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Using an Electronic Monitoring System to Link Offspring Provisioning and Foraging Behavior of a Wild Passerine (Uso de un Sistema de Monitoreo Electrónico para Conectar el Aprovechamiento de las Crías y el Comportamiento de Forrajeo en un Ave Paserina Silvestre)  
Author(s): Mylene M. Mariette, Emma C. Pariser, Amanda J. Gilby, Michael J. L. Magrath, Sarah R. Pryke and Simon C. Griffith

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## USING AN ELECTRONIC MONITORING SYSTEM TO LINK OFFSPRING PROVISIONING AND FORAGING BEHAVIOR OF A WILD PASSERINE

MYLENE M. MARIETTE,<sup>1,2,6</sup> EMMA C. PARISER,<sup>3</sup> AMANDA J. GILBY,<sup>1</sup>  
MICHAEL J. L. MAGRATH,<sup>4,5</sup> SARAH R. PRYKE,<sup>1,2</sup> AND SIMON C. GRIFFITH<sup>1,2</sup>

<sup>1</sup>Department of Biological Sciences, Macquarie University, Culloden Road, Sydney, NSW 2109, Australia;

<sup>2</sup>School of Biological, Earth and Environmental Sciences, University of New South Wales, High Street, Sydney, NSW 2052, Australia;

<sup>3</sup>School of Biology, University of St Andrews, West Burn Lane, St. Andrews, Fife, KY16 9AJ, United Kingdom;

<sup>4</sup>School of Biology, Australian National University, Daley Road, Canberra, ACT 0200, Australia; and

<sup>5</sup>Department of Zoology, University of Melbourne, Parkville, Melbourne, Victoria 3010, Australia

**ABSTRACT.**—Although the costs of parental care are at the foundations of optimal-parental-investment theory, our understanding of the nature of the underlying costs is limited by the difficulty of measuring variation in foraging effort. We simultaneously measured parental provisioning and foraging behavior in a free-living population of Zebra Finches (*Taeniopygia guttata*) using an electronic monitoring system. We fitted 145 adults with a passive transponder tag and remotely recorded their visits to nest boxes and feeders continuously over a 2-month period. After validating the accuracy of this monitoring system, we studied how provisioning and foraging activities varied through time (day and breeding cycle) and influenced the benefits (food received by the offspring) and costs (interclutch interval) of parental care. The provisioning rates of wild Zebra Finches were surprisingly low, with an average of only one visit per hour throughout the day. This was significantly lower than those reported for this model species in captivity and for most other passerines in the wild. Nest visitation rate only partially explained the amount of food received by the young, with parental foraging activity, including the minimum distance covered on foraging trips, being better predictors. Parents that sustained higher foraging activity and covered more distance during the first breeding attempt took longer to renest. These results demonstrate that in some species matching foraging activity with offspring provisioning may provide a better estimate of the true investment that individuals commit to a reproductive attempt. Received 3 May 2010, accepted 15 October 2010.

Key words: distance, foraging cost, nest visitation rate, nestling provisioning, parental care, PIT-tag, *Taeniopygia guttata*, Zebra Finch.

### Uso de un Sistema de Monitoreo Electrónico para Conectar el Aprovisionamiento de las Crías y el Comportamiento de Forrajeo en un Ave Paserina Silvestre

**RESUMEN.**—Aunque los costos del cuidado parental hacen parte de la base de la teoría sobre inversión parental óptima, nuestro conocimiento sobre los costos subyacentes está limitado por la dificultad de medir la variación en el esfuerzo de forrajeo. En este estudio medimos simultáneamente el aprovisionamiento de las crías y el comportamiento de forrajeo en una población de vida libre de *Taeniopygia guttata* empleando un sistema electrónico de monitoreo. Ajustamos transpondedores pasivos en 145 adultos y registramos sus visitas a cajas de anidación y comederos de forma continua a lo largo de dos meses. Después de validar la exactitud de este sistema de monitoreo, estudiamos cómo variaban las actividades de aprovisionamiento y alimentación en el tiempo (en el día y en el ciclo anual) y cómo influenciaban los beneficios (alimento recibido por las crías) y los costos (intervalo entre posturas) del cuidado parental. Las tasas de aprovisionamiento fueron sorprendentemente bajas, con un promedio de sólo una visita por hora a lo largo del día. Esto fue significativamente más bajo que lo que se había documentado para esta especie modelo en cautiverio y para la mayoría de otras aves paserinas en el campo. La tasa de visitas a los nidos sólo explicó parcialmente la cantidad de alimento recibida por las crías. Por su parte, la actividad de forrajeo de los padres, incluyendo la distancia mínima cubierta en los viajes de forrajeo, fue un mejor predictor. Los padres que mantuvieron una mayor actividad de forrajeo y cubrieron más distancia durante el primer intento de anidación tomaron más tiempo en volver a anidar. Estos resultados demuestran que, en algunas especies, conectar la actividad de forrajeo con el aprovisionamiento de las crías puede brindar mejores estimados de la verdadera inversión que hacen los individuos en un intento reproductivo.

<sup>6</sup>E-mail: [mmariette7@hotmail.com](mailto:mmariette7@hotmail.com)

ALTHOUGH IT IS clear that parental care is often costly (Drent and Daan 1980, Bryant and Tatner 1991), the function describing the relationship between parental provisioning and the costs to the parents is not straightforward (Clutton-Brock 1991, Sætre et al. 1995, Moreno et al. 1997, Wright et al. 1998). Indeed, even though increasing parental provisioning rate by manipulating brood size generally increases the cost to the parents (e.g., Nur 1984, Gustafsson and Sutherland 1988; but see Moreno et al. 1997, Wright et al. 1998), the cost of provisioning may vary greatly with individual quality and environmental conditions (Clutton-Brock 1991, Møller 1993, Sætre et al. 1995). In particular, as experimental evidence suggests, the cost of offspring provisioning depends on the parents' access to resources and on their energy reserves and expenditure (Wright and Cuthill 1989, Moreno et al. 1999, Verboven et al. 2001, Grieco 2002, Spencer and Bryant 2002, Clutton-Brock et al. 2003; but see Moreno et al. 1997). Overall, if parents' resource intake is lower than the resources they invest in provisioning their offspring, the cost of parental care may be carried over to future breeding via reduced parental condition. Specifically, poor condition may negatively affect parents' survival to the next breeding season (Nur 1984), their condition or fecundity in the next breeding event (Gustafsson and Sutherland 1988, Griffith 2000), or the interval to the next breeding event (Møller 1993, Verboven et al. 2001, Tinbergen and Sanz 2004). Similarly, within a breeding attempt, costs of parental care at the egg stages (laying and incubation) may negatively affect adult condition and investment in subsequent stages, including nestling provisioning (Monaghan et al. 1998, Reid et al. 2000, Perez et al. 2008). Ultimately, therefore, the effect of a breeding attempt (or stage) on future reproduction depends on the cost of acquiring resources to sustain that breeding attempt.

An individual's access to resources is determined not only by resource availability but also by its foraging capacities. Therefore, to fully appreciate a parent's investment in care we must evaluate that individual's foraging behavior. Two adults may deliver the same quantity of food to a nest, but this may represent very different costs in terms of finding and delivering the food. To date, however, attempts to link foraging behavior with offspring provisioning have been limited. The few empirical studies that have used extensive behavioral observations suggest that foraging strategy or efficiency may affect provisioning (e.g., Clutton-Brock et al. 2003, Radford and Du Plessis 2003; but see Wright et al. 1998, Stauss et al. 2005), but this observational approach is applicable only in species that forage at small spatial scales in relatively open habitats. Alternatively, a growing number of studies have successfully used global positioning systems (GPS) and data loggers on seabirds and marine mammals to record foraging activity at sea while offspring growth was monitored on shore (e.g., Weimerskirch and Lys 2000, Gray and Hamer 2001, Takahashi et al. 2003). These studies have detected differences in foraging mode or efficiency between breeding males and females that may contribute to differences in parental care between the sexes (e.g., Weimerskirch and Lys 2000, Gray and Hamer 2001). Unfortunately, the price of this equipment, and its limitation to taxa large enough to carry it, constrain the widespread use of such technology.

We used an electronic monitoring system to simultaneously study parental care and foraging behavior in a small passerine, the Australian Zebra Finch (*Taeniopygia guttata*), in its natural environment. We fitted 145 adults with uniquely coded passive

transponder tags and remotely recorded their visits to nest boxes and feeders equipped with a detector. This method provided continuous data on individual behavior for up to 68 days at multiple locations, as well as estimates of the minimum distance covered per day on foraging trips that would have been impractical to obtain by direct observation. However, because it provided only an indirect measure of bird behavior, we first validated our method using videorecorders at the nests. We then used three approaches to test the value of measuring foraging activity in conjunction with nest visitation rate for the study of investment tradeoffs. First, because reproductive investment may vary through time (Reid et al. 2000, Perez et al. 2008, Rose 2009), we studied how provisioning and foraging activities varied throughout the day and the breeding cycle in response to possible variations in offspring demand and the time available for foraging. Second, because food load may (Nolan et al. 2001) or may not (Wright et al. 1998, Sejberg et al. 2000, Grieco 2002) be constant across visits, we tested whether daily visitation rates to the nest and to the feeders were good estimates of the amount of food delivered to the offspring. Lastly, we tested the prediction that foraging activity (i.e., foraging rate and distance) provides a valid estimate of the cost of parental care by investigating the effects of foraging and provisioning activities on the latency to start another breeding attempt.

## METHODS

*Study species and study site.*—The Zebra Finch is a small, sexually dimorphic and socially monogamous passerine that inhabits the arid and semiarid zones of Australia. It is highly social and commonly breeds in loose colonies. Zebra Finches breed opportunistically and lay an average clutch of  $4.9 \pm 1.1$  eggs ( $n = 559$ ; Griffith et al. 2008; throughout, statistics are presented as means  $\pm$  SD). Both parents incubate the eggs and feed the young, and, unlike most seed-eating species, Zebra Finches feed their young exclusively with seeds and other vegetable materials (but no insects) that parents carry in their crops (Zann 1996).

Data were collected over two breeding seasons from September to December (2007 and 2008) in three nest-box breeding colonies of Zebra Finches at Fowlers Gap Arid Zone Research Station, western New South Wales, Australia ( $31^{\circ}05'S$ ,  $142^{\circ}42'E$ ). In total, there were 200 nest boxes available at Gap Hills (2007) within 1 km around a dam (Fig. 1), 51 at Saloon (2007 and 2008) in a  $200 \times 200$  m area adjacent to a dam, and 150 at West Mandelman (2008) in a  $1,500 \times 200$  m area that contained a permanent artificial pond and three semipermanent natural water holes (for further details, see Griffith et al. 2008). At each site, we provided the birds with commercial finch seed in feeders throughout the breeding season. Saloon and West-Mandelman had one permanent feeder in the center of the breeding area, whereas Gap Hills had a total of 18 feeders that were scattered around the area, although only 3 to 6 were active (i.e., full) at any one time (Fig. 1). Feeders in all areas were identical, but only at Gap Hills (2007) were they equipped with an electronic monitoring system.

*Bird capture and nest monitoring.*—Active nest boxes were monitored every 3 days over the breeding season and daily as hatching approached. We calculated the breeding interval between two consecutive attempts as the number of days between the last day of the first attempt that the parents visited the nestlings in the

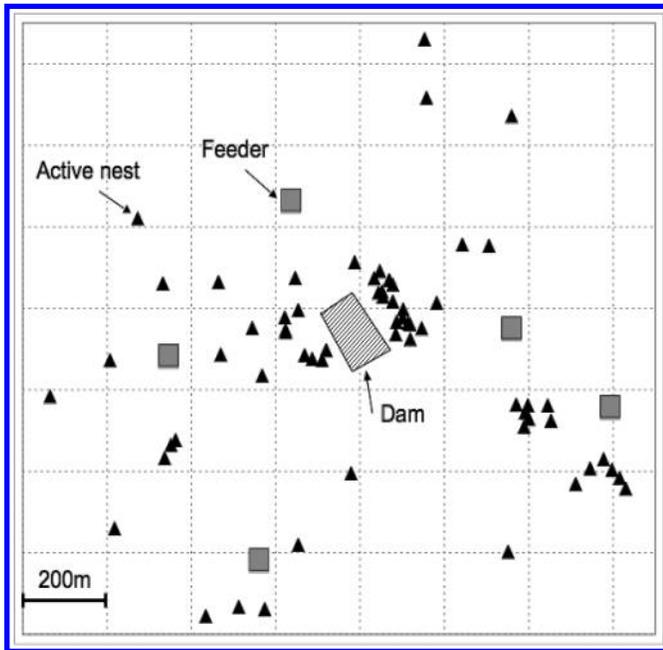


FIG. 1. Map of Gap Hills with dam (striped square), active nest boxes (from laying to fledging: small black triangles), and active feeders (large gray squares) in week 3 (15–23 October 2007).

nest (fledging day) and the day that the first egg of the following attempt was laid (laying day). When the young were 12 days old, we measured tarsus length with digital calipers (0.1 mm) and mass with an electronic scale (0.01 g) to estimate condition (residuals from the regression of mass on tarsus length). At the age of 11–12 days (i.e., 24-h intervals), we estimated crop content of the young by counting the number of seeds visible through the skin of the crop (Meijer et al. 1996, Cuthill et al. 1997). This measure has been shown to account for 90% of variation in actual seed mass in the crop (Meijer et al. 1996) and was highly correlated with the proportion of the crop that contained seeds (day 11:  $r_s = 0.747$ ,  $P < 0.001$ ,  $n = 466$  nestlings; day 12:  $r_s = 0.758$ ,  $P < 0.001$ ,  $n = 408$ ). Total seed counts per nestling on days 11 and 12 were correlated ( $r_s = 0.401$ ,  $P = 0.004$ ,  $n = 49$  nests), so we used the seed count on day 12 for all analyses (unless otherwise indicated). Because the seeds available in the feeders did not occur naturally at our study site, we differentiated commercial from natural seeds through the crop skin on the basis of seed shape and color (natural seeds were dark brown, green, or red, in the shape of a water drop or a stick, whereas exotic canary seed and white millet were lightly colored and round).

In 2007, 145 adults were captured in the morning, either at feeders early in the breeding season ( $n = 61$ , including 39 that were not recorded breeding) or at their nests when nestlings were 4–8 days old. All captured adults were measured (tarsus length and mass, similarly to nestlings) and fitted with a passive integrated transponder (PIT) tag (Trovan, Hessle, United Kingdom;  $11 \times 2$  mm, 0.1 g with band) glued onto a plastic color band (as used in, e.g., Santema et al. 2009) and with a numbered metal band (provided by the Australian Bird and Bat Banding Scheme).

*Remote recording at the nest and feeder.*—When at least one parent had been banded with a PIT-tag, the nest box was replaced

with an identical nest box equipped with a PIT-tag detection system, which consisted of a decoder (LID-665 decoder, Trovan) and a powered single-coil antenna (5 cm diameter) fitted to the inside of the entrance hole that automatically recorded the unique identification number of any tagged bird going through (or sitting within 1 cm of) the nest entrance (cf. Santema et al. 2009). We collected nest decoder data continuously for  $6.7 \pm 3.3$  days nest<sup>-1</sup> during the nestling stage only (when the young were 4–18 days old) for 66 nests ( $n = 449$  nest-days; 697 individual-days) with either one ( $n = 26$  nests) or two tagged adults ( $n = 40$  nests).

Each feeder consisted of a  $40 \times 30$  cm seed tray in a wire holding cage ( $70 \times 40 \times 50$  cm) that was partly buried in the ground. Birds got to the feeder by walking through an antenna (11 cm in diameter) fixed around an  $11 \times 11$  cm door. At Gap Hills, we collected decoder data for all active feeders (i.e., feeders containing seeds) continuously from 29 September to 5 December 2007 ( $n = 69$  days). The number of active feeders varied between 3 and 6, with an average of 5 feeders opened at any one time ( $n = 69$  days  $\times$  5.33 feeders = 368 feeder-days; we missed 19 feeder-days [4.1%] because of a technical failure or damage to the equipment by inquisitive kangaroos). On average, we obtained foraging data for  $45 \pm 19$  consecutive days per individual, from the individual's time of capture until the end of the season. This period encompassed several different stages of the breeding cycle for different individuals depending on their capture, nesting, and re-nesting dates. The positions of the feeders were rotated every week. Therefore, the distance from any particular nest to the active feeders differed each week, and the mean distance to active feeders ( $1,171 \pm 285$  m) and the distance to the closest active feeder ( $513 \pm 242$  m) differed between nests at any one time. The minimum distance covered by a breeding adult per day was calculated as the number of visits to each active feeder multiplied by the corresponding nest-feeder distance, multiplied by 2 (to account for return trip). As with other methods that record individual locations at discrete time intervals (e.g., radiotracking data), the possible detours between two recording points were not accounted for. Nonetheless, birds took longer to travel to feeders that were farther from their nests (correlation between nest-feeder distance and time interval between departure from nest and arrival at feeder, using one data point per nest and per feeder:  $r_s = 0.231$ ,  $P = 0.002$ ,  $n = 184$  nest-feeders), so the minimum distance covered on foraging trips was likely a valid proxy for the actual distance traveled. For successful breeding attempts, we considered that a bird was tied to its nest from the day it laid an egg until 10 days after the young fledged, because fledglings stay in the vicinity of the colony while dependent on parents for food (Zann 1996, M. M. Mariette pers. obs.).

*Video recording at the nest.*—In 2007, the nest cameras (Infrared Video Camera 4IRMOS408C, Avian Electronics, Switzerland) were triggered by the decoder (i.e., only when a bird entered the nest) and recorded for 2 min after each PIT-tag reading. In 2008, nests were equipped with a camera only (color CCD camera HK-C3, Handykam, Hayle, United Kingdom) that recorded continuously onto an external hard drive (Archos 605, 160 GB memory, Minidisc, Chatswood, Australia). Cameras were fixed on the inside of the nest-box lid, facing down into the nest. We collected video data from 6 nests for 92 h ( $15.4 \pm 11.8$  [SD] h per nest) in 2007 and from 14 nests for 68 hours ( $4.9 \pm 1.6$  [SD] h per nest) in 2008.

*Decoder data processing.*—For all analyses, we included only the days when the decoder recorded continuously from dawn until dusk. When visiting the nest (or the feeder), birds usually entered and exited the nest box (or the feeder) several times, sitting in the nearby vegetation between entries. The decoder took a reading every second when a PIT-tag was within the detection range of the antenna. From the nests where we simultaneously ran both a decoder and video, the decoder failed to log tagged birds exiting the nest box on 13 of 145 occasions (8.9%;  $n = 4$  nests in 2007,  $n = 15$  individual-days; entry detection probability could not be assessed because the camera was triggered by the decoder). If we missed the same proportion of entries throughout, <1% of visits ( $0.089 \times 0.089 \times 100 = 0.8\%$ ) were undetected. Our visit-rate estimate was therefore accurate but visit duration estimate was more strongly affected, because 14% of the nest visits had only one reading each (which corresponds to  $\sim 8.9\%$  exits missed +  $8.9\%$  entries presumably missed). Therefore, we present data only on nest or feeder visitation rate from decoder data, although visit duration gave similar results for most analyses.

On entering the nest, parents always moved to the back of the nest and faced the entrance while they fed the young. Birds were thus detected by the decoder when they went in and out of the box but rarely when inside the box (birds detected inside the box in 13.4% of 156 visits;  $n = 4$  nests with simultaneous decoder and video data). Similarly, birds were not detected while inside the feeder cage, because the seed tray was >5 cm from the entrance. As a result, the nest and feeder decoder data typically consisted of bouts of several readings close together in time when birds repeatedly moved in and out of the nest or feeder, separated by long intervals (often >45 min) without any reading when they were away from the nest or feeder (Fig. 2). Because we did not know for each specific reading whether the bird was going in or out of the nest or feeder, we considered that any two readings within 15 min of each

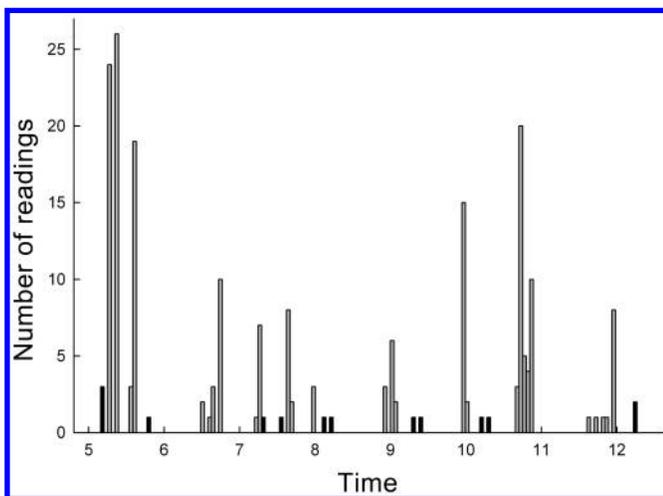


FIG. 2. Example of raw decoder output (before data processing): number of readings at the nest (gray bars) and at the feeders (black bars) for one Zebra Finch (female from nest 71) in the morning of 18 October 2007 (the x-axis shows continuous time from dawn until 1230 hours). Periods of activity around the nest are separated by long intervals without any reading. Activity at the nest and at the feeders alternates throughout the day.

other were part of the same visit and computed daily visitation rate and maximum visit interval. This 15-min threshold was used because (1) adults rarely stayed in the nest box for >15 min without leaving (91.9% of the nest entries captured on video were <15 min;  $n = 396$  entries) and (2) 15 min was almost always insufficient time to leave, forage, and return to the nest with a new crop load of food (a parent visited a feeder within a nest visit on only 2.4% of the nest visits;  $n = 6,414$  nest visits;  $n = 41$  nests with feeder and nest decoder data on the same day). When we instead applied a 10-min threshold to the decoder data, visitation rate and maximum visit interval were highly correlated with those obtained with a 15-min threshold ( $r_s = 0.934$ ,  $P < 0.001$ ,  $n = 519$  and  $r_s = 1.000$ ,  $P = 0.00$ ,  $n = 519$ , respectively).

Importantly, when we analyzed the 2008 video data (i.e., continuous recording) using the processing rules for the decoder data (i.e., the bird going through the entrance on the video was counted as a reading, but without taking note of whether it was going in or out of the nest), nest visitation rate was highly correlated with the values obtained from the actual entry and exit counts from the video data (see below;  $r_s = 0.771$ ,  $P < 0.001$ ,  $n = 26$  individuals).

*Video data processing.*—To estimate nest visitation rate and duration, we recorded the time the bird went in and out of the box and pooled entries within 15 min of each other into a single visit (see above). A single observer (A. J. Gilby) scored all videos and categorized parental behavior inside the nest as (1) feeding the young (regurgitating into the mouth of at least one offspring), (2) nest maintenance (bringing or arranging nest material or removing fecal material), and (3) brooding. In addition, we counted the number of feeds (number of times a parent made contact with a nestling's beak to regurgitate before raising its head) and the number of regurgitations per feed (characterized by an obvious heaving motion of the adult).

*Statistical analyses.*—All data were analyzed using SPSS, version 16.0 (SPSS, Chicago, Illinois) or SAS, version 9.1 (SAS Institute, Cary, North Carolina). To investigate feeder and nest visitation rates through time and how daily estimates for feeder and nest variables varied in relation to each other, we used general linear mixed models (GLMM) with individual (nested within nest) and nest as random factors to control for the fact that data from the same individuals were used for different periods. We investigated the variations in visitation rate both throughout the day (i.e., time of day) and throughout the breeding cycle (categorized by five breeding stages: eggs, young nestlings [ $<6$  days old], old nestlings [ $\geq 6$  days old], fledglings [ $\leq 10$  days after fledging], and postbreeding). Data were transformed whenever appropriate to achieve normality, and there was no major imbalance in the design. To describe the relationship between nest or feeder visitation rate and the nestlings' crop content, we included two breeding attempts for 13 pairs to increase sample size; we considered the two attempts of a pair as independent data points because they were  $19.3 \pm 5.1$  days apart, they had different brood size, and they occurred in a different nest box and with a different feeder configuration. Sample sizes vary between analyses because of missing data.

*Ethical note.*—The average mass of an adult Zebra Finch at our study site (in 2005) was  $12.0 \pm 0.1$  g and varied predictably from 11.6 g at  $\sim 0600$  hours to 13.0 g at  $\sim 1900$  hours, just before roost (one-way analysis of variance,  $F = 5.34$ ,  $df = 13$  and 390,  $P < 0.0001$ ). Therefore, the weight of the PIT-tag and band (0.1 g)

was marginal compared with natural daily fluctuations in body mass (1.4 g; 0.8% vs. 12.2% of the average body mass, respectively). Accordingly, PIT-tags had no detectable effect on bird behavior: nestling condition and crop content (mean number of seeds per brood) on day 12 were independent of whether or not the parents were tagged ( $U$ -test:  $U = 668$ ,  $n_1 = 72$  nests with at least one parent tagged,  $n_2 = 21$  control nests with untagged parents,  $P = 0.419$ ;  $U = 537$ ,  $n_1 = 71$ ,  $n_2 = 20$  nests,  $P = 0.098$ ), and the breeding interval was not affected by whether one or two partners in the pair were PIT-tagged ( $U$ -test:  $U = 116$ ,  $n_1 = 14$ ,  $n_2 = 21$  nests,  $P = 0.296$ ). In addition, the proportion of commercial seeds in the offspring crop did not affect nestling condition ( $r_s = 0.053$ ,  $n = 89$ ,  $P = 0.558$ ), which suggests that this commercial diet was appropriate.

## RESULTS

*Daily and seasonal patterns in provisioning and foraging activity.*— Individual visitation rate was low: on average, 1 visit hour<sup>-1</sup> (nest decoder data; 13.2/13.3 = 1.0 ± 0.2 visits daylight hour<sup>-1</sup>,  $n = 697$  individual-days). When all birds were active (i.e., daylight hours, 1–12 h after sunrise), nest visitation rate was relatively constant throughout the day except for the first hour after sunrise (GLMM with hourly nest visitation rate as a response variable and hours after sunrise as a fixed factor:  $F = 14.84$ ,  $df = 11$  and 1,276,  $P < 0.001$ ; Fig. 3).

The hourly feeder visitation rate was also relatively constant throughout the day, except for a small peak in the morning and another in the evening (GLMM with hourly feeder-visit rate as a response variable and hour after sunrise as a fixed factor:  $F = 17.81$ ,  $df = 11$  and 1,518,  $P < 0.001$ ; Fig. 3). Feeder visitation rate differed significantly between the stages of breeding (GLMM with natural log-transformed daily feeder visitation rate as a response variable

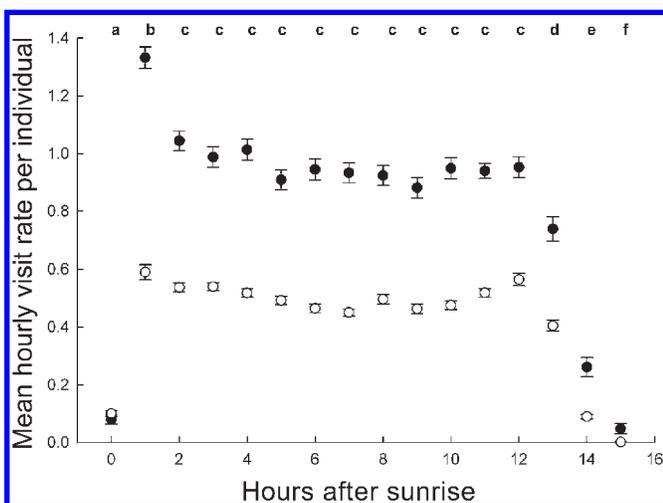


FIG. 3. Mean hourly visitation rate per individual Zebra Finch at the nest (black symbols) and at the feeders (white symbols) throughout the day (expressed as number of hours after sunrise). Letters indicate significant differences between hours according to post hoc tests for nest data. Post hoc tests for feeder data gave exactly the same pattern except that hour 12 did not differ significantly from hours 1–3.



FIG. 4. Mean visitation rate by Zebra Finches at the feeders (number of feeder visits per bird per day) for breeding stages: egg (laying or incubating), young nestling (<6 days old), old nestling (≥6 days old), fledgling (feeding dependent young ≤10 days after fledging), and post-breeding (breeding adults >10 days after fledging). The letters indicate significant differences between stages according to post hoc tests.

and breeding stage as a fixed factor:  $F = 64.01$ ,  $df = 4$  and 275,  $P < 0.001$ ; Fig. 4). In addition, the minimum distance that parents covered daily on foraging trips varied across the reproductive attempt in a similar way to the feeder visitation rate (square-root transformed daily minimum distance to feeders: GLMM,  $F = 90.20$ ,  $df = 3$  and 195,  $P < 0.001$ ). On average, active feeders were visited daily by 92.4 ± 30.6 tagged birds. Overall, 74% of the birds were detected in at least one feeder each day, and, on average across the breeding season, each individual made 6.8 visits to the feeders per day (total of 44,349 visits to the feeders).

*Linking nestling provisioning to foraging activity.*—When the young were between 6 and 18 days of age, the females fed them on 88.9% (103 of 116) of the visits and the males on 93.2% (124 of 133) of the visits (video data; Wilcoxon signed-rank paired test:  $Z = -0.772$ ,  $P = 0.440$ ,  $n = 20$ ). Feeding occurred independently of whether a parent visited the nest alone or with its partner (chi-square test on number of visits where the parent fed or did not feed when alone and with its partner:  $\chi^2 = 0.555$ ,  $P = 0.456$ ). During each entry, parents typically fed several young in turn and often fed individual nestlings more than once. On average, birds made 14.8 ± 10.6 feeds (85.6 ± 69.5 regurgitations) per feeding visit. In addition to feeding, parents brooded the young on 23% and rearranged nesting material on 31% of their visits. Most visits were short. Analysis of video data gave a median of 3.6 min in the nest per visit (mean ± SD = 8.3 ± 11.3 min) and a median of 4.1 min in and around the nest per visit (i.e., including time in the tree between entries when the bird entered the nest multiple times in a visit; mean ± SD = 11.2 ± 15.0 min).

Parental nest visitation rate (and duration; data not shown) was correlated with the number of feeds and regurgitations per day but not with nestling crop content (Table 1). On the other hand, foraging activity was correlated with the number of commercial

TABLE 1. Parental behavior at the nest and at the feeders in relation to estimates of the amount of food received by Zebra Finch nestlings (superscript 1 = from video data, superscript 2 = from decoder data).

Parental behavior	Food received by nestlings	Statistic	<i>n</i>	<i>P</i>
Nest visitation rate <sup>1</sup>	Number of feeds h <sup>-1</sup>	$r_s = 0.507$	40 individuals	0.001 <sup>a</sup>
Nest visitation rate <sup>1</sup>	Number of regurgitations h <sup>-1</sup>	$r_s = 0.420$	40 individuals	0.007 <sup>b</sup>
Nest visitation rate (old chicks and fledglings) <sup>2</sup>	Total seeds in crop, day 12	$r_s = 0.198$	60 nests	0.129
Nest visitation rate on day 12 <sup>2</sup>	Total seeds in crop, day 12	$r_s = 0.046$	54 nests	0.738
Feeder visitation rate (old chicks and fledglings) <sup>2</sup>	Commercial seeds in crop, day 12 <sup>c</sup>	$r_s = 0.296$	69 nests	0.014 <sup>d</sup>
Distance to feeders (old chicks and fledglings) <sup>2</sup>	Commercial seeds in crop, day 12 <sup>c</sup>	$r_s = 0.246$	69 nests	0.042
Feeder visitation rate on day 12 <sup>2</sup>	Commercial seeds in crop, day 12 <sup>c</sup>	$r_s = 0.324$	69 nests	0.007
Distance to feeders on day 12 <sup>2</sup>	Commercial seeds in crop, day 12 <sup>c</sup>	$r_s = 0.332$	69 nests	0.005

<sup>a</sup>When one outlier (>30 regurgitations hour<sup>-1</sup>) was omitted:  $R = 0.479$ ,  $P = 0.002$ ,  $n = 39$ .

<sup>b</sup>When one outlier (>200 regurgitations hour<sup>-1</sup>) was omitted:  $R = 0.387$ ,  $P = 0.015$ ,  $n = 39$ .

<sup>c</sup>We only considered the number of commercial seeds in relation to feeder data because natural seeds were not collected in the feeders. None of the seed counts (natural or commercial separately) were correlated with nest data, and natural seed count was not correlated with feeder data.

<sup>d</sup>See Figure 5.

seeds in the nestlings' crops (Table 1 and Fig. 5). Surprisingly, however, a nestling's condition was independent of its crop content on day 12 ( $r_s = 0.174$ ,  $P = 0.099$ ,  $n = 91$  nests) and also of nest ( $r_s = -0.179$ ,  $P = 0.191$ ,  $n = 55$  nests) and feeder visitation rate ( $r_s = 0.119$ ,  $P = 0.320$ ,  $n = 72$  nests). Lastly, pair feeder visitation rate and the minimum distance covered per day on foraging trips were correlated with brood size on day 12 ( $r_s = 0.362$ ,  $P = 0.002$ ,  $n = 73$  nests, and  $r_s = 0.348$ ,  $P = 0.003$ ,  $n = 73$ , respectively), but nest visitation rate was not ( $r_s = 0.234$ ,  $P = 0.065$ ,  $n = 63$ ).

Even though  $32 \pm 2.9\%$  of parental foraging activity did not occur at the feeders (as estimated from the proportion of natural seeds in nestlings' crops;  $n = 90$  nests), there was no evidence that individuals' foraging activity in the feeders was systematically biased. First, parents that visited the feeders less were not foraging more on natural seeds, because the proportion of commercial seeds in the nestlings' crops (i.e., number of commercial seeds/total seeds) did not increase with feeder visitation rate ( $r_s = 0.103$ ,

$P = 0.400$ ,  $n = 69$  nests), and the number of commercial seeds in the nestlings' crops was independent of the number of natural seeds ( $r_s = 0.149$ ,  $P = 0.160$ ,  $n = 91$  nests). Second, some pairs did not consistently rely on the feeders more than others, because the extent of feeder use was independent of the distance to the nearest active feeder (proportion of commercial seeds vs. distance between nest and closest active feeder:  $r_s = 0.172$ ,  $P = 0.159$ ,  $n = 69$  nests). Moreover, that the proportion of commercial seeds in crops on days 11 and 12 were not correlated ( $r_s = 0.209$ ,  $P = 0.149$ ,  $n = 47$  nests) also indicates that feeder use by different pairs was equivalent.

On average, individuals made 0.7 visits to the feeders for each visit to the nest. On a daily basis, individuals that visited their nest more often also visited the feeders more often (GLMM on first breeding attempt with nest visitation rate as a response variable, and feeder visitation rate and square-root transformed minimum distance per trip as fixed factors:  $F = 8.41$ ,  $df = 1$  and  $383$ ,  $P = 0.004$ ), regardless of the distance covered per foraging trip ( $F = 0.80$ ,  $df = 1$  and  $383$ ,  $P = 0.373$ ).

*Cost of parental care and future breeding.*—On average, breeding birds (from egg laying to caring for fledglings) covered a minimum recorded distance of  $6.4 \pm 3.8$  km daily, but that distance varied greatly among individuals ( $n = 93$  breeding individuals; range: 0.37–19.40 km). However, adult condition was not correlated with either the distance traveled (male:  $r_s = 0.158$ ,  $P = 0.274$ ,  $n = 50$ ; female:  $r_s = 0.019$ ,  $P = 0.902$ ,  $n = 47$ ) or feeder visitation rate (male:  $r_s = 0.081$ ,  $P = 0.576$ ,  $n = 50$ ; female:  $r_s = 0.061$ ,  $P = 0.686$ ,  $n = 47$ ).

Among pairs that renested within the main breeding season (September–December) after a successful breeding attempt, we did not detect any effect of the pair foraging activity during the first breeding attempt on the clutch size of the second attempt (Spearman partial correlation between second clutch size and feeder visitation rate after controlling for the size of the first clutch, during nestling and fledgling stages:  $r_s = 0.022$ ,  $P = 0.914$ ,  $n = 28$ ; nestling stage only:  $r_s = 0.075$ ,  $P = 0.709$ ,  $n = 28$ ) or the hatching rate of the second attempt (i.e., proportion of the eggs that hatched, after controlling for the size of the second clutch; nestling and fledgling stage:  $r_s = 0.089$ ,  $P = 0.692$ ,  $n = 23$ ; nestling stage only:  $r_s = -0.046$ ,  $P = 0.839$ ,  $n = 23$ ). Instead, the mean number of visits the pair made to the feeder during the first breeding

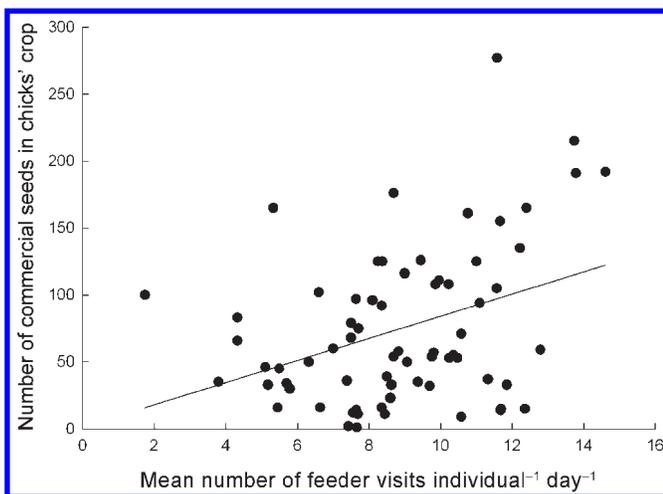


FIG. 5. Mean number of visits by parent Zebra Finches (mean of male and female partners) at the feeders per day from when nestlings were 6 days old to fledging in relation to the offspring's crop contents at 12 days of age (total number of commercial seeds in all nestlings).

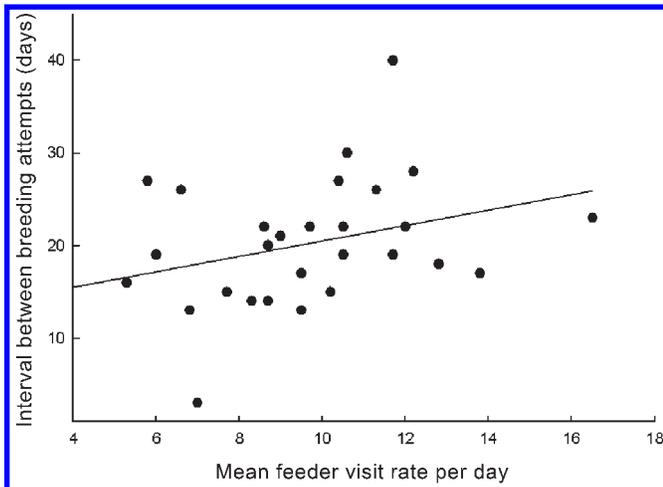


FIG. 6. Interval between the first and second breeding attempts in relation to the feeder visitation rate of Zebra Finches during nestling provisioning of the first breeding attempt. The relationship was still significant when possible outliers were omitted (interval >10 days:  $r_s = 0.419$ ,  $P = 0.023$ ,  $n = 29$ ; interval <40 days:  $r_s = 0.408$ ,  $P = 0.028$ ,  $n = 29$ ; visitation rate <16:  $r_s = 0.419$ ,  $P = 0.023$ ,  $n = 29$ ).

attempt was positively correlated with the time the parents took to renest when we considered foraging during the nestling and fledgling stages (controlling for the brood size of the first attempt:  $r_s = 0.413$ ,  $P = 0.026$ ,  $n = 30$  nests) or the nestling stage only ( $r_s = 0.436$ ,  $P = 0.018$ ,  $n = 30$ ; Fig. 6). Similarly, the total minimum distance covered by the parents per day between the feeders and their nest in the first attempt was positively correlated with the interval between breeding attempts, albeit only when both nestling and fledgling stages were considered (controlling for first brood size, nestling and fledgling stage:  $r_s = 0.370$ ,  $P = 0.048$ ,  $n = 30$ ; nestlings only:  $r_s = 0.229$ ,  $P = 0.232$ ,  $n = 30$ ). However, the number of visits to the nest during the nestling stage of the first breeding attempt had no significant effect on the latency to renest (controlling for first brood size:  $r_s = -0.359$ ,  $P = 0.092$ ,  $n = 24$ ). Lastly, the laying date of the first breeding attempt and the parents' condition were not correlated with the interval between breeding attempts (laying date:  $r_s = -0.268$ ,  $P = 0.152$ ,  $n = 30$ ; adult condition: male:  $r_s = -0.117$ ,  $P = 0.473$ ,  $n = 40$ ; female:  $r_s = -0.053$ ,  $P = 0.754$ ,  $n = 38$ ).

## DISCUSSION

Having simultaneously recorded parental care and foraging behavior of free-living Zebra Finches using an electronic monitoring system, we found that nest visitation rate of free-living Zebra Finches was surprisingly low, about one visit per hour throughout the day. Even though nestlings were fed on most visits to the nest, feeder visitation rate appeared to better approximate the nestlings' crop contents than nest visitation rate. Also, parents that visited the feeders more often and covered larger estimated distances during the first breeding attempt took longer to initiate their subsequent breeding attempt. Taken together, our results suggest that quantification of both foraging activity and nestling provisioning may improve our understanding of parental care and investment tradeoffs.

*Foraging cost and breeding interval.*—We found that parents that had a high foraging activity and covered larger distances during the first breeding attempt took longer to renest. Because parental foraging activity increased with the amount of food delivered to the nestlings, our results suggest that, as in other species, the length of the interval between breeding attempts increased with reproductive effort in the first attempt (Møller 1993, Verboven et al. 2001, Tinbergen and Sanz 2004). In captive Zebra Finches, delayed breeding has been shown to be associated with reduced feeding rates (Lemon and Barth 1992, Wiersma and Verhulst 2005) and high levels of activity in adults (Deerenberg and Overkamp 1999), although individual quality (Blount et al. 2006) and pair attributes (Adkins-Regan and Tomaszycski 2007) may also play a role. In our free-living population of Zebra Finches, foraging rate explained ~40% of the variation in breeding interval. It is possible that this effect would be larger in a population without supplementary feeding. In addition, our finding that foraging activity delayed renesting but had no detrimental effect on the clutch size of the second breeding attempt is consistent with some captive studies of Zebra Finches (Deerenberg and Overkamp 1999, Wiersma and Verhulst 2005) and some studies of free-living birds in other species (e.g., Tinbergen and Sanz 2004). Our data thus suggest that Zebra Finches may delay renesting to regain condition and mitigate the effect of previous breeding on future reproduction. Nonetheless, interclutch interval contributes significantly to lifetime reproductive success in captive Zebra Finches (Lemon and Barth 1992) and probably in the wild (Zann 1996). Indeed, we may expect selection to favor prompt renesting in such a short-lived species that breeds opportunistically in very unpredictable, arid environments where good environmental conditions typically prevail for only a short period after rain has initiated primary production (Zann 1996). It is believed that this same selection pressure has favored accelerated sexual development in this species, which can breed at the age of only 70 days (Zann 1996).

*Provisioning rates in free-living Zebra Finches.*—Zebra Finches at our study site visited their nests very infrequently, with an average of 1 visit hour<sup>-1</sup> throughout the day. We expect that the nest visitation rate would be even lower without supplementary feeding (M. M. Mariette and S. C. Griffith unpubl. data), given that birds in natural conditions may travel up to several kilometers from their nests to find food in the arid zone (Zann 1996). This frequency of nest visitation is remarkably lower than that reported for most other model passerine species, including insectivorous and seed-eating ones. Insectivore examples include European Starlings (*Sturnus vulgaris*; 8 visits h<sup>-1</sup>; Wright et al. 1998), Pied Flycatchers (*Ficedula hypoleuca*; 20 visits h<sup>-1</sup>; Moreno et al. 1999), Tree Swallows (*Tachycineta bicolor*; 20 visits h<sup>-1</sup>; Murphy et al. 2000), Blue Tits (*Parus caeruleus*; 35 visits h<sup>-1</sup>; Grieco 2002), and Barn Swallows (*Hirundo rustica*; 15 visits h<sup>-1</sup>; Spencer and Bryant 2002). Seed-eaters include House Finches (*Carpodacus mexicanus*; 6 visits h<sup>-1</sup>; Nolan et al. 2001) and House Sparrows (*Passer domesticus*; 12 visits h<sup>-1</sup>; Nakagawa et al. 2007). By contrast, the nest visitation rate of Zebra Finches is similar to that reported for some parrots (e.g., Crimson Rosella [*Platycercus elegans*]; 0.8 visits h<sup>-1</sup>). This low nest visitation rate, associated with the capacity of Zebra Finches to carry large loads of seeds in their crops to feed their nestlings, may result from the scarcity of food in the Australian semiarid habitat or from the high predation pressure on

natural nests (Zann 1996, Griffith et al. 2008), which favors a low nest visitation rate (Martin et al. 2000). This pattern of visitation also contrasts markedly with those reported for Zebra Finches in aviaries (Burley 1988, Royle et al. 2006, Foster and Burley 2007), where feeding bouts have been described as frequent (Foster and Burley 2007). Similarly, incubation bouts of wild-captured Zebra Finches in aviaries are ~50% shorter than in the wild (Zann and Rossetto 1991). This discrepancy highlights some disparities in the cost of parental care between captive and free-living populations. Although it may not invalidate the significant contribution of captive Zebra Finch studies in the field of parental care (e.g., Burley 1988, Royle et al. 2002), the difference between wild and captive populations warrants further research.

*The relevance of measuring foraging activity for the study of parental care.*—Parental foraging activity was related to the nestlings' crop contents, but nest visitation rate was not, even though (1) on a daily basis, individual nest and feeder visitation rate covaried; (2) feeding occurred on 91% of the nest visits; and (3) nest visitation rate was positively correlated with nestling feeding rate (number of feeds or regurgitations). These discrepancies may be related to variation in load size between visits and possibly in the number of seeds per regurgitation. Number of feeding trips is a reliable estimator of provisioning rate in single-prey loaders (e.g., Maigret and Murphy 1997), but nest visitation rate may be a poor estimate of the amount of food delivered to the offspring in species whose load size varies greatly between visits (e.g., Wright et al. 1998, Sejberg et al. 2000; but see Nolan et al. 2001, Grieco 2002). In any species, however, if the cost of acquiring food for the offspring varies among individuals, measuring foraging activity may prove valuable in estimating the cost of parental care, considering that foraging activity may (Weimerskirch and Lys 2000, Clutton-Brock et al. 2003, present study) or may not (Takahashi et al. 2003) be proportional to provisioning rate. Finally, whether parental foraging and provisioning rate correlate with nestling condition (e.g., Magrath et al. 2007, Schwagmeyer and Mock 2008) or do not (e.g., Sætre et al. 1995, Wright et al. 1998, Moreno et al. 1999, Takahashi et al. 2003) may depend on the determinants of offspring growth, including feeding rate but also nestling metabolic rate, environmental conditions, and parasite load (e.g., Møller 1993, Moreno et al. 1999, Ewen et al. 2009).

*PIT-tag monitoring: Pros and cons.*—To our knowledge, the present study is the first to extend the PIT-tag monitoring system to foraging, in conjunction with nest monitoring. This allowed us to continuously record, over a moderate spatial scale, the majority of parental foraging activity in free-ranging individuals. Although its use is limited to species that are drawn to fixed locations, PIT-tag monitoring could be used with a range of species, from honeyeaters (Ewen et al. 2009) to crows (e.g., Canestrari et al. 2008) or other species that can use feeders that contain seeds, sugar water, meat, or mealworms. As with other remote-monitoring systems (e.g., Rose 2009), the application of thresholds for data processing led to slight inaccuracies (see above). However, our estimate of nest visitation rate was unlikely to be greatly confounded by our processing method, because there were long intervals between bouts of activity at the nest or feeder, regardless of how we grouped these bouts of activity into visits (Fig. 2) and because video data supported our approach. In addition, the small proportion of readings that went undetected led to ~20% of visits of unknown

duration but to an overall detection probability of 99.2%. Finally, even though parents partially relied on natural food, the foraging activity that we measured at feeders was likely an unbiased estimate of overall foraging activity. Therefore, although our method was crude in comparison with fine-scale telemetry (Naef-Daenzer and Keller 1999, Canestrari et al. 2008) or the sophisticated devices used on larger taxa (e.g., Weimerskirch and Lys 2000, Gray and Hamer 2001, Takahashi et al. 2003), its limitations were partly compensated for by the large sample sizes both in number of individuals ( $n = 145$  individuals and 66 nests) and number of days per individual (mean  $\pm$  SD =  $45 \pm 19$  days). For example, we were able to show that parental foraging activity varied considerably between different stages of the breeding cycle, presumably reflecting variation in nestling food requirements and the time available for foraging (e.g., Weimerskirch and Lys 2000).

In summary, the difficulty of measuring individual variation in the cost of parental care has hindered empirical tests of family conflict theory and our understanding of investment tradeoffs (Clutton-Brock 1991, Sætre et al. 1995, Takahashi et al. 2003). Using an electronic monitoring system in a free-living population of Zebra Finches, we were able to simultaneously quantify the foraging and provisioning behaviors of parents caring for their young and demonstrate that foraging costs impinge on future reproduction. The application of this or similar technology, if combined with the manipulation of offspring demand or food-patch quality, may improve our understanding of parental care and life-history strategies in free-living populations. In addition, it may facilitate the study of optimal and social foraging strategies in the wild.

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