Food provisioning and body mass of nestling Meadow Pipits and Cuckoos

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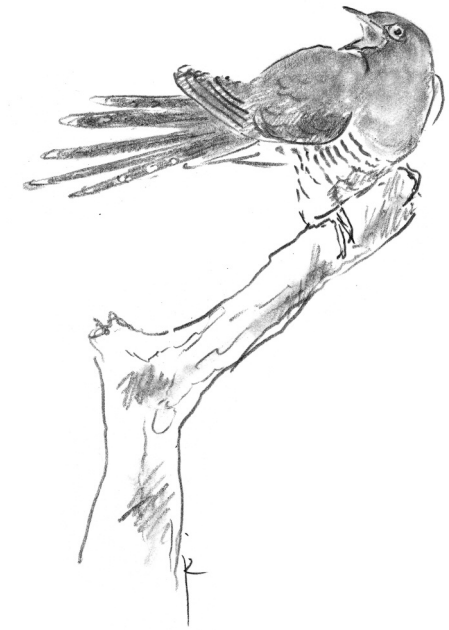

Common Cuckoos *Cuculus canorus* are obligate brood parasites, laying eggs in nests of other species. Cuckoo nestlings are often thought to be insatiable, compared to host broods. However, in Reed Warblers *Acrocephalus scirpaceus* and a few other species, cuckoo nestlings are fed at most only as frequently as a host brood. To add to the small body of knowledge on feeding frequencies and body mass development of Cuckoo nestlings, I studied Cuckoos using another host, the Meadow Pipit *Anthus pratensis*, in the Dutch dunes (2019–2021). By filming feeding parents (hosts) I determined the provisioning frequency for broods of Pipits and for nestling Cuckoos. I found that nestling Cuckoos receive on average fewer feeds per hour than broods of Meadow Pipits. Furthermore, overall Cuckoos received as many feeds during their 22-day nestling period as a brood of Pipits during their 13 days in the nest. At 13 days of age (day 1 is the day of hatching), the single Cuckoo was as heavy as a brood of four Meadow Pipits. At 22 days, the maximum weights of the nestling Cuckoos were greater than the Meadow Pipit broods and varied between 91 and 105 g. Thus, although Cuckoos are being fed less frequently, young Cuckoos are heavier at fledging than a whole brood of Pipits. This could be because Cuckoos are fed larger prey. Alternatively, Cuckoos may require less food because their thermoregulatory costs could be smaller: they have almost black skin which absorbs solar radiation efficiently, do not have to compete with siblings in the nest and, once older and feathered, have a smaller surface-to-volume ratio than a Pipit brood of four nestlings.

Key words: brood parasitism, provisioning, Meadow Pipit, Cuckoo, *Cuculus*

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The Common Cuckoo *Cuculus canorus* is an obligate brood parasite whose eggs have been found in nests of 108 bird species across Europe (Moksnes & Røskaft 1995). Diverse as the lifestyles of all hosts may be, most research in Europe has focussed on Cuckoos parasitising Reed Warblers *Acrocephalus scirpaceus*, because their densities are high and nests are readily found (Wyllie 1981, Davies 2015).

In spite of the "voracious appetite" (Chance 1940) of a young Cuckoo and in spite of a young Cuckoo being much heavier than a complete brood of nestlings, Reed Warblers actually feed a Cuckoo at about the same rate as they would a whole brood of their own (Brooke & Davies 1989, Samaš *et al.* 2019). Young Cuckoos hosted by Common Redstarts *Phoenicurus phoenicurus* received fewer feeds per hour than a brood of Redstarts (Samaš *et al.* 2018), as did nestling Cuckoos hosted by Rufous-tailed Scrub Robins *Cercotrichas galactotes* (Martín-Gálvez *et al.* 2005). Therefore, it seems possible that hosts feed young Cuckoos at about the same rate as they would feed a brood of their own.

To add to the rather small body of information on provisioning frequencies by different host species and body mass of Common Cuckoo nestlings, I report a study on nestling Cuckoos using another host, the Meadow Pipit *Anthus pratensis*, a commonly used host in Western Europe. I aimed to learn whether the provisioning frequency differed between nestling Cuckoos and broods of Meadow Pipits. Furthermore, I was interested to see how relative body mass in 'Meadow Pipit Cuckoos' develops.

METHODS

Study site

The study site Vogelduin and its immediate surroundings is part of the Noord-Hollands Duinreservaat (NHD; 52°33'N, 4°36'E) in The Netherlands, and measures approximately 136 ha. It consists of hilly open dune grasslands with scattered sandy blow-outs. The vegetation is dominated by graminoids, such as Wood Small-reed *Calamagrostis epigejos* and Sand Sedge *Carex arenaria*, herbs such as Dune Pansy *Viola curtisii*, mosses, lichens and shrubs, particularly Creeping Willow *Salix repens* and Sea-buckthorn *Hippophae rhamnoides*.

Study species

Common Cuckoo

The Common Cuckoo (adult body mass female c. 110 g), the quintessential harbinger of spring (Davies 2015) in the temperate and boreal Old World, occurs in Europe, northernmost Africa and continental Asia. As an obligate brood parasite, it mostly parasitizes nests of Reed Warblers, Dunnocks *Prunella modularis* and Meadow Pipits in Western Europe. One egg is laid per nest, with an estimated 10–20 eggs per season (Wyllie 1981; 25 under more or less experimental circumstances, Chance 1940). After hatching, the young Cuckoo evicts eggs or nestlings of the host and becomes the sole occupier of the nest. Young Cuckoos (Figure 1) stay in the nest for about 17–22 days (Chance 1940, Wyllie 1981, Samaš *et al.* 2018) and become independent about 16–22 days after fledging (Wyllie 1981, Samaš *et al.* 2018). They feed on insects, mostly caterpillars (e.g. Wyllie 1981).

Meadow Pipit

Meadow Pipits (adult body mass c. 17 g) are ground foraging insectivores which breed at temperate and boreal latitudes from Greenland to Western Siberia. They lay 3–5 eggs, 2–3 times annually in open nests built on the ground (Hötker & Sudfeldt 1982, van Oosten 2016). Young stay in the nest for about 12–13 days (Glutz von Blotzheim & Bauer 1985) and reach independence on average 13 days after fledging (Hötker 1982). In Vogelduin they nest predominantly between mid-April and July (van Oosten 2016). They forage while walking on the ground by picking prey off the ground and vegetation.

Field techniques

Nest searching

Nests of Meadow Pipits were searched for, with varying intensity, between early April and the end of July in the years 2015–2021. Although Pipits start nesting from early April, parasitized nests containing Cuckoo young were found from June onwards. Nests were found by accidentally flushing breeding females from the nest, by following feeding parents back to their nest or, in at least one occasion, by tracing begging calls of a nestling Cuckoo. Once a nest was found, the contents were checked to see whether the nest was parasitized or not. In total, 25 nests of 129 nests of Meadow Pipits were found to be parasitised. Based on focal observations, about 30–50 pairs of Meadow Pipits per year were estimated to be present in the area.

Provisioning frequency

To determine the frequency with which parents (hosts) fed their young, feeding parents were filmed at the nest

Figure 1. (A) Nestling Common Cuckoo 12 days of age. (B) Nestling on about day 8: note the black skin.

if the vegetation surrounding the nest permitted placement of a handy-cam video camera on a small tripod. The camera (either a Sony HDR-SR10E or Canon HF 10E or 100E) was camouflaged with strings of Dewberry *Rubus caesius*.

I was able to film at eight different parasitized nests (2019 and 2021), of which five were filmed for one day, two for two days and one for three days. Nests filmed for more than one day were not always filmed on consecutive days. Per nest per day, I obtained footage for a median time of 6 h and 48 min per nest (range 3 h 17 min – 7 h 35 min, total 74 h 40 min), which encompassed a median of 57.5 feedings per nest (range: 30–110, in total 698 feedings). Nests were filmed between 9 and 28 July, and the nestlings were estimated to be between 8 and 21 days of age (hatch day = 1).

In 2019, I also filmed 11 nests of Meadow Pipits with a brood of their own young, of which eight were filmed for one day and three for two days. Per day, footage was obtained for a median time of 6 h 25 min per nest (range 2 h 56 min – 8 h 45 min, total 82 h 58 min), which encompassed a median of 86 feedings per nest (range: 29–147, in total 1149 feedings). Nests contained a median of 4.0 nestlings (range 3–5) and were filmed throughout the breeding season, between 30 April and 18 July; the nestlings were between 6 and 11 days of age.

Mann-Whitney *U* tests were applied to compare median feeding frequencies of young Meadow Pipits and young Cuckoos. Pseudo-replication, because of multiple measurements on different dates for some nests, was avoided by using the median feeding frequency across dates for these nests. To test for a relation between age and feeding frequency, I calculated the Spearman's Rho correlation coefficient, again using the median value for feeding frequency for each of the measured nests.

Growth curve

Weight of the chicks of both bird species was determined with a Pesola spring scale to the nearest 0.5 g, wing length was measured as maximum stretched wing to the nearest 0.5 mm. Based on 25 measurements, partly repeat-measurements (see Table S1), from 10 nestling Cuckoos, I fitted a cubic polynomial to obtain a 'weight against wing length' growth curve, which I transformed into a 'weight against age' growth curve, based on published daily measurements of nestling Cuckoos (Werth 1947). In a similar way, I fitted a cubic polynomial to obtain a growth curve of a brood of four nestling Meadow Pipits of known age (hatching seen in field).

RESULTS

Provisioning frequency

A nestling Cuckoo was fed less frequently than a brood (median = 4 nestlings, range: 3–5 in 2019) of Meadow Pipits: median = 8.4 vs. 14.1 times per hour (Figure 2; $U = 14.5$, $P = 0.017$). No significant relation between provisioning frequency and age (between day 8 and 21) was found for nestling Cuckoos ($r_s = –0.077$, $P = 0.81$). Details of total film time and provisioning frequency are provided in Table S1.

Assuming that parents provide food to their own young and a young Cuckoo for a similar number of hours per day, multiplication of provisioning frequency times nestling days indicates that the total number of feeds received by a young Cuckoo during its 22-days' nestling period is similar to that of a brood of Meadow Pipits in 13 days, in spite of the Cuckoo spending an estimated nine days more in the nest (Table 1).

Growth curve

Maximum body mass of nestling Cuckoos was reached with a wing length of 120–130 mm (Figure 3A), corresponding with an age of 20–22 days (Figure 3B). In Table S2 the measurements of wing length and body mass are provided. A brood of four Meadow Pipits reached a maximum summed weight of 70 g at day 12 (Figure 3B). Thus, a young Cuckoo is heavier than a brood of four nestling Pipits from day 13 onwards, which is around the time that young Pipits leave their nest.

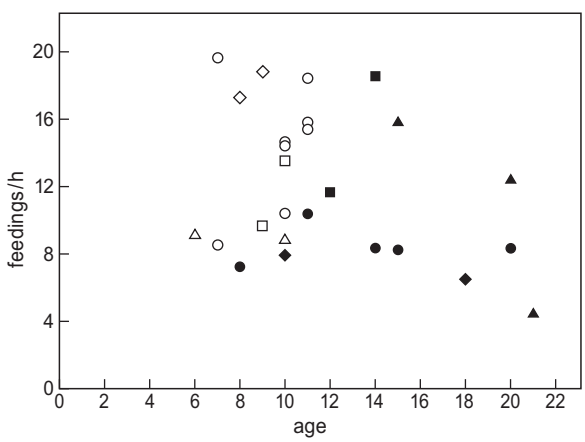

Figure 2. A nestling Common Cuckoo receives fewer feedings than a brood of Meadow Pipits: median = 8.4 vs. 14.1 feedings per hour. Dark symbols: Common Cuckoos, open symbols: Meadow Pipits. Each circle is a single nest filmed for one day. Other symbols: each symbol refers to one nest, filmed for more than one day, e.g. black squares refer to a Cuckoo's nest filmed at nestling age 12 and age 14.

DISCUSSION

The results of the present study support the earlier findings that a nestling Cuckoo is not fed more frequently than a brood of the host species (Brooke & Davies 1989, Samaš *et al.* 2018, 2019). A young Cuckoo raised by Meadow Pipits received fewer feedings per hour and as many feedings during its 22 days nestling period as a brood of Meadow Pipits in 13 days. Although Cuckoo-data were collected in two years (2019 and 2021) and the Pipit data only in 2019, it seems that feeding frequency may not differ between years: young Meadow Pipits in six nests obtained as many feedings in 2015 in Vogelduin as in 2019 (median = 12.4 with range: 7.9–18.6, similar to the 14.1, range: 8.3–18.7, in 2019; $U = 25.5$, $P = 0.48$; van Oosten unpubl. data). In line with these contemporary findings, it is of interest to note that Heinroth & Heinroth (1926) already state that raising a young Cuckoo is easier for the hosts than a brood of their own, almost a hundred years ago!

A young Cuckoo receives fewer feedings and yet it is as heavy as a whole brood of Meadow Pipits on day 13, when Pipits leave the nest. Similarly, a young Cuckoo of the same weight as a brood of Common Redstarts received fewer feedings than a Redstart brood (Samaš *et al.* 2018). How the Cuckoo manages to gain its weight with fewer feedings than the nestlings of the host species is not clear.

One way in which Cuckoos may reach the same weight as a brood of nestling Meadow Pipits is that they are fed with prey of different sizes, as reported by Martín-Gálvez *et al.* (2005). These authors found that, although young Cuckoos were fed less often than broods of Rufous-tailed Scrub Robins, Cuckoos received larger prey and hence still obtained the same amount of food as a brood of Scrub Robins. Whether Meadow Pipit Cuckoos receive larger prey than young Meadow Pipits remains to be studied.

Another intriguing possibility is that the thermoregulatory costs for the single nestling Cuckoo may not always be higher than for a brood of host nestlings. A group of huddling nestlings is able to stabilize body temperatures at an earlier age than individual nestlings, thereby saving energy (Dunn 1975, Forbes 2007). However, the skin colour of young Cuckoos turns from

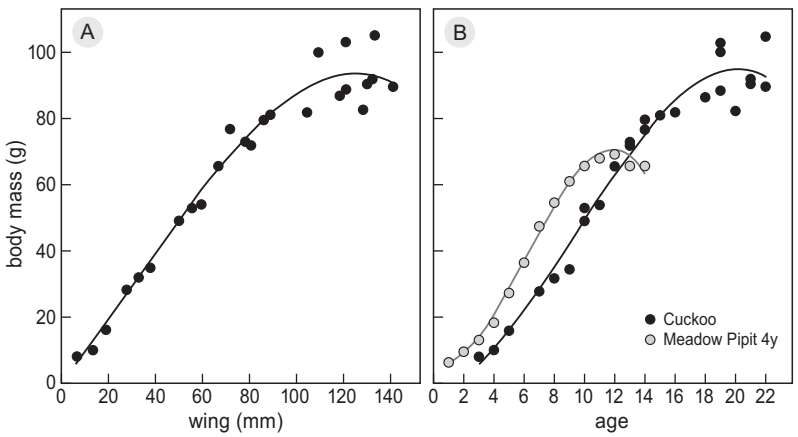

Figure 3. (A) Cubic growth curve of body mass against wing length. (B) Cubic growth curve of body mass against age for nestling Common Cuckoos (black circles), to show the summed daily mass of a brood of four nestling Meadow Pipits (grey circles). From day 13 onwards, the Cuckoo is heavier than the Pipit brood, which leave their nest at about day 13.

Table 1. Median provisioning per hour (range), nestling period (days) and total number of times a brood is fed during the nestling period (range; estimation based on the provisioning per hour and nestling period) for both species. Assuming a similar number of daily hours during which young from both species are being fed, Meadow Pipit parents feed their own young in 13 days as often as a single Common Cuckoo young in 22 days.

	Provisioning (*n*/h)	**nestling period** (d)	**Number of feedings in nestling period**
Meadow Pipit	14.1 (8.3–18.7)	13	183 (108–243)
Common Cuckoo	8.4 (4.1–18.6)	22	185 (90–409)

pink into almost black in at most three days after hatching (Figure 1B; Heinroth & Heinroth 1926, Wyllie 1981): could this be to increase heat absorption and reduce thermoregulatory costs at this scarcely feathered age? Some support for this idea comes from the Greater Roadrunner *Geococcyx californianus*, a cuckoo species living in deserts of Southwest-North America, which exposes its black skin early in the morning to absorb "the sun's radiant heat like a solar panel" (Payne 1997). Doing so, it can save up to 60% of the energy needed to increase body temperature by four degrees from night-time levels (Ohmart & Lasiewski 1971, Payne 1997). Perhaps the dark skin of a young Cuckoo at least helps it to heat up early in the morning, which may be especially important in nests located on the ground as in Meadow Pipits, because ambient temperatures are at their lowest near the ground surface.

Also, being on its own, a nestling Cuckoo does not waste energy on sibling competition over position in the nest. Once feathered, thermoregulatory costs of the not-so-young nestling Cuckoo could be smaller than of a brood of Meadow Pipits, assuming that the amount of exposed surface area per volume body mass of a Pipit brood is higher than of a single Cuckoo (Royama 1966, Dunn 1975). Taken together, perhaps nestling Cuckoos need less food than a brood of host nestlings, or less than one would expect of a single unfeathered nestling, because of having a black skin, being lethargic and, at a later stage, having a better energy conserving body-to-surface ratio.

Irrespective of exactly how nestling Cuckoos increase mass, the observed variation in maximum body mass is quite remarkable. Within the same area, the same year and the same host species, maximum body mass varied between 91 and 105 g. Indeed, maximum masses of nestling Cuckoos are known to be very variable, ranging between 51 and 137 g (across six host species; Grim & Samaš 2016, see also Werth 1947 and Wyllie 1981, for instance), mostly on average between 85 and 100 g. It is unknown why masses are this variable. Remarkably, host size has no positive effect on fledging mass of Cuckoos (Grim & Samaš 2016, contra Kleven *et al.* 1999, who noted that nestling Cuckoos raised by Great Reed Warbler *A. arundinaceus*, 28 g, were 20 g heavier at fledging than those raised by Reed Warblers of 12 g). One would think differences in food intake should play an important role in causing the observed body mass variation, perhaps in combination with variable weather circumstances, where inclement weather increases thermoregulatory costs. A good starting point would be the precise study of feeding frequencies across multiple nestling Cuckoos, in combination with a multi-day diet analysis in, for instance, Meadow Pipit Cuckoos in the rolling Dutch dunes.

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SAMENVATTING

Koekoeken *Cuculus canorus* leggen hun eieren in nesten van andere vogels. Van oudsher wordt jonge Koekoeken een enorme eetlust toegedicht, vergeleken met een broedsel van de gastheren. Echter, onderzoek naar de voerfrequentie bij Kleine Karekieten *Acrocephalus scirpaceus* en enkele andere soorten laat zien dat Koekoeken hoogstens even vaak gevoerd worden als een broedsel van de gastoudersoort. Hier doe ik verslag van een studie aan Koekoeken in nesten van Graspiepers *Anthus pratensis*, waarin ik de voerfrequentie met die van pieperbroedsels vergelijk door voerende ouders bij het nest te filmen, uitgevoerd in het Vogelduin bij Castricum (2019–2021). Het bleek dat jonge Koekoeken per uur minder vaak gevoerd worden dan een heel broedsel Graspiepers. Gedurende de 22 dagen dat een jonge Koekoek in het nest zit, wordt hij in totaal even vaak gevoerd als een broedsel jonge piepers in 13 dagen. Op een leeftijd van 13 dagen (dag 1 is dag van uitkomst ei) is de jonge Koekoek even zwaar als een broedsel van vier jonge Piepers en de maximale koekoekgewichten waren variabel, tussen de 91 en 105 g. In feite is er sprake van een paradox: ondanks een kleiner aantal voederingen zijn jonge Koekoeken toch zwaarder op dag 22 dan een broedsel Piepers. Het is onduidelijk hoe dat kan; mogelijk krijgen Koekoeken grotere prooien gevoerd of zijn de kosten voor thermoregulatie kleiner, omdat jonge Koekoeken een vrijwel zwarte huid hebben die efficiënt zonnestraling kan opnemen, omdat ze niet hoeven te bakkeleien met nestgenoten om de beste plek en omdat ze, wanneer ze eenmaal ouder en bevederd zijn, een gunstiger oppervlakte-volumerelatie hebben dan een broedsel Graspiepers. Hierdoor zou een jonge Koekoek minder voedsel nodig kunnen hebben dan vier jonge Graspiepers.

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SUPPLEMENTARY MATERIAL

Table S1. Information on the total time filmed and observed feeding frequencies at the different nests.

Common Cuckoo												
year	2019	2019	2019	2019	2019	2021	2021	2021	2021	2021	2021	2021
nest code	koek1	koek1	koek3	koek3	koek3	mv-o	mv-o	bg	nk2-0	prairie	nk3	hoek
date	9-7	11-7	18-7	23-7	24-7	12-7	20-7	13-7	20-7	13-7	28-7	20-7
total film time	6:11	3:17	7:08	6:52	7:14	6:44	5:42	7:23	7:16	5:34	3:43	7:35
age	12	14	15	20	21	10	18	20	8	14	11	15
number of feedings	69	61	111	72	30	54	37	62	53	47	39	63

Meadow Pipit														
year	2019	2019	2019	2019	2019	2019	2019	2019	2019	2019	2019	2019	2019	2019
nest code	g2	g5	g8	g9	g19	g20	g20	g25	g25	g28	g28	g34	g35	g37
date	30-4	30-4	13-5	4-6	13-6	14-6	18-6	27-6	28-6	27-6	28-6	5-7	5-7	18-7
total film time	7:53	5:01	7:12	7:44	3:09	3:28	6:32	2:56	6:18	2:58	8:05	6:45	6:12	8:45
age	11	11	7	7	10	6	10	8	9	9	10	10	10	11
number of feedings	147	81	132	64	33	32	57	51	118	29	112	95	91	107

Table S2. Wing length and body mass per date per Common Cuckoo nestling.

Nest	**Date**	**Wing** (mm)	**Body mass** (g)	**Time**
1	7-7-2021	18.5	16.25	12:05
1	12-7-2021	55	53.25	16:50
1	15-7-2021	80	72.25	16:52
1	20-7-2021	118	87.00	17:06
2	7-7-2021	71.5	77.25	10:25
2	12-7-2021	109	100.25	16:38
2	15-7-2021	133	105.25	16:40
3	12-7-2021	78	73.25	16:25
3	15-7-2021	104	82.25	17:03
3	20-7-2021	130	90.75	11:55
3	21-7-2021	141	90.00	11:30
4	13-7-2021	121	103.25	14:30
4	15-7-2021	132	92.25	16:17
5	15-7-2021	49.5	49.25	14:30
5	20-7-2021	88.5	81.25	16:41
6	15-7-2021	6	8.25	16:32
6	20-7-2021	32	32.24	16:10
6	21-7-2021	37.5	35.00	11:09
7	21-7-2021	13	10.25	10:53
7	28-7-2021	59	54.25	12:44
8	26-6-2020	27	28.25	12:30
9	9-7-2019	66	66.00	17:15
10	18-7-2019	86	80.00	16:15
10	23-7-2019	121	89.00	15:20
10	24-7-2019	128	83.00	13:55