indicator of malnutrition in older nestlings (Price 1985) and thus is included here. To allow for comparison with data from other species, body mass was the primary variable used to assess growth rate in this study.

Newly hatched (day = 1) bishop-cuckoos were not significantly heavier or larger than newly hatched yellow weaver-cuckoos (Table 4.1). After hatching, weaver- and bishop-cuckoos gained mass logistically ($r^2 = 0.91$ and 0.83 respectively, attaining half of their asymptotic mass (t_i) between days 8 and 9 (Fig 4.1). However at day 10, 4 days after the diet switch in bishop nests, bishop-cuckoos weighed significantly less and were significantly smaller than weaver-cuckoos at the same age (Table 4.1).

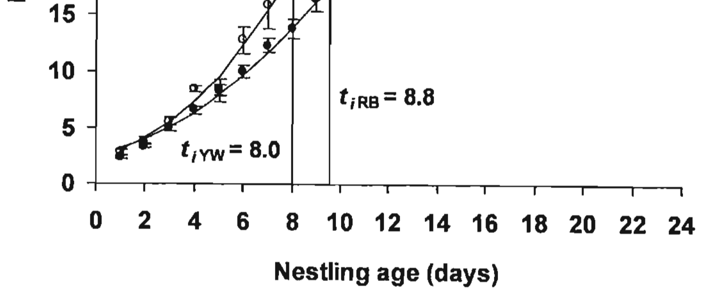

FIG. 4.1. Mean daily mass (± SE) for diderik cuckoo nestlings raised by two different hosts, the red bishop (closed circles) and yellow weaver (open circles). Cuckoos grew at a faster rate ($K = 0.35$) in yellow weaver nests than red bishop nests ($K = 0.28$). Data were fitted to the logistic growth curved using the method of Starck and Ricklefs (1998). Growth parameters (A, t_i) are included, where $_{RB}$ and $_{YW}$ indicate bishop- and weaver-cuckoos respectively. Horizontal broken line indicates the average mass of an adult cuckoo (Maclean 1993).

TABLE 4.1. Comparison of selected morphometrics between cuckoo nestlings raised by two different host species; the red bishop and yellow weaver. Day 1 = day of hatching. Values are the mean ± SD with the sample size in parentheses.

Age of cuckoo nestlings	Morphometric	Host Species		*U*-test
		Red Bishop	Yellow Weaver	
Hatching	Mass (g)	2.3 ± 0.6 (31)	2.7 ± 0.6 (4)	ns
	Wing (mm)	7.2 ± 0.8 (31)	8.4 ± 1.3 (4)	ns
	Tarsus (mm)	7.7 ± 1.1 (31)	7.7 ± 1.0 (4)	ns
10 days	Mass (g)	18.0 ± 5.5 (25)	24.1 ± 2.0 (5)	*
	Wing (mm)	27.6 ± 8.8 (25)	38.4 ± 5.0 (5)	*
	Tarsus (mm)	14.4 ± 1.6 (25)	16.0 ± 1.1 (5)	*
Fledging	Mass (g)	31.0 ± 3.6 (12)	35.0 ± 0.6 (4)	*
	Wing (mm)	71.5 ± 14.2 (12)	72.0 ± 7.6 (4)	ns
	Tarsus (mm)	18.4 ± 1.4 (12)	19.1 ± 0.6 (4)	ns

ns not significant; * $P < 0.05$

At fledging cuckoos in weaver nests were significantly heavier (Table 4.1) and fledged 3 days earlier than their bishop counterparts (19 days and 22 days, respectively). Despite the apparent rapid nestling growth in both cuckoo gentes, K was significantly higher for cuckoo nestlings raised by yellow weavers ($K = 0.35 \pm 0.02$, $n = 5$) than that recorded for bishop-cuckoos ($K = 0.28 \pm 0.01$, $n = 51$; $t_{0.001\,(2),\,535} = 3.310$, $P < 0.0001$). Thus cuckoo nestlings grew significantly faster and were heavier at fledging when raised by the larger host species than by the smaller one.

Tarsus and wing length data for cuckoo nestlings also followed the logistic growth curve (Table 4.2). Cuckoos hatched with well-developed tarsus bones and reached maximum growth rate within 3 days from hatching (Fig. 4.2A). A steady growth rate was observed for tarsus length in both cuckoo gentes for the remainder of the nestling period (Fig 4.2A).

TABLE 4.2. Estimated logistic growth parameters for cuckoo tarsus and wing lengths in red bishop and yellow weaver nests. A = asymptotic body mass, K = growth rate constant, t_i = inflection point of the growth curve. The goodness of fit of the growth function (r^2) has been included. Values are presented as the estimate ± SE with sample size in parentheses.

Host Species	A	K	t_i	r^2
Tarsus				
Red Bishop	19.10 ± 0.002 (51)	0.17 ± 0.005 (51)	3.21 ± 0.13 (51)	0.83
Yellow Weaver	19.83 ± 1.72 (5)	0.22 ± 0.07 (5)	3.16 ± 0.70 (5)	0.93
Wing				
Red Bishop	84.51 ± 5.11 (51)	0.19 ± 0.01 (51)	13.85 ± 0.76 (51)	0.83
Yellow Weaver	96.38 ± 6.54 (5)	0.23 ± 0.02 (5)	11.86 ± 0.75 (5)	0.98

However, at day 10 the tarsus and primary wing feather lengths of bishop-cuckoos were significantly shorter than recorded for weaver-cuckoos (Table 4.1). Primary wing feathers reached maximum growth rate 12-14 days after hatching, suggesting an initially slow growth of nestling primary feathers (Fig. 4.2B). The growth rate of primary feathers declined during the nestling period (Fig 4.2B), however bishop- and weaver-cuckoos attained only 60.6% and 68.2% of adult wing length at fledging, respectively (mean adult wing length = 118mm, $n = 51$; Maclean 1993). Thus, cuckoos in both gentes fledged with poorly developed primary wing feathers.

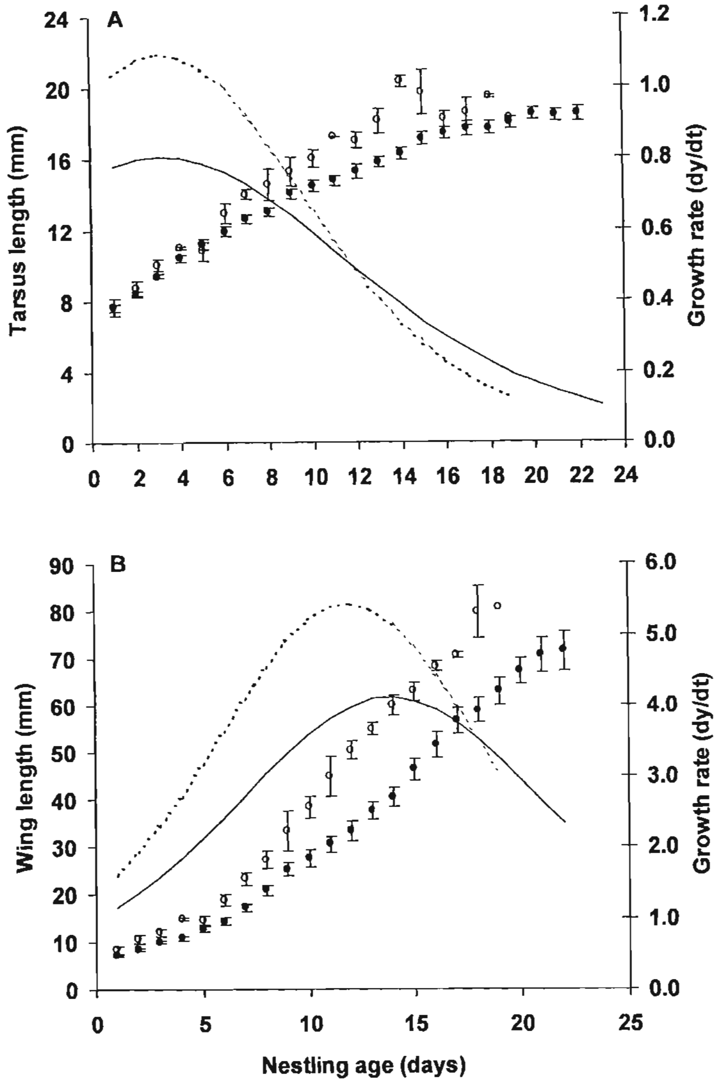

FIG. 4.2. Mean (± SE) daily measurements of (A) tarsus length and (B) wing length for diderik cuckoo nestlings raised by two different hosts, the red bishop (closed circles) and yellow weaver (open circles). The instantaneous growth rate, represented by the derivative of the logistic growth equation is included for comparison between cuckoos in red bishop (solid line) and yellow weaver nests (broken line).

The long nestling periods of cuckoos produced highly advanced fledglings relative to adult cuckoos. In terms of bone development, the tarsal lengths of cuckoo fledglings from bishop (18.4 ± 1.4mm, $n = 12$) and weaver (19.1 ± 0.6mm, $n = 4$) nests were equivalent to that of adult cuckoos (16-17mm, $n = 51$; Maclean 1993). However, cuckoos fledged from weaver nests weighing more than bishop-cuckoo fledglings. Bishop-cuckoos fledged at 89.4% of mean adult mass, compared to weaver-cuckoos that fledged at 104.7% of mean adult mass (mean adult mass = 34.6g; Maclean 1993).

Red bishop and yellow weaver nestling growth followed a logistic pattern similar to that observed in diderik cuckoo nestlings. In bishop nests, host nestlings ($K = 0.40 \pm 0.03$, $n = 161$) grew at a significantly faster rate than cuckoo nestlings ($K = 0.28 \pm 0.01$, $n = 51$; $t_{0.001\,(2),\,292} = 3.330$, $P < 0.0001$) and reached half of their asymptotic mass by day six. In contrast, yellow weaver nestlings ($K = 0.35 \pm 0.01$, $n = 95$) grew at the same rate as weaver-cuckoo nestlings ($K = 0.35 \pm 0.02$, $n = 5$) and reached half of their asymptotic mass within 7 days of hatching (Appendix 1).

DISCUSSION

This study shows significant differences in nestling growth rates (based on mass) between diderik cuckoo gentes. As predicted, in nests of the larger yellow weaver host the growth rate of cuckoo nestlings was greater than in nests of the smaller red bishop. A fast growth rate ($K = 0.375$; Starck and Ricklefs 1998) has also been recorded for a diderik cuckoo parasitising another relatively large host species, the spectacled weaver (*Ploceus ocularis*; adult mass = 28.9 g; Maclean 1993). Fast growth rates have also been reported for the smaller *Chrysococcyx lucidus* ($K = 0.35$; Gill 1983; Brooker and Brooker 1989) and

C. basalis ($K = 0.41$; Brooker and Brooker 1989), even though these cuckoo species parasitise host species that are two-three times smaller than themselves. This variation in nestling growth rate among larger and smaller *Chrysococcyx* species may reflect the general exponential inverse relationship between nestling growth rate and adult body mass, where larger species grow more slowly than smaller species (Ricklefs 1968).

The positive correlation observed in this study between the growth rate of diderik cuckoo nestlings and host body size corroborates the findings of Wiley (1986) and Kleven et al. (1999). These studies showed that the nestling growth rate of the shiny cowbird (*Molothrus bonariensis*) and European cuckoo respectively, increased significantly with host body size. Such a relationship has been explained in terms of larger hosts having the ability to provision larger amounts of food (Wiley 1986). However, this study revealed that bishop and weaver hosts provisioned the same amount of food to cuckoo nestlings, negating the influence of host size, and that selection pressure on behaviours by the cuckoo that manipulate host feeding behaviour are consequently weak (chapter three).

A more plausible explanation for the difference in growth rates between diderik cuckoo nestlings raised by yellow weavers and red bishops are the differences in diet quality. The protein-deficient diet provisioned by granivorous red bishops for more than half of the cuckoo's nestling period (chapter two) is likely to be responsible for slower growth rates in bishop-cuckoos. This is supported by several reports (e.g., Eastzer et al. 1980; Wiley 1986; Brooker and Brooker 1989; Middleton 1991; Kozlovic et al. 1996; Gill 1998) that document the frequent failure of brood parasitism in the nests of predominantly granivorous hosts. In addition to causing slower growth rates, poor diet quality (protein deficient) may have lowered fledging success for bishop-cuckoos (chapter two). Experimental manipulations of diet quantity and quality through diet supplementation (e.g.

mealworms) to cuckoo nestlings would allow for firmer conclusions in this study. Experiments of this nature were scheduled for the 3rd year (1999-2000). However, due to unexpected disruptions at the weaver study sites by the local authorities, and consequently low numbers of weaver nests, the experiments were not conducted. In addition, cuckoos did not parasitise the weaver colony during this year and thus the experiment was not conducted for bishop-cuckoos due to the lack of comparative weaver-cuckoo data. The influence of ecological factors (i.e. annual and site variation in food availability) on provisioning rates and cuckoo nestling growth cannot be ignored.

In several bird species, slow growth and/or low fledging mass decreases the probability of postfledging survival (Perrins 1965; Martin 1987; Richner et al. 1989; Magrath 1991; Gebhardt-Henrich and Richner 1998; McCarty 2001). A strong positive relationship between nestling mass and postfledging survival has been demonstrated in great spotted (*Clamator glandarius*; Soler et al. 1994) and European cuckoos (Kleven et al. 1999). In addition, Kleven et al. (1999) found a significant positive correlation between the growth rates and fledging success of European cuckoo nestlings. Although the postfledging survival of diderik cuckoos was not addressed in this study, weaver-cuckoos are likely to experience a higher probability of postfledging survival due to their relatively faster growth rates and higher fledging mass. These results lend further support to the notion that red bishops are a less suitable host species of the diderik cuckoo than the yellow weaver. Lindholm (1997) recorded similar differences in fledging mass for cuckoos parasitising lesser-masked weavers (35.6 ± 2.8g, $n = 8$) and red bishops (32.1 ± 2.9g, $n = 3$). In addition slow growth rates of bishop-cuckoos, through extended nestling periods, may reduce the number of nesting attempts by bishop hosts in a breeding season (Ricklefs

1984), which in turn will decrease the number of active nests available for parasitism by diderik cuckoos in that season.

Although the growth rates of primary wing feathers and tarsus differed between the two cuckoo gentes investigated in this study, skeletal development was independent of host selection, with both cuckoo gentes reaching adult size prior to fledging. This result was expected, as bone development is less susceptible to dietary variation than body mass and wing development (Gard and Bird 1992). Consequently, the differences recorded in fledging mass and primary feather development relative to adult cuckoos, may be used as a measure of fledgling condition and indirectly, of host suitability.

In conclusion, diderik cuckoos raised by yellow weaver hosts grew at a faster rate and fledged in better condition than their bishop counterparts. Growth rate of diderik cuckoo nestlings was primarily influenced by diet quality and not by host size. Therefore, of the two host species investigated here, the yellow weaver is the more suitable because it provisions a protein-rich diet to cuckoo nestlings. According to studies by Rothstein and Robinson (1998) and Kleven et al. (1999), the more suitable of the available host species is predicted to suffer a higher incidence of parasitism. Thus, female cuckoos should parasitise yellow weavers, more frequently than red bishops. However, this prediction does not hold for the diderik cuckoo-ploceid brood parasite system investigated in this study. Throughout this study red bishops have been shown to be the less suitable host species, nevertheless they are parasitised more often than yellow weavers and any other host species in southern Africa (Payne and Payne 1967; Reed 1968; Jensen and Vernon 1970; Rowan 1983). There are several potential explanations for this and these are addressed in the next chapter.

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APPENDIX 1. Estimated logistic growth parameters for selected variables of red bishop and yellow weaver hosts. A = asymptotic body mass, K = growth rate constant, t_i = inflection point of the growth curve. The goodness of fit of the growth function (r^2) has been included. Values are presented as the estimate ± SE with sample size in parentheses.

Species	A	K	t_i	r^2
Mass				
Red Bishop	16.02 ± 0.55 (161)	0.40 ± 0.03 (161)	5.90 ± 0.25 (161)	0.83
Yellow Weaver	23.46 ± 0.40 (95)	0.35 ± 0.01 (95)	7.11 ± 0.14 (95)	0.92
Tarsus				
Red Bishop	22.80 ± 0.69 (161)	0.28 ± 0.01 (161)	5.32 ± 0.26 (161)	0.85
Yellow Weaver	24.24 ± 0.35 (95)	0.26 ± 0.008 (95)	5.63 ± 0.14 (95)	0.94
Wing				
Red Bishop	55.07 ± 3.40 (161)	0.32 ± 0.02 (161)	8.27 ± 0.47 (161)	0.82
Yellow Weaver	62.32 ± 1.89 (95)	0.28 ± 0.01 (95)	10.08 ± 0.27 (95)	0.94

CHAPTER FIVE

Why do diderik cuckoos parasitise red bishops when they are apparently such poor hosts?

The success of brood parasitism is dependent on several factors, the following of which have previously been reported as influential in host selection:

- Host species and their nests must be abundant, so that a female cuckoo can find sufficient nests in which to lay all her eggs (Payne 1977).
- Nests must be accessible, comprising an open cup or possessing an entrance hole big enough for the cuckoo to enter and lay her egg (Wiley 1988; Johnsgard 1997; Davies 2000).
- Hosts must have a laying season that spans the breeding period of the cuckoo (Wiley 1988; Soler et al. 1999).
- Cuckoos should select hosts with a small clutch size, thereby reducing the energetic cost to the young cuckoo of ejection of the host's eggs and/or nestlings (Wyllie 1981; Soler et al. 1999).
- Host size must be similar to that of the cuckoo. Hosts must be sufficiently large to provide adequate food to support the nestling cuckoo in its later growth stages when cuckoo mass may exceed that of the host adult (Payne 1977).

- The host must provision suitable nestling diets. These are protein-rich diets (Klasing 1998) comprising mainly invertebrates (Payne 1977, 1998; Davies and Brooke 1989a; Marchetti 1992).
- Nestling behaviour of the parasite and the host should be compatible, e.g., there should be some similarity between the begging behaviour of host and parasite nestlings (Payne 1977).

Two of these factors were the focus of this study, namely the quality of the diet fed by host parents to nestlings (chapter two) and the ability of the host to provision sufficient food (chapter three) to support the demands of the growing nestling parasite. Brood-parasites must select a host that not only accepts its egg but also is capable of successfully rearing the parasite to fledging. Although the quality of host species varies, brood parasites appear to avoid hosts that are likely to reject their eggs, that are an inappropriate size (too small or too big), or that feed their nestlings inadequate or insufficient food (reviewed by Rothstein & Robinson 1998).

In the diderik cuckoo-ploceid brood parasite system, cuckoo nestlings were provisioned the same diet as southern red bishop or yellow weaver host nestlings. Although bishop and weaver hosts provisioned the same amount of food to cuckoo nestlings, bishop-cuckoos received a protein-deficient seed diet for most of their nestling period. As a correlate, cuckoos in bishop nests grew at a slower rate and fledged in a poorer condition, three days later than their yellow weaver counterparts. Despite slower growth rates, poorer condition and lower fledging success experienced by the bishop-cuckoo, bishop hosts are nevertheless frequently parasitised. The final task of this thesis is to provide an explanation for this seemingly non-adaptive behaviour.

The high frequency of parasitism of red bishops may be due to their longer breeding season that coincides more closely with that of the diderik cuckoo than does most weaver species. In addition, red bishops appear to be more recent hosts of the diderik cuckoo than other ploceids and are at an early stage in the evolutionary arms-race. The latter is evident from the lack of egg rejection behaviours, and the lack of defences against brood parasitism by red bishops (Davies and Brooke 1989b). The bishop egg is immaculate and easily mimicked by the cuckoo and red bishops are less discriminating of the cuckoo's egg than most ploceids (Lawes and Kirkman 1996).

Lawes and Kirkman (1996) have suggested another possible explanation for the lack of egg rejection behaviour by red bishops. They suggest that an evolutionary equilibrium may exist between red bishop hosts and diderik cuckoos in which discrimination against the cuckoo egg by the bishop cannot improve because of the closed (i.e. dark) nest structure and mimetic cuckoo egg. In turn, the cuckoo is unable to exploit this constraint because of the colonial breeding behaviour of the red bishop and the improved corporate vigilance and defence of the colony that arises as a consequence. Thus, diderik cuckoos exploit bishops only in small, low density and poorly defended colonies (Ferguson 1994; Lawes and Kirkman 1996). Unless the nest structure or breeding behaviour of the red bishop changes, it is possible that the system will remain in equilibrium.

Rejection rates of cuckoo eggs by weavers are comparatively higher and weavers appear to be at a more advanced stage of the evolutionary arms-race (Lindholm 1997). The latter is most convincingly indicated by the considerable intraspecific variability in egg colouration and maculation in the weavers, including the yellow weaver (Lindholm 1997). This is made all the more interesting by the fact that the red bishop cuckoo gens is highly specialised on its host while the yellow weaver cuckoo gens appears to parasitise several *Ploceus* weaver species that all lay similar variably coloured and spotted eggs (Jensen and Vernon 1970). Weaver species are therefore arguably more difficult to parasitise by diderik cuckoos. However, where the cuckoo egg is accepted and incubated by the weaver, the cuckoo nestling can expect a greater likelihood of fledging and postfledging survival than in a bishop nest, because it is fed sufficient insect-rich food to ensure good condition at fledging and it approximates adult size and weight (chapter four).

Thus in the diderik cuckoo-ploceid brood parasite system, two strategies of host choice by the cuckoo appear to exist – cuckoos either choose hosts that are:

1. easily parasitised because they have low egg rejection rates, but that have a relatively low nestling survival rate (i.e. provision a poor-quality diet to the cuckoo nestling), or are;
2. difficult to parasitise due to high egg rejection rates, but that have a high nestling survival rate (i.e. provision high-quality diets to the cuckoo nestling).

There is no doubt that the diderik cuckoo-red bishop brood parasite system is successful, in spite of the poor quality of the host compared to weavers. The only way in which these two contrasting systems survive is if cuckoo fledging success from bishop nests is similar to that from weaver nests. Given that the former is relatively low, diderik cuckoos must parasitise red bishops more frequently than yellow weavers. Ultimately, both systems represent compromises for the diderik cuckoo, emphasising the flexible nature of brood parasite behaviour.

FUTURE RESEARCH

This study was primarily a descriptive assessment of the diderik cuckoo-ploceid breeding system, focussing on nestling diet, host-provisioning rates to cuckoo nestlings and cuckoo nestling growth. Inferences regarding nestling growth and diet quality are made in this study, based on an important assumption derived from the literature, that seeds are protein-poor and insects are protein-rich. Consequently, much of the data presented here are correlative. Experimental manipulations would greatly improve future research on this brood parasite system. These should include i) a comparison of the nutritional content of the seed and insect provisioned by red bishops with that of the insect provisioned by weaver hosts, ii) daily supplementation of host and cuckoo nestling diets with mealworms (high protein) in the field, iii) careful consideration of cross-fostering experiments and iv) using a small camera in the nest to observe provisioning rates more accurately.

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