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RESEARCH ARTICLE

Unusual diet of brood parasitic nestlings and its fitness consequences

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ABSTRACT

Avian brood parasitism provides a tractable system within which to study diverse aspects of animal ecology and evolution. Yet, parasite–host research has focused on specific adaptations and counter-adaptations, such as egg rejection by hosts and egg mimicry by parasites, leaving other aspects of these relationships poorly studied, including general life history traits of hosts that did not evolve as specific antiparasite defenses. In particular, the diet and fledging parameters (age, mass, success) of parasitic nestlings are poorly known, although they are central to our understanding of host selection and the potential for coevolution in parasite–host relationships. We focused on the diet composition and fledging parameters of parasitic Common Cuckoo (*Cuculus canorus*) nestlings raised by their only regular cavity-nesting host, the Common Redstart (*Phoenicurus phoenicurus*). In addition to invertebrates, both Common Cuckoo and Common Redstart nestlings were fed fruits and lizards by some host pairs. This is the first record of lizards being fed to Common Cuckoo nestlings by any host. Capitalizing on this unusual diet and between-host-pair variation (statistically confirmed by high repeatability of diet composition across host pairs), we tested for the first time whether nestling diet variation affected Common Cuckoo breeding success. Common Cuckoos, but not Common Redstarts, fed a combination of plants and vertebrates showed decreased fledging masses and delayed fledging. Common Cuckoos fed with plants (but not vertebrates) also had lower fledging masses. Vertebrates alone did not have any effects. Fledging success was not influenced. These patterns could not be explained by various potential confounding effects, including seasonal effects or inferior provisioning capacities of Common Redstarts feeding unusual diets. This suggests that plant and vertebrate material is digestible by Common Cuckoo nestlings but might cause ontogenetic stress. We show for the first time that diet composition may affect parasite success, not only at the level of host species, as documented by previous studies, but also intraspecifically (i.e. at the level of individual host pairs). Host diet selection may represent an important general life history trait that affects brood parasite fitness, even though it most likely did not evolve as a specific antiparasite defense.

Keywords: Common Cuckoo, diet, fitness, fledging success, host selection, Common Redstart

Dieta inusual de polluelos parásitos de nidada y sus consecuencias en la adecuación biológica

RESUMEN

El parasitismo de nidada de las aves representa un sistema manejable para estudiar diversos aspectos de la ecología y la evolución animal. Sin embargo, la investigación de parásitos y hospederos se ha enfocado en adaptaciones específicas y contra-adaptaciones, como el rechazo del huevo por parte del hospedero y el mimetismo del huevo por parte del parásito, dejando otros aspectos de las relaciones poco estudiados, incluyendo los rasgos generales de la historia de vida del hospedero que no evolucionaron como defensas antiparasitarias específicas. En particular, los parámetros de la dieta y de emplumamiento (edad, masa, éxito) de los polluelos parásitos son poco conocidos, aunque son centrales para nuestro entendimiento de la selección del hospedador y del potencial de coevolución en las relaciones parásito-hospedero. Nos enfocamos en la composición de la dieta y en los parámetros de emplumamiento de los polluelos parásitos de *Cuculus canorus* en su único hospedero regular que anida en cavidades, *Phoenicurus phoenicurus*. Además de invertebrados, tanto los individuos de *C. canorus* como los de *P. phoenicurus* fueron alimentados con frutos y lagartijas por algunas parejas de hospederos. Este es el primer registro de lagartijas en la dieta de los polluelos de *C. canorus* para cualquier hospedero. Capitalizando esta dieta inusual y la variación entre parejas hospederas (estadísticamente confirmada por la alta repetitividad de la composición de la dieta a lo largo de las parejas de hospederos), evaluamos por primera vez si la variación de la dieta de los polluelos afecta el éxito de cría de *C. canorus*. Los individuos de *C. canorus*, pero no los de *P. phoenicurus*, alimentados con una combinación de plantas y vertebrados mostraron una disminución en el peso en la etapa de emplumamiento y un retraso en el emplumamiento. Los individuos de *C. canorus* alimentados con plantas (pero no vertebrados) también tuvieron menor peso en la etapa de emplumamiento. Los vertebrados solos no tuvieron ningún efecto. El éxito de emplumamiento no se vio influenciado. Estos patrones no podrían ser explicados por varios factores de confusión potenciales, incluyendo efectos estacionales o una capacidad inferior de aprovisionamiento por parte de individuos de

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P. phoenicurus que alimentan con dietas inusuales. Esto sugiere que el material de plantas y vertebrados es digestible para los polluelos de *C. canorus* pero podría causar estrés ontogenético. Por primera vez mostramos que la composición de la dieta podría afectar el éxito del parásito no solo a nivel de la especie hospedera, como han documentado estudios previos, pero también intra-específicamente, i.e., a nivel de parejas hospederas individuales. La selección de la dieta del hospedero podría representar un rasgo general importante de la historia de vida que afecta la adecuación biológica de los parásitos de nidada, a pesar de que probablemente no haya evolucionado como una defensa antiparasitaria específica.

Palabras clave: adecuación biológica, *Cuculus canorus*, dieta, éxito de emplumamiento, *Phoenicurus phoenicurus*, selección del hospedero

INTRODUCTION

Provisioning of suitable food is crucial for proper nestling development and thus parental fitness (Ricklefs 1968). The composition of diets delivered to nestlings varies greatly, both within and among species (del Hoyo et al. 2016). This variation may be particularly important in cases when nestlings are not fed by their own parents but by members of another species, that is, in the context of interspecific brood parasitism (Davies 2015). Indeed, nestling diet is one of the main factors that seems to govern host selection by parasitic birds (Soler et al. 1999, but see Grim et al. 2011). Specifically, plant-dominated diets fed by potential hosts to nestlings are fatal to parasitic progeny of both Brown-headed Cowbirds (*Molothrus ater*; Middleton 1977) and Common Cuckoos (*Cuculus canorus*; hereafter, cuckoos; Glue and Morgan 1972).

Early studies assumed that hosts of the cuckoo feed parasitic nestlings with insects and other invertebrates (Baker 1942, Wyllie 1981). Wyllie (1981:73) asserted that "nestling parasitic cuckoos are fed, of course [sic], on whatever food each particular host species normally brings to its own young." However, this claim was not substantiated by any empirical evidence. Indeed, later studies showed that hosts sometimes fed different proportions of particular prey items to parasitic vs. their own nestlings (Brooke and Davies 1989, Grim and Honza 1997, 2001, Martín-Gálvez et al. 2005). This led Soler (2008) to suggest that hosts may specifically feed parasitic nestlings with less profitable prey as a special form of foreign nestling discrimination (Grim 2006a).

However, the poor taxonomic metareplication (sensu Johnson 2002) of dietary studies (i.e. low number of studied hosts) makes it difficult to assess the generality of such differences. Cuckoo nestling diet composition has been quantified, often with very small sample sizes, for just 4 hosts: Eurasian Reed-Warblers (*Acrocephalus scirpaceus*; Brooke and Davies 1989, Grim and Honza 1997, 2001, Grim 2006b), Great Reed-Warblers (*A. arundinaceus*; Mayer 1971, Trnka 1995), Rufous-tailed Scrub-Robins (*Cercotrichas galactotes*; Martín-Gálvez et al. 2005), and Great Tits (*Parus major*; Grim et al. 2014a). Yang et al. (2013) reported that Verditer Flycatchers (*Eumyias thalassinus*) effectively killed cuckoo hatchlings by feeding them only insects protected by thick exoskeletons (beetles and grasshoppers), but their study did not quantify diet composition. In comparison with nestling diet research, by a decade ago the number of cuckoo host species employed in egg discrimination experiments was 54 (Grim 2007a), and dozens of new hosts have been tested since then (e.g., Martín-Vivaldi et al. 2013, Yang et al. 2013).

Thus, cuckoo nestling diet—similarly to other aspects of cuckoo nestling biology (Grim 2007a)—remains poorly known. Additionally, only a few previous studies have reported quantitative data on cuckoo fledging ages and masses (reviewed by Grim 2006c, Grim and Samaš 2016). The rarity of both types of study may explain why no previous studies have examined how intraspecific variation in diet composition affects cuckoo fledging parameters and reproductive success across host nests. Consequently, the relationship between host diet composition, both within and among species, and parasitic nestling fitness represents a crucial missing link in our understanding of host selection by cuckoos and other parasitic birds (Ladin et al. 2015).

To ameliorate this knowledge gap, we studied cuckoo nestling diet composition and its effects on fledging parameters when raised by the Common Redstart (*Phoenicurus phoenicurus*; hereafter, redstart). Unlike all other cuckoo hosts, this species is the only known regular cavity-nester (Rutila et al. 2002, Samaš et al. 2016, Thomson et al. 2016, Grim and Rutila in press). Redstarts often breed in ground cavities (Glutz von Blotzheim et al. 2001, T. Grim, Z. Tyller, and P. Samaš personal observations) and, in contrast to other common cuckoo hosts (such as *Acrocephalus* species; Grim and Honza 1996), redstarts regularly collect food from the ground surface (Glutz von Blotzheim et al. 2001). This may increase the potential for revealing unusual items in nestling diets. Indeed, although cuckoo nestlings are considered purely insectivorous, we found that some host pairs (but not others) also fed them plants and vertebrates (see Results). This among-host-pair variation allowed us to examine for the first time whether diet composition affected cuckoo breeding success at the host's intraspecific level (i.e. across different host pairs). It may be expected that host and parasitic nestlings are not equally adapted to different food types (Rothstein 1976, Yang et al. 2013); thus, differences

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in performance (growth, fledging age, and fledging success) may also be expected.

Fruits represent an insufficient diet for many birds, and a purely plant-based diet always causes the death of cuckoo nestlings (Glue and Morgan 1972, Davies 2015; for a similar pattern in Brown-headed Cowbirds see Rothstein 1976, Middleton 1977). However, fruits may be acceptable to insectivorous birds as a complement to animal foods (Sedinger 1990). According to the nutritional deficiency hypothesis (Izhaki and Safriel 1989), fruits generally represent an inferior diet for any bird, as the assimilation efficiency (i.e. "the efficiency with which ingested food is converted to usable energy"; Castro et al. 1989:271) for fruits (41%) is only approximately half that for invertebrates (74%; table 4 in Castro et al. 1989). Lizards, like other animal food (see small vertebrates in Castro et al. 1989), show a high assimilation efficiency (78%), but this holds for carnivorous birds, namely falcons and owls; the assimilation efficiency for a vertebrate diet in otherwise insectivorous passerine nestlings is unknown (Castro et al. 1989). Regardless, switching between diets, e.g., plant and animal foods, is known to be costly in terms of compromised digestive efficiency (Levey and Karasov 1989). Further, lizards, like any large prey item, may be difficult for altricial nestlings to swallow (Turtumøygard and Slagsvold 2010), and such items have been shown to retard nestling growth (Slagsvold and Wiebe 2007). In general, both plant and animal diets of inferior quality cause subnormal fledging masses and delayed fledging (Johnston 1993). Based on all of these empirically known patterns, we predicted that cuckoos fed with fruits and/or vertebrates would show decreased fledging masses and increased fledging ages (indicative of ontogenetic stress; Grim et al. 2009a) and decreased fledging success.

METHODS

Study Area and General Procedures

We collected data on diet composition from parasitic cuckoo and host redstart nestlings using nest boxes in pine forests near Ruokolahti (61°24′N, 28°37′E) in southeastern Finland from May to July, 2012–2016 (see Grim et al. 2009a, 2009b, 2014a and Samaš et al. 2016 for details on logistics and field procedures). This study population shows a high parasitism rate (31%, $n = 392$ nests).

The quality of parents could differ between naturally parasitized and naturally unparasitized nests: Female cuckoos may target hosts of higher quality (Polačiková et al. 2009) or may disproportionally parasitize host individuals of lower quality due to structural habitat constraints (Grim 2002). In either case, such nonrandom host targeting might confound dietary comparisons if individual host quality covaries with individual host prey selection. Therefore, we randomly removed the cuckoo egg from some parasitized nests and cross-fostered it to another nest. Thus, we created 4 groups of nests: naturally parasitized nests that either remained parasitized ($n = 31$) or were experimentally unparasitized by us ($n = 15$), and naturally unparasitized nests that either remained unparasitized ($n = 55$) or were experimentally parasitized by us ($n = 51$, using 15 cuckoo eggs from 15 experimentally unparasitized nests and additional 36 cuckoo eggs from nests that were not followed in the present study). To test for nonrandom individual host selection by cuckoo females, we included the predictor of original "parasitism status" (i.e. before cross-fostering) in our statistical models. Because of the randomization and interspersion created via cross-fostering, it was not strictly necessary to control for host pair quality (Hurlbert 1984); however, we conservatively measured host pair quality as provisioning effort (feedings hr^{-1}) and tested its potential covariation with diet composition.

We regularly checked nests throughout the nestling period to video-record host provisioning. Before expected fledging, we measured nestling mass using a digital scale (model AMW-600; American Weigh Scales, Cumming, Georgia, USA) with precision to ±0.1 g. Fledging parameters could be determined for only a subset of video-recorded nests ($n = 120$ out of 152) because some nestlings and broods did not fledge due to predation ($n = 5$) or inclement weather ($n = 1$) or were not followed through to fledging due to logistic reasons ($n = 26$; i.e. too many synchronous nests in too-distant parts of our large study area, which covered 25 × 7 km; see figure 1 in Samaš et al. 2016). Sample sizes vary slightly (Results) because we failed to record complete data for some nests.

We used 3 methods specifically developed to prevent potential effects of video-recording and observer visitation on nest success. First, cameras were inconspicuously hidden in wooden nest box extensions (see figure 2b in Samaš et al. 2016). Second, we excluded most nest predators mechanically: At the start of the incubation period, we inserted 2 nails into the nest box entrance hole so that redstarts could enter but predators were excluded (see figure 2a in Samaš et al. 2016); this worked because predation rates were almost nil (4%, $n = 126$ nests). We removed the nails from the nest boxes with cuckoo nestlings shortly before expected fledging; there was no need to do this for the nest boxes with redstart fledglings because host nestlings were small enough to move freely between the nails. Video-recordings confirmed that cuckoo nestlings did not try to fledge before we removed the nails. Third, fledging time was primarily determined from long-term microcamera recordings, which started a day or 2 before the expected fledging date for a particular nest and thus eliminated the necessity of repeated nest checks by a human observer during the period shortly before nestlings

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SUPPLEMENTAL MATERIAL VIDEO S1. Common Redstart male feeding a parasitic Common Cuckoo nestling with a viviparous lizard. https://www.youtube.com/watch?v=FLjuMDgwGg8

fledge when human nest checks may trigger premature fledging (see also Grim 2007b).

We defined fledging success as the proportion of hatchlings that fledged. For redstart broods, each nest represented 1 data point (i.e. the proportion of hatchlings that fledged from each nest). In mixed broods, we scored cuckoo and redstart nestlings separately. Shortly before expected fledging, nest boxes with cuckoos were checked daily and those with redstarts every 1–3 days. For fledging success analyses, the a priori temporal criterion for successful redstart fledging was that nestlings survived to 11 days of age (following Järvinen 1990). For cuckoos, the criterion was 18 days (Grim 2006c), with the day of hatching = day 0 (Li et al. 2016). We managed to follow all cuckoos and all but 1 redstart brood through to fledging; thus, we applied the temporal criterion to only 1 nest. Nests that failed due to predation ($n = 5$) or inclement weather ($n = 1$) were excluded in fledging age, mass, and success analyses because we wanted to test only for potential effects of diet type.



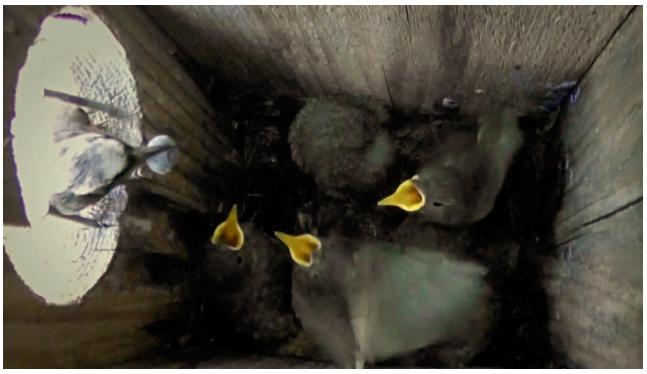
SUPPLEMENTAL MATERIAL VIDEO S2. Common Redstart male feeding his own nestling with a viviparous lizard. https://www.youtube.com/watch?v=eeBbii18itc



SUPPLEMENTAL MATERIAL VIDEO S3. Common Redstart female feeding a parasitic Common Cuckoo nestling with a lingonberry. https://www.youtube.com/watch?v=i0anKhxo5Ss

Video-recording

Using 2 types of cameras, we video-recorded nestling provisioning from hatching (day 0) to fledging. This whole period covered up to the age of 14 days in redstart nestlings and 20 days in cuckoo nestlings (Grim et al. 2009a, Grim and Samaš 2016). During each day of the nestling period, we video-recorded 15–39 nests with redstart nestlings and 13–37 nests with cuckoo nestlings. Due to this extensive sampling, we were able to identify unusually high (compared with typical dietary studies) numbers of prey items for both host (243–1,003 items per day) and parasitic nestlings (73–827 items per day). Nestlings older than the typical fledging age (i.e. >14 days for redstarts and >20 days for cuckoos) are naturally uncommon (due to fledging), but we managed to video-



SUPPLEMENTAL MATERIAL VIDEO S4. Common Redstart male feeding his own nestling with a whortleberry. https://www.youtube.com/watch?v=-bxKLRz3gS8

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record 1–11 nests for each day up to the age of 17 days in redstarts and 27 days in cuckoos.

Some nests (10%) were video-recorded during the whole day (24-hr period), but 90% of nests were recorded only between 0800 and 1900 hours (EEST). Each nest was video-recorded 1–18 times (median = 4), always on separate days, and each recording lasted 1.0–4.0 hr, depending on weather conditions, predation, and logistic constraints. In contrast to all previous studies of cuckoo diet, and most studies of avian nestling diet, our recordings covered the whole period from hatching to fledging.

We placed each camcorder at the top of the nest box, where it was attached to a wooden nest box extension (16 cm depth × 15 cm width × 20 cm height; see figure 2b in Samaš et al. 2016). The lens of the camera pointed down into the box, covering both the nest cup and the nest box entrance in its field of view (Grim et al. 2014a). Thus, the recordings allowed us to clearly identify which species of nestling (cuckoo or redstart) got fed in all broods, including mixed broods (i.e. nests in which host and parasitic nestlings shared the nest; Grim et al. 2009a). We used Panasonic HDC-HS80 camcorders (HD quality; Panasonic, Kadoma, Osaka, Japan), which allowed us finer taxonomic identification of prey items (Appendix Table 2, Supplemental Material Video S1, Video S2, Video S3, and Video S4). Additionally, we used lower-resolution recordings from infrared microcameras (CCD Bird Box Camera 420TVL; SpyCameraCCTV, Bristol, UK) located inside nest boxes; each microcamera was connected to a digital video-recorder (Wireless 2.4 GHz 1 Channel D1 Mini DVR Recorder; SpyCameraCCTV) hidden in an underground box below the nest. Microcameras were primarily used to determine the exact time of fledging of host and parasitic nestlings, as they allowed us to record the brood undisturbed for several days without the need to check the nest in person, which may cause premature fledging (Grim 2007b). However, we also took advantage of these microcamera recordings to determine dietary items, although necessarily at a lower level of taxonomic detail (invertebrate, vertebrate, and plant).

When categorized by the 4 types of nest parasitism status, we video-recorded the following numbers of nests: 31 naturally parasitized, 51 experimentally parasitized, 15 experimentally unparasitized, and 55 naturally unparasitized. We cross-fostered randomly selected cuckoo eggs, and some of the cuckoo nestlings did not successfully evict all host progeny. This was not a result of cross-fostering because mixed broods were similarly frequent among naturally (9 out of 31) and experimentally parasitized nests (9 out of 51; Pearson's $\chi^2 = 1.46$, $P = 0.23$), reflecting the natural situation in this cuckoo–host system (Rutila et al. 2002, Grim and Samaš 2016, Samaš et al. 2016, Thomson et al. 2016). This resulted in 64 "solitary" cuckoo broods (nests with 1 cuckoo that successfully evicted all host progeny; Grim et al. 2009a), 70 unparasitized host redstart broods, and 18 "mixed" broods that included 17 cuckoo–redstart broods (nests with 1 cuckoo that did not evict all host progeny and both species were raised jointly; see Grim et al. 2009a) and 1 brood of 2 cuckoo nestlings that both survived to fledging. This last case was a natural case of successful double parasitism; the cuckoos evicted all redstart progeny but neither cuckoo nestling managed to evict the other. Excluding this nest had a negligible effect on quantitative parameter estimates and no effect on our conclusions.

Analyses of Video-recordings

Identification of prey items to a fine level of taxonomical precision (i.e. to genus or species) almost always requires the examination of prey items under a microscope (e.g., Mayer 1971, Trnka 1995, Grim and Honza 1997). Thus, prey items must be removed from studied nestlings via neck-collars (e.g., Trnka 1995, Grim and Honza 1997, 2001). Such methods are invasive, may increase nestling mortality, and are no longer considered ethically acceptable. Therefore, we used less invasive and ethically sound video-recordings, whereby a researcher (Z. Tyller) visually inspected all food items that were visible on our video-recordings of feeding events (Martín-Gálvez et al. 2005, Grim et al. 2014a). This prevented us from detailed taxonomic identification of prey: the majority of feedings (79% out of 20,975, including 8,757 to solitary cuckoos, 1,934 to cuckoos in mixed broods, 1,963 to redstarts in mixed broods, and 8,321 to unparasitized redstarts) contained unidentifiable small insects; identification was not possible because redstart parents moved too fast, prey was too damaged, prey was hidden in the parent's bill, or prey was of typically small body size (see also Grim et al. 2014a). Note that even the determination of prey items collected with invasive neck collars, potentially the most precise method possible, was often unsuccessful, as seen from "indet." prey items in such dietary studies (e.g., Trnka 1995, Grim and Honza 1997). This does not necessarily represent a disadvantage for any dietary study, including the present one, because various types of insect show similar nutritional and energetic values (more similar to each other than to other diet types such as fruits; Castro et al. 1989).

The snout-vent length (SVL) of lizards was estimated by a professional herpetologist (M. Veselý) using the known length of host redstart bills as a reference. The mass of lizards was then estimated based on the known allometric relationship between SVL and mass (Meiri 2010).

In the analyses of fledging mass, age, and success, we present results partitioned into 4 categories of nestling diet. "Plant" included nests where whortleberries (*Vaccinium myrtillus*) and lingonberries (*Vaccinium vitis-idaea*) were detected in addition to typical invertebrate diet items. "Vertebrate" included nests where viviparous lizards (*Zootoca vivipara*) were detected in addition to typical

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TABLE 1. Prey abundance (n = number of food items), dominance (D, %), and frequency (F, %) of food items (see Appendix Table 2 for definition of these terms), and number of nests where each type of prey was fed by Common Redstarts to parasitic Common Cuckoo nestlings (n = 4,998 items from 10,691 feedings of 83 nestlings in 82 nests) and to their own nestlings (n = 4,413 items from 10,284 feedings of 86 broods in 86 nests; data from 1 out of 87 video-recorded broods were missing). Numbers of items are lower than numbers of feedings because dietary composition of many feedings could not be determined. Note that at some nests both plants and vertebrates were consumed, and therefore total sample sizes (nest, above) are smaller than the simple summary of number of nests in the table would suggest. Invertebrates were fed to nestlings in all nests. See Appendix Table 2 for a more detailed taxonomic determination of invertebrate diet items and Supplemental Material Video S1, Video S2, Video S3, and Video S4 for examples of feedings.

	Common Cuckoo				Common Redstart			
Prey type	*n*	*D* (%)	*F* (%)	Nests	*n*	*D* (%)	*F* (%)	Nests
Plants	74	1.48	0.69	9	79	1.79	0.77	4
Vertebrates	8	0.16	0.09	4	10	0.23	0.09	6
Invertebrates	4,916	98.36	99.27	82	4,324	97.98	99.15	86

invertebrate diet items. Nests where nestlings were fed both vertebrates and plants in addition to invertebrates were classified as "Both." We did not detect any other plant or vertebrate species in nestling diets. All of the other video-recorded nests were assigned to the category "Invertebrate." We managed to collect data on dietary items (Table 1) for 83 cuckoo nestlings (64 solitary plus 19 nestlings in 18 mixed broods) and 86 redstart broods (70 unparasitized plus 16 in mixed broods; i.e. we failed to record any dietary information for redstarts in 1 of the mixed broods).

Sampling: Effort and Limitations

Despite massive sampling effort, and similarly to any other dietary study, we cannot exclude the possibility that we did not detect vertebrate or plant dietary components at nests included in the "Invertebrate" category. However, such misclassification would only introduce noise into our analyses and decrease the power of our tests to detect statistically significant differences among groups. We also stress that our temporal coverage of nests from hatching to fledging is much longer than that of any typical avian dietary study. This is because it is not possible to apply neck collars to freshly hatched nestlings or to nestlings shortly before fledging (see any of the dietary studies that we have cited above), but cameras can be used to cover the complete nestling period (this study). Also, the majority of dietary studies have not sampled particular nests repeatedly (as we have done), including statistically controlling for such repeated sampling (see Statistical Analyses, below). Crucially, the focal prey types of interest in our study (i.e. fruits and lizards) were easier to identify than the more common food items (invertebrates) due to their uniquely large size (lizards) and color (fruits; Supplemental Material Video S1, Video S2, Video S3, and Video S4). Fruits were further unambiguously confirmed by the color of feces of nestlings from the same nests, even after fledging (T. Grim, Z. Tyller, and P. Samaš personal observations). Thus, any biases in the present study will be smaller than those in typical avian dietary studies.

Sampling in the present study can be considered sufficiently representative: Data were collected over 5 breeding seasons (compared to 1–3 seasons used in previous studies), and numbers of sampled nestlings and numbers of samples (~20,000 feedings) are much larger than those in previous studies (typically several dozens of feedings). On the other hand, the total number of successfully identified prey items is smaller. This follows from host feeding strategies and logistic constraints. First, unlike some passerines that bring a single large food item per feeding (e.g., tits; Naef-Daenzer and Keller 1999, Barba et al. 2009), redstarts typically bring multiple small items per feeding (similarly to, e.g., reed-warblers; Grim and Honza 1996, Davies 2015). Second, these multiple food items are largely hidden inside the bill cavity, preventing their identification without invasive methods such as neck collars (Grim and Honza 1996).

Finally, our samples were not well balanced between typical purely invertebrate-fed nestlings and broods and those fed additionally with plants or vertebrates, both for cuckoos (69 vs. 11 nestlings) and for redstarts (78 vs. 9 broods). Note that the unbalanced samples resulted from biological reality, that is, low numerical dominance of alternative food types, and not from poor sampling effort (which was massive by any standards).

As in all previous studies (Introduction), several items (e.g., a caterpillar, a spider, and an unidentified insect) could be identified in a single feeding. We simply analyzed all items from all feedings and present the data pooled per whole study population (Table 1, Appendix Table 2). This approach parallels all previous studies and makes our results comparable with previous work.

Statistical Analyses

First, we tested whether diet composition was specific to host pairs. Using repeated samples per pair (1 sample = a

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single 1-hr video-recording per nest per day, i.e. there was no more than 1 sample from the same nest and day), we calculated the repeatability of diet composition per host (parent) pair. Nests that provided only a single sample, e.g., due to early predation, were naturally excluded from repeatability analyses. Because unusual food items were not provided during the first week of nestling development (Results), we estimated repeatability only for the later part of the nestling period, when both usual and unusual diet items were provided. However, including data from the first week of nestling development led to virtually the same parameter estimates (results not shown). We scored the data as a binary variable: unusual food items (i.e. fruits and lizards pooled) present vs. absent. Further, we calculated repeatability separately for "fruits" and "lizards." Repeatability estimates and their 95% CIs were calculated using a generalized linear mixed model with a binary response (logit link), using the formula $r = \mathrm{VB} / (\mathrm{VB} + \mathrm{VE} + \pi^2/3)$, where VB denotes between-individual variance, VE is the residual variance (always fixed to 0 for binary response variables), and $\pi^2/3$ is the inherent distribution-specific variance (for details see Nakagawa and Schielzeth 2010, Samaš et al. 2011, Grim et al. 2014b).

Next, we calculated 8 linear mixed models separately for each combination of nestling species (redstart, cuckoo) and fledging (mass, age, success) or provisioning parameter (parental provisioning effort). We used generalized linear mixed models with identity links when analyzing the continuous response variables of nestling fledging mass (g), fledging age (days), and provisioning effort (feedings hr^{-1}). We employed a generalized linear mixed model with a logit link when analyzing the binomial response variable of fledging success (fledged vs. died in the nest).

All models contained "diet type" (categorical variable, with the categories "Invertebrate," "Vertebrate," "Plant," and "Both") as a fixed predictor. In the fledging success analysis, the predictor "diet type" had just 2 categories ("Invertebrate" and "Noninvertebrate"). We pooled the "Vertebrate," "Plant," and "Both" categories into a single "Noninvertebrate" category for this particular analysis because all nestlings fed with lizards successfully fledged (thus, there was no variation in the data and the model failed to converge). We summarized the fit of models using marginal (R^2_m) and conditional (R^2_c) R-squared accompanied by Akaike's Information Criterion corrected for small sample sizes (AIC_c), as recommended by Nakagawa and Schielzeth (2013) and Lefcheck (2015).

In analyses with a fledging parameter as the response variable (fledging mass, age, success), we controlled for temporal between-year variation by including the variable "year" (5 levels, 2012–2016) as a random effect because we did not have any specific year-based predictions (Bolker 2015). Each redstart nest had several nestlings and thus we additionally controlled for within-nest variability by including the random effect redstart "brood ID." This was applied only to models with the response variables "fledging mass" and "fledging age" because for "fledging success" all predictors and the response were quantified at the brood level (fledging success was defined as the proportion of hatchlings that fledged per whole brood). In analyses with provisioning effort as the response variable, we controlled for variation in both nestling age and brood ID by employing a random slope model (i.e. nestling age was statistically nested within brood ID, following the guidelines of Bolker 2015). This model took into account the fact that provisioning rate in relation to nestling age differed across broods. Further, nestling growth performance and fledging success may vary because of cohabitation (Grim et al. 2009a) and individual host quality (Polačiková et al. 2009). Therefore, we additionally tested for the potential confounding effects of "brood type" (categorical variable: mixed or not) and "parasitism status" (categorical variable: nest originally parasitized by a cuckoo female or not).

The timing of breeding within a season in relation to the occurrence of an unusual diet was controlled for by the binary variable "fruit availability" (yes or no) in each particular season. The onset of ripe berries typically comes in the middle of the redstart breeding season, so each year we had active nests when fruits were both unavailable and available. The year-specific date of whortleberry ripening was obtained from Metla (http://www.metla.fi/cgi-bin/feno/kuvasarja/mu/10.5/30.8/3/en). The occurrence of young lizards has not been monitored in southeastern Finland, and thus we did not have any specific predictor for the availability of vertebrates; however, anecdotal data suggest that lizards, including young ones, are available throughout the whole redstart breeding season (J. Rutila personal communication).

If fruit was available only later in the season, and if late nests produced fledglings of lower mass overall, then there would be a potential problem: the effect of "fruit availability" on fledging parameters would be confounded with seasonal effects. An alternative way to control for the potential effects of fruit availability would be to include only nests that had nestlings in the period when fruits were available. However, such data trimming would have caused us multiple problems. First, we would have had to exclude ~70% of our data points, leading to poor statistical power of our tests. Second, excluding data from the early part of the season, when fruits were not available, would have automatically excluded some of our (already limited) sample of nests where lizards were fed to nestlings (lizards were available the whole season, independently of fruits), leading to even poorer statistical power. These limitations, of course, do not solve the potential issue of "fruit availability" being confounded with seasonal effects. Therefore, we ran separate alternative analyses in which

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we directly tested whether seasonal effects could explain the fledging patterns. We removed the predictor "fruit availability" and instead included a new predictor, "hatching date" (the rest of the models remained identical to models reported in Appendix Tables 3 and 4). Hatching date was centered on the mean within each year to exclude any confounding effects of between-year variation (following Grim et al. 2011). We ran these models for fledging mass, age, and success. Hatching date was not statistically significant in either full or final models, the statistical significance of the other predictors did not change qualitatively (i.e. no nonsignificant predictors became significant, and vice versa), and parameter estimates remained similar to those in our original analyses (i.e. analyses with "fruit availability"). Although the conclusions remained the same when we used "fruit availability" and "hatching date," we preferred using the former predictor because it directly reflected biological reality (i.e. the availability of the alternative plant diet item in each specific season), whereas the latter predictor merely assumed in an unspecific way that conditions were poorer at the end of the season. However, this assumption was not supported by our data: "weather" (see below) was not correlated with "hatching date" for cuckoos ($r = 0.02$, $P = 0.88$, $n = 74$) or redstarts ($r = -0.19$, $P = 0.11$, $n = 72$).

Weather, including precipitation and temperature, may affect food supply and nestling growth (Pérez et al. 2016). Weather data were acquired from the Finnish Meteorological Institute (https://en.ilmatieteenlaitos.fi/open-data). We tested potential weather effects with 2 predictors, total daily rainfall (a continuous variable measured in mm per day) and average daily temperature (a continuous variable measured in °C). In the analyses of fledging parameters, we averaged rainfall and temperature for the whole nestling period for each particular brood (i.e. from the date of hatching till the date of fledging). We detected high collinearity between the predictors of rainfall and temperature (variance inflation factor: VIF $>$ 7; Zuur et al. 2010); the variables were strongly negatively correlated (Pearson's $r = -0.87$, $P < 0.001$). Thus, we used principal component analysis (PCA) to create a new single variable, "weather," representing both predictors. The first principal component, PC1, explained 94% of the total variance and was positively correlated with rainfall (Pearson's $r = 0.65$, $P < 0.001$) and negatively correlated with temperature (Pearson's $r = -0.51$, $P < 0.001$). In the analyses of provisioning effort, we controlled for weather on the particular day of video-recording of provisioning behavior. There was no collinearity between the 2 predictors in this case (i.e. rainfall and temperature at the day level); therefore, we used both as separate predictors in the provisioning effort analyses.

In the analysis of fledging mass, we included an additional predictor of nestling age (continuous variable, measured in days) when fledging mass was measured ("age weighed"; this was always after nestlings reached the asymptotic phase and shortly before they fledged). For analyses of redstart data, we additionally included another potential predictor, "brood size" (as a continuous variable). Brood size was not included in parasitic nestling models because brood size did not vary for solitary cuckoos (brood size always = 1), whereas it was always larger than 1 for mixed broods; therefore, there would be multicollinearity between "brood size" and "brood type." In the analyses of provisioning effort we included the additional predictors "daytime" (continuous; in hours) and its quadratic term "daytime^2" (because provisioning effort can be expected to be nonlinearly related to the hour of the day, with increased feeding in the morning and evening) and the "date" of video-recording (because food availability may theoretically decline late in the season leading to lowered provisioning effort).

We present results from both the full (as recommended by Forstmeier and Schielzeth 2011) and final reduced models (as recommended by Grafen and Hails 2002). We used backward elimination of nonsignificant terms. We kept the main predictor of interest, i.e. "diet type," in the models until the final step, regardless of its significance (following Grafen and Hails 2002). Additionally, in another series of analyses, we added each previously removed covariate (separately, one by one) and confirmed that it was nonsignificant in all the final models. In models with identity links, we checked the assumptions of normality of residual errors, linearity of effect, and homogeneity of variances by visual inspection (Ieno and Zuur 2015), and found them satisfactory.

We were specifically interested in differences between the potential effects of the following diet combinations: invertebrate vs. vertebrate, invertebrate vs. plant, and invertebrate vs. both. We did not have any specific predictions about differences between plant vs. vertebrate diet effects: both effects should be detrimental, but we did not find any information in the published literature to allow us to predict the absolute or relative magnitude of the 2 effects. Thus, there were no grounds to predict whether the effect of fruits would be larger or smaller than that of vertebrates. Therefore, we used post hoc Dunnett's tests with invertebrate diet (typical for both redstart and cuckoo nestlings; Glutz von Blotzheim et al. 2001) set as a reference level. The results of the post hoc tests remained the same when applied to both full and final models (Appendix Tables 3–5). For simplicity, we present results based on final models (Figure 1). All analyses were performed in R 3.3.2 (R Core Team 2016). All estimates are means ± SE.

RESULTS

Redstarts fed both their own and cuckoo nestlings with mostly insects and spiders (overall $n = 20{,}975$ feedings;

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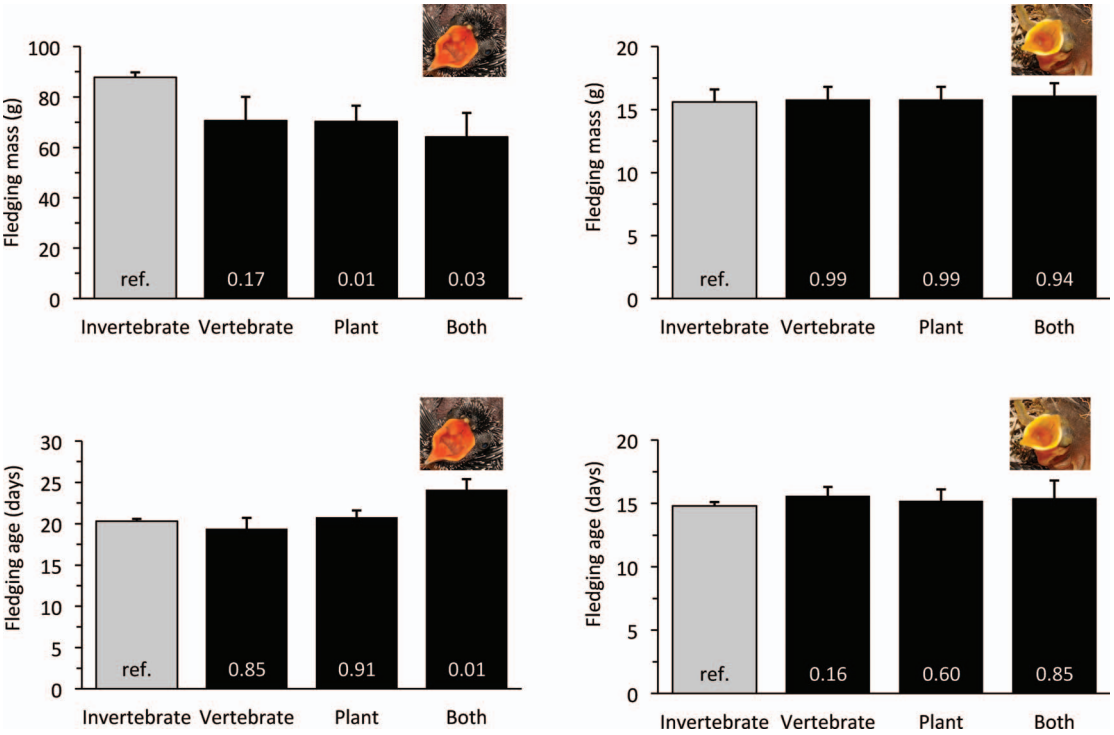


FIGURE 1. (**A**) Fledging mass and (**B**) age of Common Cuckoo nestlings provisioned by Common Redstart hosts with either a typical diet of insects (Invertebrate, $n = 62$ nestlings), or a diet containing additionally either young lizards (Vertebrate, $n = 2$), fruits (Plant, $n = 7$), or both lizards and fruits (Both, $n = 2$). (**C**) Fledging mass and (**D**) age of Common Redstart broods (brood averages, i.e. without pseudoreplication) provisioned by their parents with either a typical diet of insects (Invertebrate, $n = 60$ broods) or a diet that also (i.e. additionally to invertebrates) contained either young lizards (Vertebrate, $n = 5$), fruits (Plant, $n = 3$), or both lizards and fruits (Both, $n = 1$). Total sample sizes are smaller than those for diet composition (Table 1) due to predation, weather effects, and logistic reasons. Numbers within bars are *P*-values from post hoc Dunnett's tests comparing Invertebrate (reference category, gray bars) with either Vertebrate, Plant, or Both (black bars). Values are least square means + SE from final models controlling for other significant predictors where appropriate (see Appendix Table 3).

Table 1) that, in most cases, could not be identified more precisely (for explanation, see Methods). However, identifiable items (Table 1, Appendix Table 2) were often unique: juvenile viviparous lizards (Supplemental Material Video S1 and Video S2) and fruits (*Vaccinium* spp.; Supplemental Material Video S3 and Video S4). The snout-vent length of lizards ($n = 18$) was 2–4 cm (2.6 ± 1.3 cm), with corresponding estimated mass of 0.5–3.0 g (1.16 ± 0.20 g). Neither the snout-vent length (Welch's $t_{13,3} = 0.05$, $P = 0.96$) nor the mass of lizards (Welch's $t_{15,0} = 0.11$, $P = 0.91$) differed between lizards fed to cuckoo vs. redstart nestlings. Redstarts consumed viviparous lizards when broods were 5–14 days old (10.0 ± 0.9 days, $n = 6$ broods), and cuckoos ate lizards when nestlings were 6–19 days old (11.9 ± 1.4 days, $n = 4$). Redstarts received fruits when broods were 9–15 days old (12.0 ± 0.6 days, $n = 4$ broods) and cuckoos when nestlings were 8–20 days old (16.1 ± 1.0 days, $n = 9$). The occurrence of unusual food items did not covary with original parasitism status (whether the nest was naturally parasitized or not; Pearson's $\chi^2 = 0.76$, $P = 0.38$).

Overall, redstarts and cuckoos received similarly low numbers of both plants (i.e. fruits) and vertebrates (i.e. lizards; Table 1). Females were more often recorded feeding nestlings with both fruits (females: $n = 93$ fruits, males: $n = 60$ fruits), and lizards (females: $n = 12$ lizards, males: $n = 6$ lizards).

Diet composition repeatability (invertebrate vs. unusual diet) was high for redstarts provisioning both cuckoo nestlings ($r = 0.69$, 95% CI = 0.52–0.81) and redstart broods ($r = 0.60$, 95% CI = 0.31–0.79). There was very high repeatability for feeding a fruit diet (cuckoo: $r = 0.80$, 95% CI = 0.67–0.88; redstart: $r = 0.92$, 95% CI = 0.84–0.97) and moderate repeatability for feeding a vertebrate diet (cuckoo: $r = 0.45$, 95% CI = 0.21–0.64; redstart: $r = 0.32$, 95% CI = –0.04 to 0.61).

Cuckoo fledging mass varied by diet type (Figure 1A, Appendix Table 3). Nestlings fed an unusual diet, either fruits or a combination of fruits and lizards, fledged at much lower masses than nestlings in whose diet we did not detect unusual prey types; the change was most pronounced when nestlings were fed both fruits and lizards

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(see Figure 1A for effect sizes based on final models). Cuckoo fledging age did not differ significantly with diet type, except when both fruits and lizards were fed (Figure 1B, Appendix Table 3). In contrast, diet type did not covary with the fledging mass (Figure 1C, Appendix Table 3) or the fledging age of redstarts (Figure 1D, Appendix Table 3).

Overall, fledging success was very high: 57 out of 62 invertebrate-fed cuckoos successfully fledged (average fledging success = 0.92), and 9 out of the 11 plant-fed and vertebrate-fed cuckoos fledged (average fledging success = 0.82). The 2 cuckoos that did not survive to fledging were from plant-fed mixed broods; these 2 were the only mixed broods for which an unusual diet was detected. Fledging success did not differ between cuckoo nestlings fed an unusual diet (plant and vertebrate diets pooled because of low sample sizes) or a typical diet of invertebrates (chi-square test: $\chi^2 = 0.24$, $P = 0.62$, $n = 73$; see also Appendix Table 4). There was partial prefledging nestling mortality in both invertebrate-fed ($n = 63$ broods [with 360 nestlings], average fledging success = 0.86) and plant- and vertebrate-fed redstart broods ($n = 9$ broods [with 46 nestlings], average fledging success = 0.80; chi-square test with Yate's correction: $\chi^2 = 0.56$, $P = 0.45$; see also Appendix Table 4).

Cuckoo fledging success was not statistically different between nestlings in mixed broods (0.82, $n = 17$) and solitary nestlings (0.93, $n = 56$; chi-square test with Yate's correction: $\chi^2 = 0.67$, $P = 0.41$; see also Appendix Table 4). Redstart fledging success was significantly lower in mixed broods (0.48, $n = 15$ broods [with 69 nestlings]) compared with unparasitized broods (0.93, $n = 57$ broods [with 337 nestlings]; chi-square test: $\chi^2 = 88.8$, $P < 0.0001$; see also Appendix Table 4). The fates of cuckoo nestlings and redstart nestlings were independent within the same nests ($r_s = 0.02$, $P = 0.99$; tested following recommendations of Nakagawa and Schielzeth 2010).

Provisioning capacity measured by feeding frequency did not vary across host pairs that fed cuckoo nestlings with different diet types (i.e. Invertebrate, Plant, Vertebrate, Both; Appendix Table 5).

DISCUSSION

Contrary to traditional views, cuckoos raised by redstarts were able to consume, digest, grow, and successfully fledge on a diet containing fruits and small lizards. A thorough literature review (T. Grim and P. Procházka personal observations) showed that no lizards or any other reptiles have ever been previously reported in the cuckoo nestling diet, and fruits have been reported in only one prior study (Martín-Gálvez et al. 2005). The presence of these unusual dietary components generally showed very high repeatability across redstart pairs; that is, parents (individual host pairs) behaved consistently with regard to the composition of the diets that they fed to nestlings. We did not find any other study that quantified such diet composition repeatability; thus, the present study seems to be the first to test for and find such patterns. Importantly, this unusual diet had consequences for cuckoo nestling quality: Nestlings whose diet contained plants, vertebrates, or a combination of plants and vertebrates had 20%, 20%, and 27% lower fledging masses, respectively, than nestlings that were fed only invertebrates (Figure 1A). These differences were statistically significant, except for cuckoo nestlings fed vertebrates. Cuckoo nestlings whose diet contained both fruits and vertebrates also fledged later (~4 days) than other nestlings (Figure 1B). Parasitism rates did not differ between nests where redstarts provisioned nestlings with unusual diet items vs. only invertebrates. This suggests that cuckoos do not target host pairs that bring more suitable food (invertebrates) or do not avoid host pairs that bring less suitable diet items (fruits, vertebrates; cf. Grim 2002, Polačiková et al. 2009).

The effects of a few unusual dietary items or their combinations might seem hard to reconcile with the low numbers of these items that we detected (Table 1). However, the numbers inevitably reflect the length of our video-recordings: we, just like any other study, did not record nests continuously, but rather used sampling (on average, ~10 hr of recordings per nest per whole nestling period; see Methods). Given that cuckoos were fed with unusual items from the age of ~1 week onward (Results), they were exposed to these foods for up to ~2 weeks (because fledging age is typically ~3 weeks; Grim and Samaš 2016). Redstarts provisioned both their own nestlings and cuckoos throughout most of the day (due to its latitude, our study site experiences virtually continuous light during the summer breeding season). Thus, the raw numbers (Table 1) should not be considered in isolation; instead, the raw numbers should only be included in estimates of proportions of unusual dietary items. Most importantly, the mass of the unusual food items—instead of numerical dominance—should also be taken into consideration (see the section "Unusual Prey Items"). The mere raw numbers presented in Table 1 underestimate the real total (i.e. cumulative per whole nestling period) consumption and, by implication, the effects of unusual diets by 1 or even 2 orders of magnitude.

Alternative Explanations

Theoretically, poorer fledging parameters of cuckoos fed with unusual dietary items could be a by-product of individual host pair selection by cuckoos, that is pair quality (Grim 2002, Polačiková et al. 2009). We excluded this potential confounding factor experimentally by cross-fostering randomly selected cuckoo eggs between naturally parasitized and unparasitized nests (see Methods). We also explicitly statistically tested this potential confounding

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effect (Appendix Tables 3–5). None of the various fitness-related parameters covaried with host parasitism status for cuckoo nestlings. To our knowledge, cross-fostering was done in only one previous dietary study (Martín-Gálvez et al. 2005), which highlights that the results of the present study should be robust.

However, randomization via cross-fostering does not automatically ensure interspersion of treatments (Hurlbert 1984). Despite our efforts, we could still have inadvertently assigned cuckoos to host pairs that showed overall poorer provisioning capacity, because of which they may have fed nestlings with unusual diet items, although we find it extremely improbable that such a coincidence would have arisen in 5 separate breeding seasons. In this scenario, hosts of lower quality would have collected suboptimal prey to feed to nestlings. Clearly, this scenario is unlikely because the redstart nestlings fed with fruits and lizards did not show poorer fledging parameters (Figure 1). Indeed, we did not detect any differences in provisioning capacity (i.e. feeding frequency) between hosts feeding cuckoos with the different types of diet (Appendix Table 5).

Importantly, host vs. parasite fledging success was not correlated within mixed broods. These analyses clearly reject the alternative "poor parent" scenario and further support our prediction (Introduction) and results that the presence of fruits and lizards in the diet is causally responsible for the poorer fledging parameters of cuckoo nestlings.

Finally, poor foraging conditions could also have caused the observed patterns. Poor conditions could manifest themselves either spatially (at particular nests located in poor habitats) or temporally (in particular years or particular parts of the breeding season with inclement weather).

A spatial confounding effect is highly unlikely for 3 reasons. First, our study sites were highly homogeneous because they were all located in industrial forests of similar age (Samaš et al. 2016). Consequently, the structure of the vegetation layers, and prey availability, was highly uniform. Second, we randomly cross-fostered cuckoo eggs among available synchronous redstart nests, eliminating any potential confounding effect of spatially specific poor conditions: Nests with host vs. parasite nestlings were interspersed in space (sensu Hurlbert 1984). Third, no matter how "poor conditions" may have been manifested, we established quantitatively and statistically that nestlings who were fed with unusual food items were fed at similar frequencies as nestlings fed with "standard" invertebrates.

A temporal confounding effect is also highly unlikely, for 2 reasons. First, parasitized and unparasitized nests were interspersed in time (sensu Hurlbert 1984) across each of the 5 breeding seasons that we sampled; thus, nests with both cuckoo and redstart nestlings were synchronous and therefore experienced similar weather conditions. This is inevitable in mixed broods in which both parasitic and host nestlings experience identical conditions. Second, we explicitly quantified and statistically tested for potential confounding weather effects (rain, temperature); as expected due to the previous point (synchrony), the patterns of nestling growth and success that we detected were not explained by weather (cf. Pérez et al. 2016). Analyses based on the alternative predictor of "hatching date" did not change our conclusions. There was no decline in provisioning rates late in the season for redstarts and there was an increase for cuckoos (Appendix Table 5), and cuckoos survived better (not worse) overall when fruits were generally available (Appendix Table 4). These patterns are mostly the opposite of what would be expected under the assumption of confounding seasonal effects, and therefore provide strong support for our conclusions (causal effect of unusual dietary items).

Thus, although prey availability may vary in space and both within and between breeding seasons, such confounding effects were excluded in the present study via experimental design and statistical control (see full models including all these covariates; Appendix Tables 3–5). Previous studies of cuckoo diet rarely adopted an experimental approach (Martín-Gálvez et al. 2005) and never tested for potential confounding effects (e.g., Trnka 1995, Grim and Honza 1997, 2001). We believe that future studies would benefit from employing these improvements because they allow the detection of correlates and causes of parasite and host nestling fitness.

In summary, we attempted to control for many potential confounding factors (Appendix Tables 3 and 4). Based on these analyses, we suggest that the decreased mass and delayed fledging of cuckoo nestlings fed with some unusual diet items were not by-products of the timing of nesting within the breeding season, between-year variation, parasitism status (with cuckoo females targeting hosts that did not produce nestlings with better fledging parameters), or other confounding factors whose potential effects we statistically excluded (final models) or controlled for (full models). Fledging mass patterns were not confounded by the nestling age at which the fledging mass was measured; this is not surprising because we measured all nestlings shortly before fledging and always after they reached the growth asymptote.

Potential Fitness Consequences

Lower mass at fledging and delayed fledging suggest a dietary cost of some noninvertebrate diets (Figure 1), which may affect postfledging survival and recruitment and thus a brood parasite's fitness (Ladin et al. 2015). For example, Naef-Daenzer et al. (2001) found that Great Tit fledglings that died soon (<20 days) after fledging had ~5% lower fledging mass than fledglings that survived. In our study, cuckoo nestlings that were fed plants, verte-

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brates, or both had lower fledging masses (by 20%, 20%, and 27%, respectively) than purely invertebrate-fed cuckoos. Fledging age was prolonged by 19% in cuckoos fed both fruits and vertebrates, but did not differ between the other diet categories.

These substantial values strongly suggest that the unusual fruit and lizard diet (the latter only in combination with the former) may indeed translate into decreased parasite fitness during the postfledging period. This view is further supported by quantitatively similar fledging mass decreases between plant- and vertebrate-fed solitary cuckoos and those sharing the nest with host redstart nestlings in a previous study in the same study site (Grim et al. 2009a): Cuckoos in mixed broods had 26% lower mass than solitary cuckoos (i.e. cuckoos raised alone) and their fledging age was prolonged by 15%. Cuckoos in mixed broods suffered drastic prefledging mortality, with fledging success decreased to 44% of that of solitary cuckoos (Grim et al. 2009a; see also Grim and Samaš 2016). In contrast, in the present study, both plant- and vertebrate-fed cuckoos all fledged (predation and weather effects excluded). However, poor body condition at fledging of cuckoos with unusual diets suggests that mortality may have taken its toll shortly after fledging. Indeed, preliminary data on postfledging dispersal and survival show that cuckoo nestlings from mixed broods always die within several days after fledging (Grim and Rutila in press).

Host nestlings fed lizards or fruits did not show statistically significantly lower fledging success, mass, or delayed fledging. This was despite the fact that redstart nestlings consumed such items at relative ages similar to those of cuckoos, namely in the last two thirds of the nestling period. This finding is roughly parallel to that of Yang et al. (2013), who reported that Verditer Flycatcher nestlings were able to digest insects with hard exoskeletons, whereas cuckoo nestlings fed with the same prey items grew poorly and even died long before potential fledging. The same applies to plant-provisioning hosts of Brown-headed Cowbirds (Rothstein 1976).

There was partial prefledging mortality in redstart host broods fed with invertebrates and plants, but not vertebrates. However, these differences were not statistically significant. The potential causes of this mortality in our redstart population include inclement weather conditions (e.g., O'Connor and Morgan 1982), partial predation (e.g., Thompson et al. 1999), hatching asynchrony (e.g., Slagsvold and Wiebe 2007), and a beak deformity that was observed in one of the dead nestlings.

Unusual Prey Items

Fruits have previously been reported in the redstart nestling diet (Glutz von Blotzheim et al. 2001) but only once in the diet fed by other hosts to cuckoos (Martín-Gálvez et al. 2005). Thus, one could expect the effect of unusual plant items to be larger for cuckoos than for host nestlings, that is, a large effect of novel prey to which they are not adapted on parasitic nestlings vs. little effect of the same prey on host nestlings who are at least partly adapted. Indeed, as predicted, cuckoo nestlings fed plants showed lower fledging masses (but not delayed fledging), but there was no such effect for host nestlings.

Lizards were by far the largest prey brought to nestlings by hosts, with an estimated body mass of several grams. In contrast, typical insects brought by hosts to cuckoos were several orders of magnitude smaller, with body masses at the scale of dozens of milligrams (Grim and Honza 1997). For example, the body mass of a single lizard (0.5–3.0 g) is equal to 13 to 75 caterpillars (1 fully grown caterpillar weighs 40 mg; Naef-Daenzer and Keller 1999). This comparison refers to caterpillars that are at their maximum size; redstarts, of course, also fed smaller, not fully grown caterpillars to nestlings. Thus, comparing simple number dominance of prey items (Table 1) massively underestimates the contribution of lizards to the diet. This is even more pronounced because caterpillars were by far the largest insect items that redstarts brought to their own or parasitic nestlings. Therefore, the mass and, by implication, the energy content of lizards are ~2–3 orders of magnitude larger than their numerical dominance (Table 1) would suggest. In light of these differences, it can be reasonably expected that feeding lizards to cuckoo nestlings will affect them.

However, lizards might be too rare as food items to cause detrimental effects by themselves (Table 1). Indeed, the significant combined effects of plants and vertebrates in the diet, coupled with the nonsignificant effects of lizards alone, in the analyses of both fledging mass (Figure 1A) and fledging age (Figure 1B) suggest that lizards only exacerbate the negative effects of plants (which also show statistically significant negative covariation with cuckoo fledging mass when fed without lizards). Still, we note that the effect of lizards on fledging mass (but not on fledging age) is in the predicted direction and the lack of statistical significance may stem from the low number of nestlings that were fed only lizards (i.e. not also plants) in conjunction with invertebrates. In general, large prey items, such as lizards that are several centimeters long, may be problematic for small altricial nestlings to swallow (Turtumøygard and Slagsvold 2010) and may impair growth (Slagsvold and Wiebe 2007). Yet, observations of feeding events involving lizards did not suggest that either host (Supplemental Material Video S2) or parasitic nestlings (Supplemental Material Video S1) had any problem swallowing these food items. Therefore, we hypothesize that the decreased growth and delayed fledging of parasitic nestlings fed lizards in combination with plants might have been caused by variation in

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digestive efficiency between host and parasitic nestlings. Digestive efficiency has not been studied in the cuckoo and represents a potentially fruitful avenue for future research (see also Soler et al. 2014).

A literature review suggests that the range of the cuckoo nestling diet may be much broader than previously thought (T. Grim and P. Procházka personal observations). For example, anecdotal records report relatively large vertebrates in the diets of host Great Reed-Warblers, namely fish (common carp [*Cyprinus carpio*]; Mayer 1971, Mikulica et al. 2017) and amphibians (the European tree frog [*Hyla arborea*]; Trnka 1995, Mikulica et al. 2017). Our work further widens the range of these unconventional vertebrate dietary components.

Soler (2008) suggested that feeding parasitic nestlings with unusual prey items represents a subtle form of nestling discrimination. However, in this study, the numbers of unusual prey items fed to cuckoo and redstart nestlings were similar. Generally, we doubt that hosts are able evolve specific cuckoo nestling feeding habits as a form of nestling discrimination. First, nestling discrimination is typically represented by dramatically different host behavior toward alien offspring, in the form of starvation, desertion, pecking, or outright nestling removal (reviewed by Grim 2006a, 2011). Second, changing diet composition would provide a very inefficient antinestling defense (Yang et al. 2013). This is because shifting dietary habits would not ameliorate the majority of parasitism-related costs. First, eviction of the host's own progeny by the cuckoo hatchling typically occurs before the death of the cuckoo nestling due to an unsuitable diet (Grim et al. 2009b, 2011). Second, shifting dietary habits would be costly to hosts because it would affect most of the host's biology unrelated to parasitism (Yang et al. 2013). This would be especially so in the case of lizards, which show low availability simply because their body size is much larger than that of insect or spider prey. Lizards also surely require more effort to catch, handle, and transfer than typical invertebrate food items ("loading effect" sensu Carlson and Moreno 1982). Instead, we suggest that host diet selection may represent a general life history trait (sensu Grim et al. 2011) that either facilitates (Brooke and Davies 1989) or prevents (Yang et al. 2013) coevolution between parasites and (potential) hosts, even though it most likely did not evolve as a specific antiparasite defense.

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Author contributions: All authors contributed to study design, data collection, analyses, and writing.

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APPENDIX TABLE 2. Detailed taxonomic composition of the invertebrate diet delivered by Common Redstarts to parasitic Common Cuckoo nestlings and their own nestlings. With each feeding, Common Redstarts brought multiple small prey items that were often fully hidden inside the bill (this did not apply to lizards and fruits; see Table 1 and Supplemental Material Video S1, Video S2, Video S3, and Video S4); therefore, it was not possible to reliably determine the taxonomic identity of some of the small invertebrates. Sample sizes are smaller than the total number of feedings (20,975) for the same reason: In many cases, we could not reliably determine the diet composition even at the highest taxonomic level, e.g., spider, insect, or isopod. Therefore, such feedings were excluded here. n = number of food items or nests where each diet taxon was detected. D is dominance = (number of items of respective taxon / total number of items) × 100. F is frequency; for food items, F = (number of feedings in which items of respective taxon appeared / total number of feedings) × 100, and for nests, F = (number of sampled nests in which items of respective taxon appeared / total number of sampled nests) × 100.

	Food items			Nests	
Prey type	*n*	*D* (%)	*F* (%)	*n*	*F* (%)
Common Cuckoo					
Araneida	767	16	8.22	58	71
Hymenoptera	719	15	8.11	44	54
Lepidoptera	430	9	4.42	44	54
Diptera	208	4	2.32	34	41
Orthoptera	162	3	1.82	29	35
Coleoptera	83	2	0.90	25	30
Blattodea	23	<1	0.26	8	10
Odonata	16	<1	0.17	9	11
Heteroptera	15	<1	0.17	5	6
Neuroptera	13	<1	0.15	7	9
Chilopoda	12	<1	0.13	11	13
Diplopoda	12	<1	0.14	6	7
Hemiptera	2	<1	0.01	2	2
Isopoda	1	<1	0.01	1	1
Earthworms	—	—	—	—	—
Trichoptera	—	—	—	—	—
Dermaptera	—	—	—	—	—
Insecta indeterminate	2,453	50	79.25	79	96
Total	4,916	100		82	
Common Redstart					
Araneida	779	18	9.33	61	70
Hymenoptera	486	11	5.47	43	49
Lepidoptera	191	4	3.88	44	51
Diptera	150	3	1.80	34	39
Orthoptera	73	2	0.95	20	23
Coleoptera	55	1	0.77	29	33
Blattodea	12	<1	0.14	9	10
Odonata	7	<1	0.08	6	7
Heteroptera	14	<1	0.17	2	2
Neuroptera	16	<1	0.18	9	10
Chilopoda	6	<1	0.06	5	6
Diplopoda	8	<1	0.08	6	7
Hemiptera	1	<1	0.01	1	1
Isopoda	—	—	—	—	—
Earthworms	5	<1	0.06	5	6
Trichoptera	2	<1	0.02	2	2
Dermaptera	1	<1	0.01	1	1
Insecta indeterminate	2,518	57	79.33	86	100
Total	4,324	100		86	

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APPENDIX TABLE 3. Effects of diet composition and covariates on fledging mass (g) and fledging age (days) of parasitic (Common Cuckoo) and host (Common Redstart) nestlings. Results are from general linear mixed models with normal distributions and identity links. We show statistics and parameter estimates from both the full models (as recommended by Forstmeier and Schielzeth 2011) and final reduced models (as recommended by Grafen and Hails 2002). *P*-values were computed using *F*-tests with Kenward-Roger corrected denominator degrees of freedom (Luke 2016); numerator degrees of freedom were always 1 (i.e. predictors were either continuous or categorical with 2 levels), except for "Diet type," which had numerator degrees of freedom = 3. The fit of models is summarized using marginal (R^2_m) and conditional (R^2_c) *R*-squared accompanied by Akaike's Information Criterion corrected for small sample sizes (AIC_c; Nakagawa and Schielzeth 2013, Lefcheck 2015). "Diet type" (categories: "Invertebrate," "Vertebrate," "Plant," and "Both"; Figure 1) was a predictor of key interest and was therefore retained in models regardless of its significance (as recommended by Grafen and Hails 2002). See Figure 1 for differences between the 4 diet type categories and for post hoc Dunnett's test results. Removal of the "Diet type" predictor (when nonsignificant in a particular model) did not affect conclusions. To control for temporal between-year variation, we included the variable "Year" as a random effect (we did not have any specific year-based predictions). To control for within-brood variation in Common Redstart nests, we included the random effect "brood ID." The predictor variable "Weather" was created from strongly negatively correlated variables "Rainfall" and "Temperature" using principal component analysis. "Rainfall" represented average daily rainfall (mm) and "Temperature" represented average daily temperature (°C) over the whole nestling period (i.e. from the date of hatching till the date of fledging). "Brood size" was always 1 for Common Cuckoo nestlings; therefore, we removed this predictor from Common Cuckoo models (Bolker 2015). Reference levels of categorical variables are given in square brackets.

	Common Cuckoo							
	Full model				Final model			
Predictor	df	*F*	*P*	Estimate ± SE	df	*F*	*P*	Estimate ± SE
Fledging mass	$R^2_m = 0.32$, $R^2_c = 0.32$, $AIC_c = 547.1$				$R^2_m = 0.31$, $R^2_c = 0.31$, $AIC_c = 538.5$			
Intercept	—	—	—	100.5 ± 17.2	—	—	—	87.8 ± 1.9
Diet type	45.9	2.97	0.04	—	5.0	56.20	0.004	See Figure 1
Fruit availability [no]	57.9	0.22	0.64	−1.7 ± 3.6	—	—	—	—
Brood type [mixed]	54.5	14.24	<0.001	8.4 ± 2.1	61.4	17.38	<0.001	8.5 ± 1.9
Parasitism status [parasitized]	56.2	0.34	0.56	−1.3 ± 2.1	—	—	—	—
Brood size	—	—	—	—	—	—	—	—
Age weighed	57.5	0.41	0.53	−0.6 ± 0.9	—	—	—	—
Weather	2.2	0.00	0.96	−0.1 ± 1.2	—	—	—	—
Fledging age	$R^2_m = 0.21$, $R^2_c = 0.26$, $AIC_c = 273.2$				$R^2_m = 0.13$, $R^2_c = 0.16$, $AIC_c = 266.9$			
Intercept	—	—	—	20.2 ± 0.4	—	—	—	20.3 ± 0.3
Diet type	53.9	2.86	0.05	—	57.0	2.86	0.04	See Figure 1
Fruit availability [no]	57.8	0.94	0.34	0.5 ± 0.5	—	—	—	—
Brood type [mixed]	57.9	3.70	0.06	−0.5 ± 0.3	—	—	—	—
Parasitism status [parasitized]	57.7	2.14	0.15	0.4 ± 0.3	—	—	—	—
Brood size	—	—	—	—	—	—	—	—
Weather	3.1	1.05	0.38	0.2 ± 0.2	—	—	—	—

	Common Redstart							
	Full model				Final model			
Predictor	df	*F*	*P*	Estimate ± SE	df	*F*	*P*	Estimate ± SE
Fledging mass	$R^2_m = 0.07$, $R^2_c = 0.49$, $AIC_c = 853.0$				$R^2_m = 0.05$, $R^2_c = 0.46$, $AIC_c = 834.2$			
Intercept	—	—	—	15.7 ± 0.8	—	—	—	15.8 ± 0.1
Diet type	47.4	0.27	0.85	—	51.1	0.21	0.89	See Figure 1
Fruit availability [no]	58.2	0.36	0.55	−0.1 ± 0.2	—	—	—	—
Brood type [mixed]	61.6	0.37	0.54	−0.1 ± 0.2	—	—	—	—
Parasitism status [parasitized]	47.4	4.07	0.05	−0.3 ± 0.2	31.1	4.45	0.04	−0.3 ± 0.1
Brood size	54.8	0.25	0.62	−0.1 ± 0.1	—	—	—	—
Age weighed	14.9	0.03	0.88	0.0 ± 0.1	—	—	—	—
Weather	20.3	0.34	0.56	−0.1 ± 0.1	—	—	—	—
Fledging age	$R^2_m = 0.22$, $R^2_c = 0.98$, $AIC_c = 265.3$				$R^2_m = 0.21$, $R^2_c = 0.98$, $AIC_c = 261.8$			
Intercept	—	—	—	14.9 ± 0.4	—	—	—	14.8 ± 0.3
Diet type	56.3	0.53	0.66	—	59.1	0.83	0.48	See Figure 1
Fruit availability [no]	56.5	1.09	0.30	0.2 ± 0.2	—	—	—	—
Brood type [mixed]	58.1	21.38	<0.001	−1.1 ± 0.2	61.3	22.40	<0.001	−1.0 ± 0.2
Parasitism status [parasitized]	58.1	4.80	0.03	0.5 ± 0.2	61.1	4.60	0.04	0.4 ± 0.2
Brood size	58.4	10.00	0.002	0.5 ± 0.1	60.2	9.40	0.003	0.4 ± 0.1
Weather	30.2	0.23	0.64	−0.1 ± 0.2	—	—	—	—

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APPENDIX TABLE 4. Effects of diet composition and covariates on fledging success (fledged vs. died in the nest) of parasitic (Common Cuckoo) and host (Common Redstart) nestlings. Results are from generalized linear models with binomial distributions and logit links. We show statistics and parameter estimates from both the full models (as recommended by Forstmeier and Schielzeth 2011) and final reduced models (as recommended by Grafen and Hails 2002). *P*-values were computed using Wald chi-square tests (thus, both the numerator and denominator degrees of freedom were 1). The fit of models is summarized using marginal (R^2_m) and conditional (R^2_c) *R*-squared accompanied by Akaike's Information Criterion corrected for small sample sizes (AIC_c; Nakagawa and Schielzeth 2013, Lefcheck 2015). "Diet type" (categories: "Invertebrate," "Noninvertebrate") was a predictor of key interest and was therefore retained in models regardless of its significance (as recommended by Grafen and Hails 2002). Within the predictor variable "Diet type," we pooled the categories of "Vertebrate," "Plant," and "Both" into the single category of "Noninvertebrate" because a lack of variability in the "Vertebrate" and "Both" categories (all nestlings fledged) caused model convergence failure. Removal of this predictor (when nonsignificant in a particular model) did not affect conclusions. To control for temporal between-year variation, we included the variable "Year" as a random effect (we did not have any specific year-based predictions). The predictor variable "Weather" was created from strongly negatively correlated variables "Rainfall" and "Temperature" using principal component analysis. "Rainfall" represented average daily rainfall (mm) and "Temperature" represented average daily temperature (°C) over the whole nestling period (i.e. from the date of hatching till the date of fledging). "Brood size" was always 1 for Common Cuckoo nestlings; therefore, we removed this predictor from Common Cuckoo models (Bolker 2015). Reference levels of categorical variables are given in square brackets.

	Common Cuckoo					
	Full model			Final model		
Predictor	χ^2	*P*	Estimate ± SE	χ^2	*P*	Estimate ± SE
Fledging success	$R^2_m = 0.54$, $R^2_c = 0.80$, $AIC_c = 45.8$			$R^2_m = 0.55$, $R^2_c = 0.81$, $AIC_c = 44.7$		
Intercept	—	—	−0.8 ± 1.6	—	—	0.2 ± 1.4
Diet type [Invertebrate]	1.52	0.22	−2.0 ± 1.8	2.28	0.13	−2.4 ± 1.9
Fruit availability [no]	4.79	0.03	3.5 ± 2.1	5.36	0.02	4.1 ± 2.4
Brood type [mixed]	1.38	0.24	1.6 ± 1.3	—	—	—
Parasitism status [parasitized]	8.01	0.004	4.4 ± 2.3	7.80	0.005	4.7 ± 2.6
Brood size	—	—	—	—	—	—
Weather	5.58	0.02	1.4 ± 0.7	5.12	0.02	1.4 ± 0.7
	Common Redstart					
	Full model			Final model		
Predictor	χ^2	*P*	Estimate ± SE	χ^2	*P*	Estimate ± SE
Fledging success	$R^2_m = 0.38$, $R^2_c = 0.46$, $AIC_c = 163.7$			$R^2_m = 0.37$, $R^2_c = 0.45$, $AIC_c = 162.8$		
Intercept	—	—	1.8 ± 0.6	—	—	0.7 ± 0.5
Diet type [Invertebrate]	3.13	0.08	1.3 ± 0.7	3.40	0.07	0.0 ± 0.5
Fruit availability [no]	4.98	0.03	−1.0 ± 0.4	6.84	0.01	−1.1 ± 0.4
Brood type [mixed]	24.56	<0.001	2.0 ± 0.4	27.08	<0.001	2.1 ± 0.4
Parasitism status [parasitized]	4.41	0.04	−1.2 ± 0.6	4.17	0.04	−1.1 ± 0.6
Brood size	1.65	0.20	0.2 ± 0.2	—	—	—
Weather	2.70	0.10	0.5 ± 0.3	4.11	0.04	0.6 ± 0.3

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APPENDIX TABLE 5. Effects of diet composition and covariates on provisioning effort (feedings hr^{-1}) to parasitic (Common Cuckoo) and host (Common Redstart) nestlings. Results are from general linear mixed models with normal distributions and identity links. We show statistics and parameter estimates from both the full models (as recommended by Forstmeier and Schielzeth 2011) and final reduced models (as recommended by Grafen and Hails 2002). *P*-values were computed using *F*-tests with Kenward-Roger corrected denominator degrees of freedom (Luke 2016); numerator degrees of freedom were always 1 (i.e. predictors were either continuous or categorical with 2 levels), except "Diet type," which had numerator degrees of freedom = 3. The fit of models is summarized using marginal (R^2_m) and conditional (R^2_c) *R*-squared accompanied by Akaike's Information Criterion corrected for small sample sizes (AIC_c; Nakagawa and Schielzeth 2013, Lefcheck 2015). "Diet type" (categories: "Invertebrate," "Vertebrate," "Plant," and "Both"; see Figure 1) was a predictor of key interest and was therefore retained in models regardless of its significance (as recommended by Grafen and Hails 2002). Removal of this predictor (when nonsignificant in a particular model) did not affect conclusions. There was no collinearity between "Rainfall" and "Temperature" at the day level and thus we used both as separate predictors in these provisioning effort analyses (cf. the use of the predictor "Weather" in analyses reported in Appendix Tables 3 and 4). Reference levels of categorical variables are given in square brackets.

	Common Cuckoo							
	Full model				Final model			
Predictor	df	*F*	*P*	Estimate ± SE	df	*F*	*P*	Estimate ± SE
Provisioning effort	$R^2_m = 0.08$, $R^2_c = 0.35$, $AIC_c = 2{,}092.4$				$R^2_m = 0.05$, $R^2_c = 0.32$, $AIC_c = 2{,}078.5$			
Intercept	—	—	—	13.4 ± 2.4	—	—	—	11.3 ± 1.0
Diet type	27.9	0.16	0.92	—	29.7	0.13	0.94	—
Date	75.5	6.78	0.01	0.1 ± 0.1	73.8	6.17	0.02	0.1 ± 0.0
Daytime	291.2	1.58	0.21	−0.1 ± 0.1	—	—	—	—
Daytime^2	298.9	2.94	0.09	−0.0 ± 0.0	—	—	—	—
Brood type [mixed]	68.5	2.03	0.16	1.2 ± 0.8	—	—	—	—
Parasitism status [parasitized]	37.0	0.15	0.70	0.3 ± 0.6	—	—	—	—
Brood size	—	—	—	—	—	—	—	—
Rainfall	283.6	1.33	0.25	0.1 ± 0.1	—	—	—	—
Temperature	258.9	1.77	0.18	−0.2 ± 0.1	—	—	—	—
	Common Redstart							
	Full model				Final model			
Predictor	df	*F*	*P*	Estimate ± SE	df	*F*	*P*	Estimate ± SE
Provisioning effort	$R^2_m = 0.11$, $R^2_c = 0.55$, $AIC_c = 1{,}499.4$				$R^2_m = 0.10$, $R^2_c = 0.55$, $AIC_c = 1{,}486.2$			
Intercept	—	—	—	12.8 ± 4.1	—	—	—	14.2 ± 1.6
Diet type	18.7	0.66	0.59	—	16.1	1.70	0.21	—
Date	37.5	0.41	0.53	0.0 ± 0.1	—	—	—	—
Daytime	181.7	0.41	0.52	−0.1 ± 0.1	186.8	0.40	0.53	−0.1 ± 0.1
Daytime^2	165.0	9.26	0.003	0.1 ± 0.0	169.4	9.11	0.003	0.1 ± 0.0
Brood type [mixed]	110.6	0.01	0.93	0.2 ± 2.5	—	—	—	—
Parasitism status [parasitized]	100.7	0.90	0.34	1.0 ± 1.0	—	—	—	—
Brood size	85.8	14.10	<0.001	2.0 ± 0.5	62.9	14.40	<0.001	1.8 ± 0.4
Rainfall	179.5	0.72	0.40	−0.1 ± 0.1	—	—	—	—
Temperature	137.1	0.00	0.97	−0.0 ± 0.2	—	—	—	—

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