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FEATURED STUDENT RESEARCH PAPER

Visitation rate, but not foraging range, responds to brood size manipulation in an aerial insectivore

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Abstract

Life history theory predicts that increased investment in current offspring decreases future fecundity or survival. Avian parental investment decisions have been studied either via brood size manipulation or direct manipulation of parental energetic costs (also known as handicapping). However, we have limited experimental data on the potential interactive effects of these manipulations on parent behavior. Additionally, we know little about how these manipulations affect spatial foraging behavior away from the nest. We simultaneously manipulated brood size and parental costs (via added weight in the form of a GPS tag) in wild female barn swallows (*Hirundo rustica*). We measured multiple aspects of parent behavior at and away from the nest while controlling for measures of weather conditions. We found no significant interactive effects of manipulated brood size and parental costs. Both sexes increased their visitation rate with brood size, but nestlings in enlarged broods grew significantly less post-brood size manipulation than those in reduced broods. Foraging range area was highly variable among GPS-tagged females but was unaffected by brood size. As such, increased visitation rate in response to brood size may be more energetically costly for far-ranging females. GPS-tagged females did not alter their visitation rate relative to un-tagged birds, but their mates had higher visitation rates. This suggests that GPS tagging may affect some unmeasured aspect of female behavior, such as prey delivery. Our findings indicate that investigation of foraging tactics alongside visitation rate is critical to understanding parental investment and the benefits and costs of reproduction.

Significance statement

Avian parental investment decisions have been studied by either brood size manipulation or direct manipulation of parental costs, but rarely both simultaneously. We simultaneously manipulated brood size and parental costs (via addition of a GPS tag) in a wild avian system, allowing us to examine interactive effects of these manipulations. Additionally, studies of parental investment often examine behaviors at the nest, but measurements of parental care behavior away from the nest are rare. Our study is unique in that we measured multiple aspects of parental care, including spatial foraging behavior tracked with GPS tags. We found no interactive effects of manipulated brood size and parental costs on visitation rate or nestling growth, and spatial foraging behavior of females was individually variable. Documenting foraging tactics alongside visitation rate is critical to understanding parental investment because the same visitation rate might be more costly for far-ranging females.

Keywords Brood size manipulation · GPS tagging · *Hirundo rustica* · Life-history trade-offs · Parental care · Spatial foraging behavior

Introduction

Life-history theory predicts that parents caring for dependent offspring face trade-offs among current reproduction, future reproduction, and survival (Williams 1966; Stearns 1992). Increased parental investment in a breeding attempt may result in more offspring or offspring with a greater chance of surviving to reproduce, but may also reduce future fecundity and survival of the parents, which is

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referred to as the cost of reproduction (Clutton-Brock 1991). Numerous studies have examined parental investment decisions in avian systems through either brood size manipulation, where the number of offspring a parent cares for is altered (e.g., Gow and Wiebe 2014; Baldan et al. 2019), or through direct manipulation of parental costs—e.g., increasing flight costs by adding weight or clipping feathers (e.g., Harrison et al. 2009; Serota and Williams 2019). Important knowledge gaps remain in the study of parental investment: brood size manipulation and direct manipulation of parental costs are rarely conducted simultaneously, limiting our ability to understand the interactive effects of offspring demand and parental condition on parent behavior (but see Wright and Cuthill 1990a, b; Ratz and Smiseth 2018). In addition, most brood size manipulation studies have focused on parent behavior at the nest, such as visitation rate, and, as such, we know little about spatial foraging behavior away from the nest (Madden 2020).

Brood size manipulation involves altering nestling demand by adding and/or removing nestlings and measuring parent response. Short-term brood size manipulations, where brood size is manipulated for a day or two, are used to examine the behavioral responses of parents to change in brood size (e.g., Magrath et al. 2007; Koenig and Walters 2012; Gow and Wiebe 2014). Long-term manipulations, where brood size is manipulated early in the rearing period and then maintained until fledging, are used to assess both behavioral responses of parents and costs of increased parental care for parents (e.g., Horak et al. 1998; Fokkema et al. 2016). In short-lived species, where current reproduction may be favored over survival (Stearns 1992), parents are expected to scale their investment to brood size, increasing their investment in enlarged broods because they have a greater potential reproductive output and decreasing their investment in reduced broods because the costs of maintaining effort are no longer warranted by the lower potential reproductive output (Williams 1966; Winkler 1987). Parental investment decisions are generally assessed by measuring parental care, such as nest visitation rates: increased visitation rate to enlarged broods is interpreted as willingness to increase investment in current offspring if offspring demand and potential reproductive output are increased (Gow and Wiebe 2014; Madden 2020). Consistent with theoretical expectations, in short-lived species, parents of both sexes generally increase their visitation rate with brood size, perhaps reflecting increased willingness to invest in reproduction at a cost to survival (Gow and Wiebe 2014; Madden 2020; e.g., Garcia-Navas and Sanz 2010; Koenig and Walters 2012). In some cases, parents may show non-linear responses to manipulation, with parental care and energy expenditure leveling off at high brood sizes (e.g., Tinbergen and Verhulst 2000).

Parental investment is also studied via direct manipulation of parental costs (sometimes called handicapping), in which parents' flight costs are increased by attaching weights or feather clipping, which increases the energy required for both self-maintenance and caring for offspring and thus may affect parental condition (e.g., Harrison et al. 2009; Serota and Williams 2019). Most studies on short-lived birds report decreases in parental care when parental costs are increased, which is interpreted as decreased investment in current offspring due to increased costs of care (e.g., Tajima and Nakamura 2003; Harrison et al. 2009). In some cases, increasing parental costs does not affect parental care, which may reflect willingness of parents to maintain investment in current offspring despite increased costs of care (e.g., Sanz et al. 2000; Griffioen et al. 2019). Surprisingly, some studies report that increasing parental costs leads to increased parental care (e.g., Ratz and Smiseth 2018; Ratz et al. 2020). This may occur if increased energetic costs trigger a terminal investment pattern, where parent condition drops below a threshold value, reducing future survival prospects, and thus parents invest heavily in reproduction (Ratz et al. 2020). Studies manipulating parental costs also examine conflict between mates over level of investment in offspring. When energetic costs of one partner are experimentally increased, unmanipulated parents often partially compensate for decreases in their mate's parental care by increasing their own parental care, but in some cases, unmanipulated parents fully compensate for their mate or do not compensate at all (Harrison et al. 2009).

Our understanding of life history trade-offs is limited by lack of simultaneous manipulations of nestling demand via brood size manipulation and parental condition via increased energetic costs of care (but see Wright and Cuthill 1990a, b; Ratz and Smiseth 2018). Brood size manipulation and increased parental costs are expected to have interactive effects on parent investment if the costs of caring for large broods are substantially increased relative to small broods, while interactive effects are not expected if manipulated parental costs lead to only a small divergence in cost of care for large broods (Ratz and Smiseth 2018). Of the few studies that have performed simultaneous manipulations of brood size and parental costs, empirical results have been mixed. Some studies found interactive effects of brood size and parental costs on parental care (Wright and Cuthill 1990a), while others found no interactive effects of the treatments (Wright and Cuthill 1990b; Ratz and Smiseth 2018). Further investigation of interactive effects of brood size and parental costs on parent behavior is warranted, and this necessitates studies performing both manipulations in concert.

Visitation rate is the most common measure used to investigate avian parental investment decisions following brood size manipulation or direct manipulation of parental costs (brood size manipulation: Gow and Wiebe 2014;

Madden 2020; manipulation of parental costs: Serota and Williams 2019 and references therein). This frequent use of visitation rate likely reflects that many studies focused on physiological and fitness costs of reproduction, rather than parental care, track visitation rate as a “proof of concept” to ensure that brood size manipulation or manipulation of parental costs had some effect on parent behavior. However, central place foraging theory (Orians and Pearson 1979) suggests that parental investment may be poorly captured by measuring visitation rate alone, because parents may be able to increase visitation rate while altering other aspects of foraging behavior to avoid costs: when nestling demand is increased (e.g., via brood size manipulation), parents may increase visitation rate and reduce search time and/or travel distance while foraging, resulting in delivery of smaller prey loads or lower quality prey per visit (Houston and McNamara 1985; Mathot et al. 2017; Baldan et al. 2019). A growing number of studies have tracked aspects of parental behavior other than visitation rate during nestling provisioning, including prey type, prey load size, and diversity of prey items delivered (Madden 2020). As predicted, some have reported that manipulation of brood size or parental costs affects prey type and/or load size (e.g., García-Navas and Sanz 2010; Mathot et al. 2017; Serota and Williams 2019), but others have found no effects on prey delivered (e.g., Hinde and Kilner 2007).

As most studies have not been able to directly track individual parents using GPS tags when they are providing parental care, we have limited understanding of how spatial foraging behavior, such as travel distance during foraging, changes with brood size manipulation and direct manipulation of parental costs. To our knowledge, only two brood size manipulation studies have examined spatial foraging behavior (Aho et al. 2010; Gow and Wiebe 2014). Aho et al. (2010) tracked spatial foraging behavior of Eurasian treecreepers with control and manipulated broods by directly observing foraging behavior. They reported that males with enlarged brood foraged closer to the nest than control males in one year, while females showed no difference in foraging distance. Gow and Wiebe (2014) tracked spatial foraging behavior of Northern Flickers using radiotelemetry and reported decreased visitation rate to reduced broods relative to control broods, but no effect of brood size manipulation on foraging distance from the nest. Additionally, Serota and Williams (2019) manipulated parental costs in European starlings via wing-clipping and used automated radiotelemetry to detect decreased overall parent activity, despite maintenance of visitation rate. This finding may indicate shifts in spatial foraging behavior, but movements were not tracked. Advances in tracking technology, including the recent advent of miniaturized GPS tags which can be deployed on small songbirds (Hallworth and Marra 2015), are now providing new opportunities to accurately track parent movements.

Here, we experimentally manipulated both brood size and parental costs (through the addition of a 1-g GPS tag) in wild female barn swallows. Our study is unique in that (1) our simultaneous manipulation of brood size and parental costs allows us to study potential interactions, which are poorly understood, and (2) we examined multiple dimensions of parental care behavior, including spatial foraging behavior, which is now possible with recent advances in tracking technology. The addition of a GPS tag is expected to increase flight costs in two ways: by increasing mass and by increasing drag. Geolocators placed on birds significantly increase drag during flight (Bowlin et al. 2010); we expect similar effects of GPS tags. Due to their energetically demanding flight behavior and extensive parental care, barn swallows are an ideal study system to examine potential interactions between brood size and parental costs. Both sexes feed altricial offspring, but females provide the majority of parental care (songbirds: Trivers 1972; barn swallows: Aberle 2014; Costantini et al. 2014). Additionally, we have limited understanding of how brood size and parental costs affect spatial dimensions of parental care in aerial insectivores like swallows. In this study, we addressed the following questions: (1) How do brood size manipulation and manipulation of parental costs via GPS tagging affect female visitation rate, and how does brood size manipulation affect female foraging distance from the nest? (2) How do brood size manipulation and mate tagging affect male visitation rate? (3) How do brood size manipulation and GPS tagging of females affect nestling growth? Graphical representations of our predictions are outlined in Fig. 1. Because environmental variables are known to affect aerial insect abundance and parental care behavior of aerial insectivores (e.g., Grüebler et al. 2008; Schifferli et al. 2014; Cinque et al. 2021), we extracted temperature, wind speed, and precipitation data from weather stations close to each field site for the duration of the study.

Methods

Study sites

We carried out our brood size manipulation and GPS tagging experiment at 14 barn swallow breeding sites in Boulder County, CO (40.0150° N, 105.2705° W; Table S1 – Online Resource 1) from June 14th to July 13th, 2019, and from June 6th to July 5th, 2020. Details of treatment assignment are in the supplementary methods (Online Resource 1). To accurately record nest phenology, nests at study sites were checked every three to 4 days from mid-May through late-August using an 88-cm telescoping lighted mirror (EEEkit, San Ramon, CA, USA). Candidate experimental nests were checked every other day around their estimated hatch date.

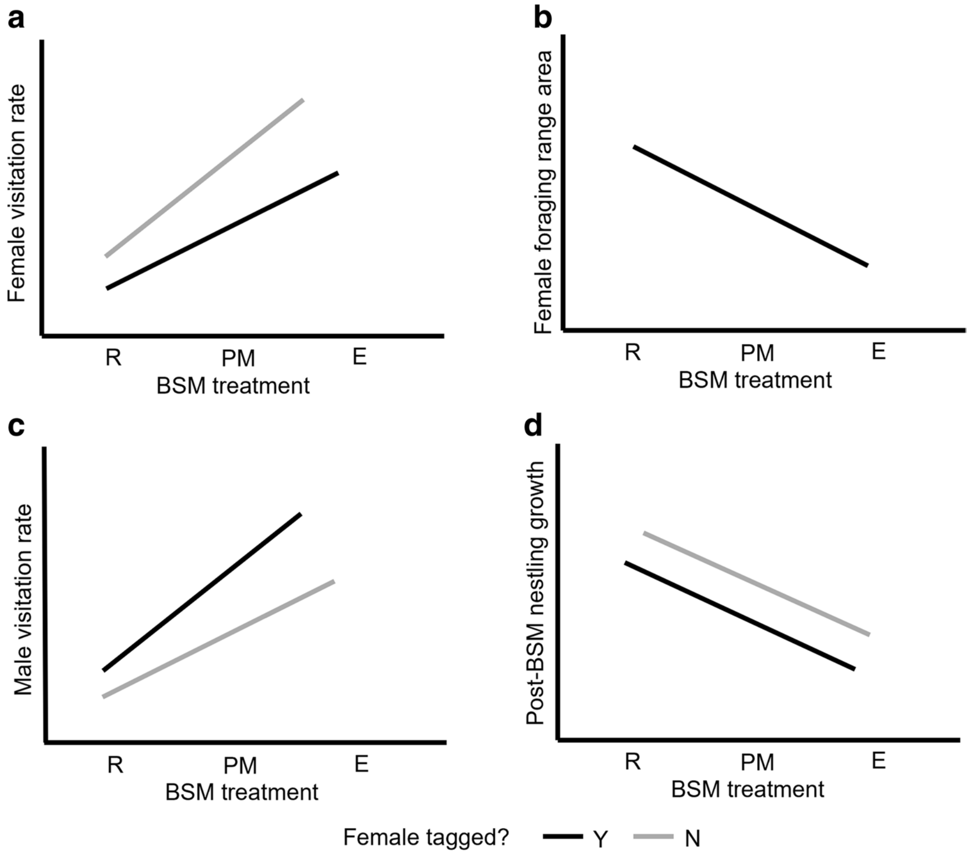

Fig. 1 Graphical predictions for effects of brood size manipulation (BSM; R = reduced, PM = pre-manipulation, E = enlarged) and GPS tagging of females (female tagged = black, female not tagged = gray) on (**a**) female visitation rate, (**b**) female foraging range (measured for tagged females only), (**c**) male visitation rate, and (**d**) post-brood size manipulation nestling growth. We expected that both sexes would increase their total visitation rate following brood enlargement and decrease their total visitation rate following brood reduction (**a** and **c**). We also expected that GPS-tagged females would have lower visitation rates than non-tagged females, and that males of tagged mates would have higher visitation rates than males with non-tagged mates (**a** and **c**). Based on the framework of Ratz and Smiseth (2018), we predicted that the increase in self-maintenance and reproductive costs caused by the GPS tag would lead to interactive effects of brood size manipulation and tagging on female visitation rate (**a**). However, it is also feasible that we might not observe interactive effects if manipulated parental costs lead to only a small divergence in cost of care for large broods. Similarly, we expected interactive effects of brood size manipulation and tagging of their mates on male visitation rate, as males might be more willing to compensate for reduced mate care at high brood sizes (**c**; Wright and Cuthill 1990a). For tagged females only, we expected that brood enlargement would lead to decreased foraging range area, while brood reduction would lead to increased foraging range area (**b**). Finally, we predicted that post-manipulation nestling growth would be lower in enlarged than reduced broods and lower in nests with tagged females than those with non-tagged females, but we did not expect interactive effects on nestling growth (**d**). Figure created using PowerPoint (Microsoft Corporation 2021)

Capture and GPS tagging

We captured all experimental females ($n = 36$) and most experimental males ($n = 30$) with mist nets or by hand four to six days post-hatch, prior to the brood size manipulation (Fig. 2). Captured birds were equipped with US Geological Survey aluminum-numbered bands (National Band and Tag CO., Newport, KY, USA) and, to allow identification by sight from a distance, unique plastic color band combinations. We fitted females in the tagged treatment ($n = 20$) with a 1-g “PinPoint 10” GPS tag (Lotek Wireless, Inc., Newmarket, ON, Canada), using a Rappole leg-loop harness of elastic beading string (Stretch Magic) and crimping beads. We chose to GPS-tag only females because we wanted to maximize our sample size for a single sex and females provide the majority of parental care (songbirds Trivers 1972; barn swallows Aberle 2014; Costantini et al. 2014). These tags provide high-resolution spatial data with an accuracy of ~ 10 m (Hallworth and Marra 2015). We programmed the GPS tags to record coordinates every 10 min from 0700 to 0900 h each morning, during the peak foraging time for barn swallows (Maguire and Safran 2010; Hund et al. 2015), when nestlings were 6–12 days old. This schedule maximized the

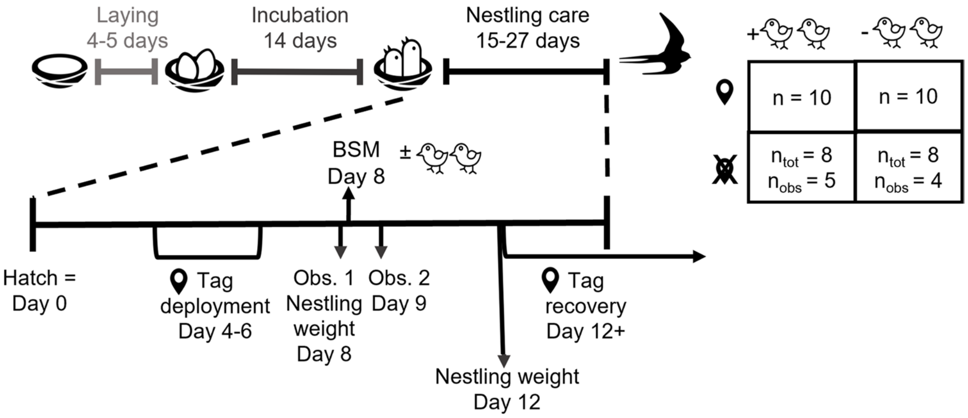

Fig. 2 A visual depiction of our brood size manipulation (BSM) and GPS tagging experiment design. We deployed GPS tags on some experimental females 4 to 6 days post-hatch and later recovered tags. Eight days post-hatch, we manipulated the brood size of all experimental nests. Nestlings were weighed on day eight and day 12, allowing us to calculate post-manipulation growth. Immediately prior to brood size manipulation and one day after manipulation, we completed behavioral observations at experimental nests. Behavioral observations were carried out at all nests with GPS-tagged females, but at only some nests with control females. For non-tagged nests, n_{obs} gives the sample size of nests where observations were completed, while n_{tot} gives the total sample size of all manipulated nests where nestling growth was measured. Details on nesting chronology are from Brown and Brown (2020). The icons are from the Noun Project: nests by Nick Bluth, swallow by Laymik, and nestling by darwis. Figure created using PowerPoint (Microsoft Corporation 2021)

frequency at which coordinates were recorded while still allowing us to obtain GPS data for several days before and after brood size manipulation (see below). Once nestlings were 12 days old, we began efforts to recapture birds to recover GPS tags.

Brood size manipulation experiment

When nestlings in an experimental nest were eight days old, within a few hours after the first behavioral observation (see "Behavioral observations" below), two nestlings were marked with color bands to allow identification and transferred from the reduced to the enlarged nest in a cloth bag placed in a plastic container with no lid (Fig. 2). Details about selection of nestlings for transfer are in the supplementary methods (Online Resource 1). We minimized the time that nestlings spent out of the nest (range = 2–45 min, mean = 26 min; Table S2). We viewed a female's initial brood size as the optimal number of nestlings for her current condition (Drent and Daan 1980) and thus transferred a fixed number of nestlings (two), as opposed to creating broods of pre-determined sizes (e.g., reduced = 2, enlarged = 6). To minimize loss of experimental nests to predators, we manipulated brood size 8 days post-hatch because mortality due to predation occurs more frequently in younger nestlings (RJS, unpubl. data). Transferred nestlings remained in their new nests until fledging 11–20 days after the brood size manipulation.

Behavioral observations

Focal observations were conducted at each nest before and after brood size manipulation to estimate visitation rate. Trained observers conducted two 1-h in-person or camera-recorded observations of each nest: one observation on day eight post-hatch prior to the brood size manipulation and a second observation on day nine (day 10 for one nest) after the BSM (Fig. 2). We expected one day to be long enough for parents to respond to changes in brood size based on reports of rapid behavioral adjustments to brood size manipulation (e.g., Magrath et al. 2007; Koenig and Walters 2012). This study design allowed us to compare visitation rates following brood enlargement or reduction to pre-manipulation measures for the same nest, such that each individual parent could serve as their own control. It was not possible for us to randomize the order of our pre-manipulation "control" measure and our treatment measures because we needed to maintain the brood size manipulation through fledging as part of a concurrent study of the physiological and fitness costs of reproduction (McDermott 2022). As such, pre-manipulation measures always occurred when nestlings were one day younger than treatment measures. We expect visitation rate to increase with age (Zielinski and Wojciechowski 1999), which should be considered when interpreting our results.

At peak foraging time, and concurrent with the data collected by GPS tags, behavioral observations were carried out between 0600 and 1030 h (following Vitousek et al. 2017). For in-person observations, observers watched the nest from a blind 2–13 m from the nest, with the exact placement dependent on the layout of the site. Before starting an observation, observers waited in the blind for at least 15 min or until parents had stopped alarm calling and resumed normal activities, up to 25 min. Behavioral observations were carried out at the nests of all GPS-tagged birds but only some non-tagged birds due to limited field time (see Fig. 2 for sample sizes).

Eight of the 22 separate parental behavior observations in 2020 were recorded using a Hero Session or Hero4 Session Go Pro camera (GoPro Inc., San Mateo, CA, USA) and later scored by a single observer (SAM) who had also conducted most in-person behavioral observations. For camera-recorded observations, we set up cameras 0.94–1.02 m from the nest. We used the same 15–25-min acclimation period for camera-recorded observations as for in-person observations. Camera-recorded observations were equally distributed across brood size manipulation and tagging treatments.

For both in-person and camera-recorded observations, observers logged parental care behavior on iPads or iPhones (Apple Inc., Cupertino, CA, USA) using “Animal Behavior Pro” (Newton-Fisher 2020). Birds were sexed based on unique combinations of color bands, the presence of the GPS tag on the female, and sexual dimorphism in breast color and tail streamer length. Breeding pairs often had very distinct color combinations and color bands on different legs, aiding in identification. In 30-min test observations, behavioral observation data were highly consistent among observers (Table S4 – Online Resource 1) and between in-person and camera-recorded observations (Table S5 – Online Resource 1). It was not possible to record parental care data blind because our study involved observation of focal animals in the field, and the brood size and tagging status of individuals could not be hidden.

We calculated visitation rate from behavioral observation records as the number of visits to the nest per hour because all types of visits are a form of parental investment. Parents fed nestlings on most visits to the nest, and also sometimes brooded nestlings, rearranged nest contents, removed nestling fecal sacs, or perched on the nest rim. Similarly, per-capita visitation rate was calculated as the number of visits per hour per nestling.

Post-manipulation nestling growth

Nestlings from experimental nests were weighed eight days post-hatch during the brood size manipulation and 12 days post-hatch. At 12 days, they were banded with US Geological Survey aluminum-numbered bands (National Band and Tag CO., Newport, KY, USA). We calculated per-capita post-manipulation nestling growth by subtracting the average nestling mass on day eight from the average mass on day 12, resulting in one measure of nestling growth for each experimental nest.

Statistical analyses

Estimating foraging range area

We filtered GPS locations to have a dilution of precision (a measure of the accuracy of GPS locations) of less than five, which is the recommended level for good quality data (Lotek Wireless Inc. 2018). We then estimated the minimum convex polygon foraging range area for each female parent on days 7–8 prior to brood size manipulation and 9–10 after manipulation using the R package “adehabitatHR” version 0.4.18 (Calenge 2006) in R version 3.6.1 (R Core Team 2020). The number of GPS locations used to estimate each foraging range area ranged from 8 to 26, with a median of 23. The nature and significance of our results were unaffected by using other measures of foraging distance from the nest, including average or maximum distance from the nest per day calculated using R package “geosphere” version 1.5.10 (Table S3 – Online Resource 1; Hijmans 2019). The GPS data from one reduced treatment bird was not analyzed because the tag battery died before day seven. For another bird in the reduced treatment, we have only a pre-manipulation foraging range because the tag recorded data through day seven. A limitation of our study is that our foraging range area estimates may capture both foraging and non-foraging behaviors away from the nest, such as resting or seeking extra-pair copulations. Our GPS tags do not provide sufficient information to investigate what behaviors females may have been performing away from the nest.

Model building and diagnostics

We ran linear mixed models (LMMs) using the package “lme4” version 1.1.23 (Bates et al. 2015) in R version 3.6.1 (R Core Team 2020) to test the effects of brood size manipulation and GPS tagging on total and per-capita visitation rates of both sexes and post-manipulation nestling growth, and to test the effects of brood size manipulation on female foraging range area. To account for effects of environmental variation on parental behavior, we included weather variables as covariates in our analyses. Details about weather data are in the supplementary methods (Online Resource 1). We started with models containing the relevant subsets of the following predictor variables: brood size manipulation treatment (three levels, reference = pre-manipulation (PM), enlarged (E), reduced (R)), tag treatment (all models except foraging range area; two levels, reference = no (N), yes (Y)), year (two levels, reference = 2019, 2020), an interaction between brood size manipulation and tag (all models except foraging range area), important weather variables (see “Accounting for Weather Conditions”—Online Resource 1), and an individual ID random intercept nested within a site ID random intercept. Our LMMs to test effects of brood size manipulation and GPS tagging on post-brood size manipulation nestling growth had the following differences: BSM treatment had only two levels, enlarged (reference) and reduced, and there was no individual ID random effect because there was only a single growth measurement per nest. We chose to model brood size manipulation as a categorical treatment variable, rather than modeling the effects of brood size itself, because we were most interested in the effects of change in brood size relative to the female's initial brood.

We tested the significance ($\alpha = 0.05$) of all fixed predictors and interactions using F tests with a Kenward-Roger Approximation in the package "pbkrtest" version 0.5.1 (Halekoh and Højsgaard 2014). To select our final models, we retained fixed effects critical to study design (BSM treatment, tag, year) and random effects regardless of significance, and we used backward stepwise selection for other variables (interaction between brood size manipulation treatment and tag, weather variables). Bolker et al. (2009) assert that backward stepwise selection is an appropriate strategy when used for hypothesis testing for a small number of predictors, as done here. When the effect of brood size manipulation treatment was significant, we further tested whether the enlarged and reduced treatments differed from pre-manipulation measures by calculating the differences in least squares (LS) means using the Kenward-Roger approximation in the package "lmerTest" version 3.1.2 (Kuznetsova et al. 2017). Marginal and conditional R^2 values were estimated for each model using R package "MuMIn" version 1.43.17 (Barton 2020). Marginal R^2 gives the variance explained by fixed effects alone, while conditional R^2 gives the variance explained by the full model, including fixed and random effects (Nakagawa and Schielzeth 2013).

We checked our models for violations of the assumptions of LMMs via visual inspection of diagnostic plots and Shapiro–Wilk tests, and we transformed response variables when necessary. Foraging range area was right-skewed, and thus was log-transformed in LMMs, which sufficiently improved normality and homogeneity of variance. We identified points with a Cook's distance of greater than one or a studentized residual values greater than three using the "car" package version 3.0.9 (Fox and Weisberg 2019), and when these influential outliers were present, we compared analyses including and excluding them (models with outliers: Table S6 – Online Resource 1).

Results

Pre-manipulation brood size and hatch date did not significantly differ between brood size manipulation or tagging treatment groups for the datasets used to analyze treatment effects on visitation rate and foraging range area (Tables S7–S8). For the dataset used to analyze treatment effects on post-brood size manipulation nestling growth, pre-manipulation brood size was significantly higher in non-tagged nests than tagged nests (Tables S7–S8), but initial differences are unlikely to strongly bias our results because our measure of growth involves change in weight within nests. Hatch date of experimental birds was significantly later in 2019 than 2020 for all subsets of data (Tables S7–S8).

Visitation rate (visits/hour)

Brood size manipulation affected both female and male barn swallow visitation rates (Fig. 3a,d; Tables 1, 2). Specifically, females increased their visitation rate by 3.72 visits per hour following brood enlargement (differences of LSmeans PM-E, $t_{34.5} = -2.37$, $P = 0.02$) and decreased their visitation rate 4.17 visits per hour following brood reduction (differences of LSmeans PM-R, $t_{34.9} = 2.58$, $P = 0.01$). Similarly, males increased their visitation rate by 5.24 visits per hour following brood enlargement (differences of LSmeans PM-E, $t_{33.3} = -3.31$, $P = 0.002$) and decreased their visitation rate by 4.94 visits per hour following brood reduction (differences of LSmeans PM-R, $t_{33.6} = 3.04$, $P = 0.005$). GPS-tagged females did not have significantly lower visitation rates than non-tagged females (Fig. 3a; Table 1), but males responded to mate handicapping nonetheless: males with tagged mates visited 5.32 times more per hour than those with non-tagged mates (Fig. 3d; Table 2). The effect of brood size manipulation on visitation rate did not differ by tagging treatment (interaction not significant) for either sex (females $\text{mean}_{TE} + SE = 0.92 + 3.38$, $\text{mean}_{TR} + SE = -0.41 + 3.62$, $F_{2,\,32.44} = 0.05$, $P = 0.96$; males $\text{mean}_{TE} + SE = 0.67 + 3.44$, $\text{mean}_{TR} + SE = -1.73 + 3.69$, $F_{2,\,31.11} = 0.13$, $P = 0.88$). Both female and male visitation rates were higher in 2020 than 2019 and significantly increased with temperature (Tables 1, 2).

Per-capita visitation rate did not differ significantly by brood size manipulation or GPS tagging treatment for either sex (Tables 1, 2). The effect of brood size manipulation on per-capita visitation rate did not depend on tagging treatment (interaction not significant) for either sex (females $\text{mean}_{TE} + SE = 0.46 + 1.05$, $\text{mean}_{TR} + SE = -0.58 + 1.12$, $F_{2,\,33.05} = 0.23$, $P = 0.79$; males $\text{mean}_{TE} + SE = -0.61 + 0.96$, $\text{mean}_{TR} + SE = -0.21 + 1.03$, $F_{2,\,28.49} = 0.22$, $P = 0.81$). Female and male per-capita visitation rates were not significantly affected by year but did increase with temperature (Tables 1, 2).

Foraging range area (MCP area)

Female barn swallows did not alter their foraging range area in response to brood size manipulation (Fig. 3c; Table 1), but foraging range area was highly variable

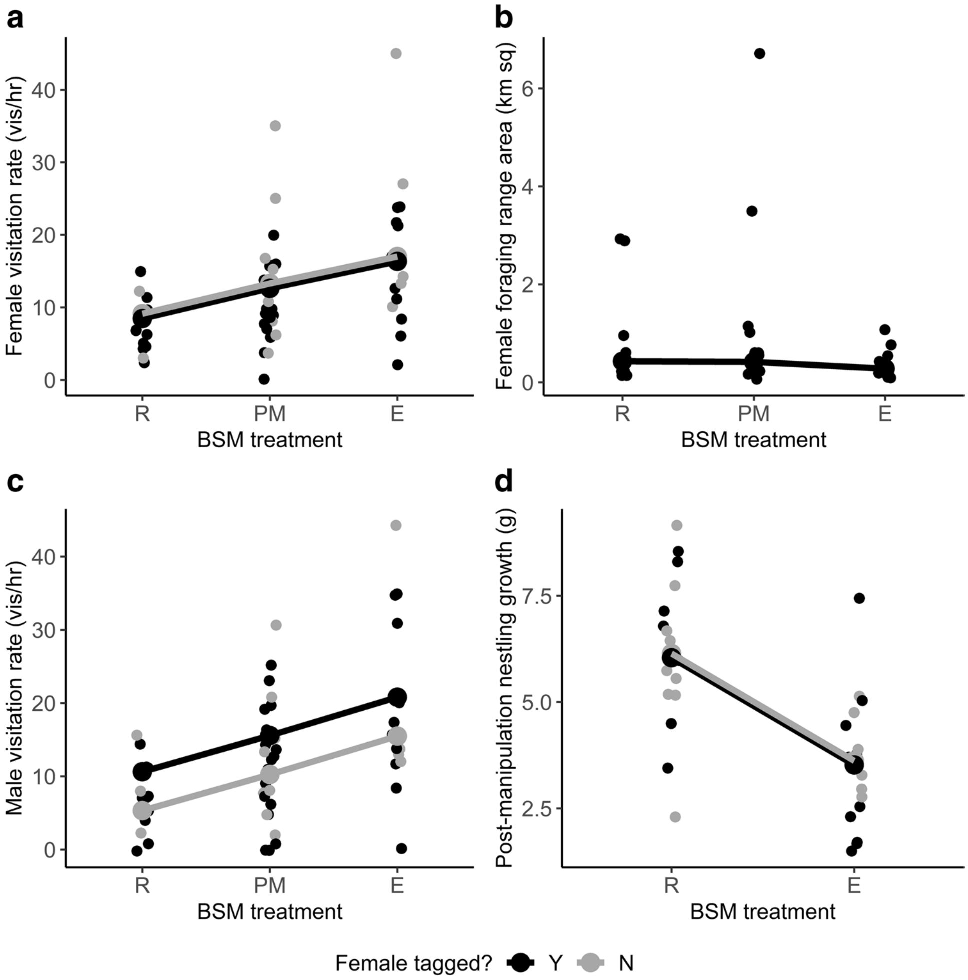

Fig. 3 The effects of brood size manipulation (BSM; R reduced, PM pre-manipulation, and E enlarged) and female GPS tagging (female tagged = black, female not tagged = gray) on (**a**) female visitation rate, (**b**) female foraging range area (BSM only), (**c**) male visitation rate, and (**d**) post-brood size manipulation nestling growth of barn swallows in Boulder County, CO. The small points show the raw data. The large points and lines show predicted results from linear mixed models averaged across two study years. All models included random intercepts for breeding site ID and individual ID (not visualized). Foraging range area was log-transformed in the model but is visualized back transformed here. For female and male visitation rate, the effects of brood size manipulation and tagging are shown at the average temperature across the study period. Influential outliers were excluded from the model results. Figure created using ggplot2 version 3.3.4 (Wickham 2016)

across individual females, ranging from 0.07 to 38.28 (mean = 1.82) km^2 (Fig. 4, Fig. S1, S2 – Online Resource 1). Foraging range area was not significantly affected by any tested weather variables. The conditional R^2 for the foraging range area model was much higher than the marginal R^2, indicating that random effects explained more variance than fixed effects. We removed an influential outlier from the model of foraging range area, but inclusion of the outlier did not affect the significance of our results (Table S6 – Online Resource 1).

Post-manipulation nestling growth (grams/nestling)

Brood size manipulation significantly affected per-capita post-brood size manipulation nestling growth, with nestlings in reduced broods gaining an additional 2.52 g more than those in enlarged broods over 5 days following manipulation (Fig. 3f; Table 3). GPS tagging did not significantly affect per-capita post-manipulation nestling growth (Table 3). Nestling growth was not significantly affected by any tested weather variables or year (Table 3). The effect of brood size manipulation on nestling growth did not depend on GPS tagging (no significant interaction; $\text{mean}_{\text{TR}} + \text{SE} = 0.69 + 1.26$, $F_{1,\,27.53} = 0.16$, $P = 0.69$).

Discussion

We examined how barn swallow parents responded to brood size manipulation and direct manipulation of parental costs in the form of a 1-g GPS tag, controlling for various weather conditions, but did not find any interactive effects of these treatments. While many studies have independently manipulated brood size or parental costs, ours is one of only a few to conduct these manipulations simultaneously (but see Wright and Cuthill 1990a, b; Ratz and Smiseth 2018). We also sought to understand the effects of brood size and GPS tagging on multiple dimensions of parental care behavior, including visitation rate and spatial foraging behavior. Parent visitation rate increased with brood size, perhaps indicating willingness to increase investment in reproduction at a potential cost to survival. In contrast, we found that female foraging range area was unaffected by brood size but was individually variable.

Table 1 Linear mixed models (LMMs) to examine the effects of brood size manipulation (BSM; reference = pre-manipulation), GPS tagging (reference = no tag), year (reference = 2019), and weather conditions on the total and per-capita visitation rate and log-transformed foraging range area (tagged birds only) of female barn swallows. F-statistics, numerator (Ndf) and denominator (Ddf) degrees of freedom, and *P*-values are provided for F tests with Kenward-Roger approximation. There were no significant interactions between brood size manipulation and GPS tagging (see "Results"), so interaction terms were not retained in our final models. Random effect variances are given for the individual ID and site ID random effects. Sample size (n) and marginal ($R^2_{\mathrm{LMM(m)}}$) and conditional ($R^2_{\mathrm{LMM(c)}}$) R^2 values are given for each model. Influential outliers were excluded from models depicted here

Female visitation rate	Fixed effects	Estimate	SE	F	Ndf	Ddf	*P*
***n* = 58**	BSM treatment	3.72	1.54	7.16	2	35.25	0.002*
$R^2_{\mathrm{LMM(m)}} = 0.40$	Enlarged	−4.17	1.58	4.88	1	25.46	0.04*
$R^2_{\mathrm{LMM(c)}} = 0.69$	Reduced	4.95	2.10	0.09	1	22.03	0.76
	Year	−0.67	2.09	17.90	1	39.58	0.0001*
	Tag	0.85	0.19				
	Temperature (°C)						
	Random effects	**Variance**	**SD**				
	Individual ID (29)	6.46	2.54				
	Site ID (13)	13.49	3.67				
	Residual	20.67	4.55				
Female per-capita visitation rate	**Fixed effects**	**Estimate**	**SE**	**F**	**Ndf**	**Ddf**	***P***
***n* = 58**	BSM treatment	−0.30	0.48	2.23	2	35.99	0.12
$R^2_{\mathrm{LMM(m)}} = 0.20$	Enlarged	0.96	0.50	2.67	1	26.18	0.11
$R^2_{\mathrm{LMM(c)}} = 0.46$	Reduced	1.05	0.62	0.03	1	24.81	0.87
	Year	−0.11	0.64	5.00	1	35.84	0.03*
	Tag	0.14	0.06				
	Temperature (°C)						
	Random effects	**Variance**	**SD**				
	Individual ID (29)	0.99	1.00				
	Site ID (13)	0.00	0.00				
	Residual	2.07	1.44				
Log-transformed female foraging range area	**Fixed effects**	**Estimate**	**SE**	**F**	**Ndf**	**Ddf**	***P***
***n* = 36**	BSM treatment	−0.40	0.36	0.62	2	21.41	0.55
$R^2_{\mathrm{LMM(m)}} = 0.06$	Enlarged	0.03	0.39	0.53	1	14.74	0.48
$R^2_{\mathrm{LMM(c)}} = 0.39$	Reduced	−0.31	0.40				
	Year						
	Random effects	**Variance**	**SD**				
	Individual ID (19)	0.15	0.39				
	Site ID (7)	0.26	0.51				
	Residual	0.74	0.86				

$^{*}\alpha < 0.05$

GPS-tagged females did not measurably alter their visitation rate, but their mates visited more often, suggesting that some unmeasured aspect of female parental care, such as the size or quality of prey delivered, may have changed.

Contrary to predicted interactive effects between brood size and handicapping (Wright and Cuthill 1990a; Ratz and Smiseth 2018), but consistent with some empirical studies (Wright and Cuthill 1990b; Ratz and Smiseth 2018; but see Wright and Cuthill 1990a), we found that brood size manipulation and GPS tagging did not have interactive effects on the visitation rate of either sex or post-brood size manipulation nestling growth. Based on predictions laid out in Ratz and Smiseth (2018), the lack of interactive effects in our study may indicate that GPS tagging does not substantially increase the costs of providing parental care to large broods relative to their reproductive value. Our sample sizes for parental visitation rates are small when divided across all GPS tagging and brood size treatments, and we may not have had sufficient power to detect interactive effects. However, we had larger sample sizes for examining nestling growth and still did not observe an interactive effect, suggesting that the joint effects of brood size manipulation and handicapping may be simply additive on nestling outcomes.

As predicted (Fig. 1a, c) and consistent with many other brood size manipulation studies on short-lived birds (Gow and Wiebe 2014; barn swallows: Costantini et al. 2014), both female and male barn swallows increased their total visitation rate with brood size, which may suggest willingness to increase investment in the current brood at a potential cost to survival. However, parental care behavior is not a perfect measure of investment, and particularly on short-time scales, changes in visitation rate and other aspects of care may reflect response to immediate begging conditions of the clutch or their mate's behavior rather than or in addition to parental decisions about potential reproductive output (e.g., Hinde and Kilner 2007). Our results contrast with those of an earlier study on our study population that did not find differences in total visitation rates unless a predator was present (Vitousek et al. 2017), perhaps due to their use of a different control group rather than a repeated-measures design as used in our study. Brood size manipulation did not significantly affect per-capita visitation rate of either sex, suggesting

Table 2 Linear mixed models (LMMs) to examine the effects of brood size manipulation (BSM; reference = pre-manipulation), GPS tagging of their mate (reference = no tag), year (reference = 2019), and weather conditions on the total and per-capita visitation rate of male barn swallows. F-statistics, numerator (Ndf) and denominator (Ddf) degrees of freedom, and *P*-values are provided for F tests with Kenward-Roger approximation. There were no significant interactions between brood size manipulation and GPS tagging (see "Results"), so interaction terms were not retained in our final models. Random effect variances are given for the individual ID and site ID random effects. Sample size (*n*) and marginal ($R^2_{\text{LMM(m)}}$) and conditional ($R^2_{\text{LMM(c)}}$) R^2 values are given for each model. Influential outliers were excluded from models depicted here

Male visitation rate	Fixed effects	Estimate	SE	F	Ndf	Ddf	*P*
***n* = 58**	BSM treatment	5.24	1.55	11.44	2	33.77	0.0002*
$R^2_{\text{LMM(m)}} = 0.36$	Enlarged	−4.94	1.59	8.55	1	22.18	0.008*
$R^2_{\text{LMM(c)}} = 0.80$	Reduced	7.31	2.37	4.68	1	19.13	0.04*
	Year	5.32	2.35	20.11	1	38.95	< 0.0001*
	Tag	0.99	0.21				
	Temperature (°C)						
	Random effects	**Variance**	**SD**				
	Individual ID (29)	8.28	2.88				
	Site ID (13)	37.46	6.12				
	Residual	20.32	4.51				
Male per-capita visitation rate	**Fixed effects**	**Estimate**	**SE**	**F**	**Ndf**	**Ddf**	***P***
***n* = 58**	BSM treatment	−0.46	0.44	1.43	2	30.70	0.25
$R^2_{\text{LMM(m)}} = 0.13$	Enlarged	0.58	0.45	2.19	1	27.50	0.15
$R^2_{\text{LMM(c)}} = 0.76$	Reduced	1.40	0.90	1.92	1	24.71	0.18
	Year	1.35	0.93	4.95	1	51.94	0.03*
	Tag	0.16	0.07				
	Temperature (°C)						
	Random effects	**Variance**	**SD**				
	Individual ID (29)	3.11	1.76				
	Site ID (13)	0.94	0.97				
	Residual	1.52	1.23				

$^*\alpha < 0.05$

that parents fully compensated visitation rate for changes in brood size, similar to some previous studies (e.g., Parejo and Danchin 2006; Sousa and Marini 2013), but in contrast with others in which large broods received lower per-capita visitation rates (e.g., Tinbergen and Verhulst 2000; Gow and Wiebe 2014). In our study, the sizes of enlarged broods were within the range of natural variation for the species, which may explain why parents were able to fully compensate for increased brood sizes in terms of visitation rate (Tinbergen and Verhulst 2000). Visitation rate differed between years in our 2-year study, highlighting the importance of multi-year brood size manipulation experiments.

Because our brood size manipulation involved transferring the largest and smallest nestling from the reduced to the enlarged brood (Online Resource 1), only enlarged broods contained foreign nestlings and there may have been greater variation in nestling mass in enlarged than reduced broods. However, there is evidence that parents in our study system cannot distinguish between foreign vs. natal nestlings (Medvin and Beecher 1986; Hubbard 2014), and paternity does not affect feeding rates (Maguire and Safran 2010). Although parents do not seem to recognize their offspring, barn swallow nestlings with unrelated brood mates may beg louder (Boncoraglio and Saino 2008). As such, our reported effects of brood size enlargement may represent combined effects of both increased brood size and increased begging intensity. Even if this is the case, our enlarged treatment would have resulted in higher perceived nestling demand, which was the desired effect. Another limitation of our study is that our pre-manipulation measures occurred when nestlings were one day younger than brood size manipulation treatment measures. Although we conducted our pre-manipulation and treatment measures only one day apart to minimize differences in age, increased age in our treatment groups still may have affected our results. Feeding rate increases with age in barn swallows (Zielinski and Wojciechowski 1999), but we reported decreased visitation rate to reduced broods despite the increase in age, suggesting that parents did respond to our brood size manipulation treatment.

Contrary to our predictions (Fig. 1c) and despite the effects of brood size manipulation on visitation rate, female foraging range area was unaffected by brood size manipulation but was exceptionally individually variable. Some

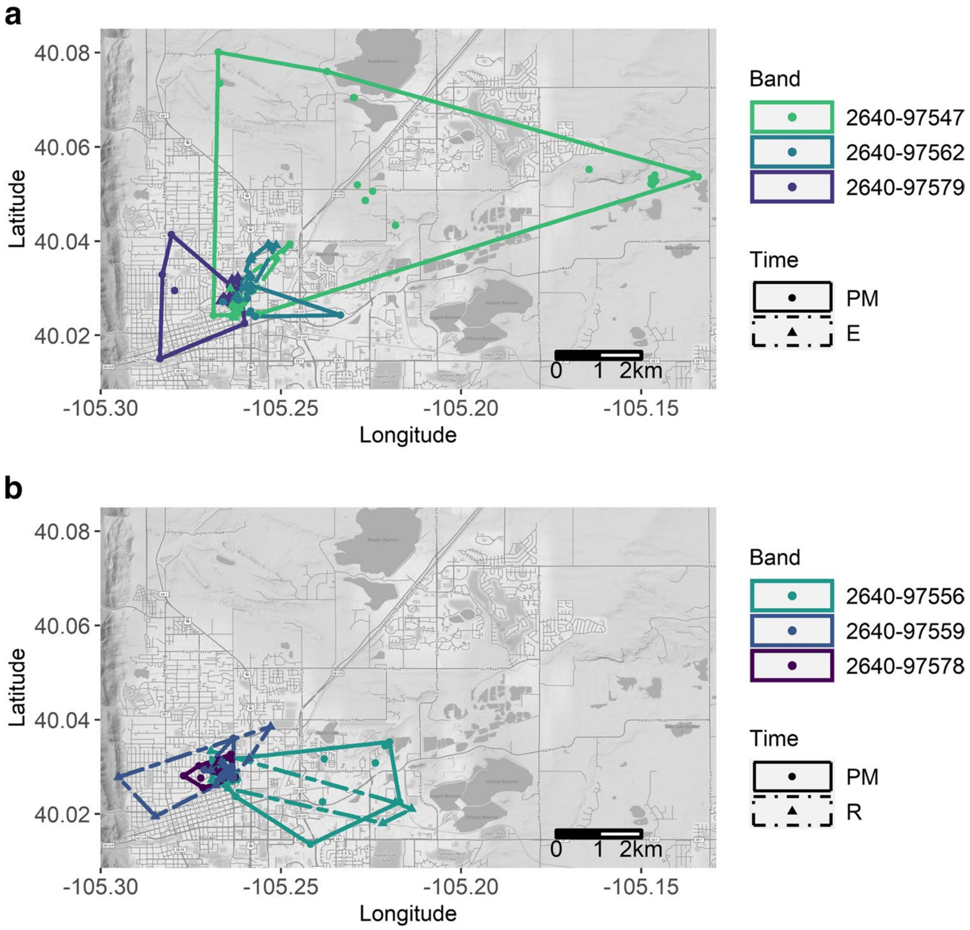

Fig. 4 Foraging range areas of female barn swallows at a single study site (Folsom) before and after brood size (**a**) enlargement or (**b**) reduction. Each band number and shade represent an individual bird. For clarity, data from only six of 20 GPS-tagged birds (those from a single breeding site) are shown here. Lines show the estimated minimum convex polygon (MCP) foraging ranges and points show individual GPS locations for each female before manipulation (PM = pre-manipulation; circles and solid lines) and after manipulation (E = enlarged, R = reduced; triangles and two-dashed lines). Figure created using ggmap version 3.0.0 (Kahle and Wickham 2013) and PowerPoint (Microsoft Corporation 2021)

individuals traveled as far as 11.26 km from the nest (mean maximum foraging distance from the nest = 1.26 km, range 0.11 to 11.26 km), suggesting that barn swallows forage further from the nest than has previously been recorded (maximum foraging distance in Bryant and Turner 1982 = 0.6 km). Individual identity and site explained more variation in foraging distance than brood size treatment, pointing to the potential importance of female quality or external factors such as locations of profitable foraging spots. Barn swallows preferentially forage over pastures with cattle (Evans et al. 2007; Henderson et al. 2007) and may also visit water sources due to the importance of insects with an aquatic

Table 3 Linear mixed models (LMMs) to examine the effects of brood size manipulation (BSM; reference = enlarged), GPS tagging of the female parent (reference = no tag), and year (reference = 2019) on post-manipulation nestling growth rate (gain in mass from days 8 to 12 post-hatch). F-statistics, numerator (Ndf) and denominator (Ddf) degrees of freedom, and *P*-values are provided for F tests with Kenward-Roger approximation. There were no significant interactions between brood size manipulation and GPS tagging (see "Results"), so interaction terms were not retained in our final models. Random effect variances are given for the individual ID and site ID random effects. Sample size (*n*) and marginal ($R^2_{\mathrm{LMM(m)}}$) and conditional ($R^2_{\mathrm{LMM(c)}}$) R^2 values are given for each model. Influential outliers were excluded from models depicted here

Post-manipulation nestling growth	Fixed effects	Estimate	SE	F	Ndf	Ddf	*P*
$\boldsymbol{n = 33}$	BSM	2.52	0.62	14.76	1	28.37	0.0006*
$\boldsymbol{R^2_{\mathrm{LMM(m)}} = 0.38}$	Year	−0.45	0.63	0.46	1	27.95	0.50
$\boldsymbol{R^2_{\mathrm{LMM(c)}} = 0.38}$	Tag	−0.10	0.63	0.02	1	24.06	0.89
	Random effects	**Variance**	**SD**				
	Site ID (14)	0.00	0.00				
	Residual	2.99	1.73				

$^*\alpha < 0.05$

life stage for aerial insectivore development (Twining et al. 2016), which may constrain foraging range such that it cannot be adjusted to brood size. However, our measure of foraging range area may also capture non-foraging behaviors, such as searching for extra-pair matings. Thus, it is possible that behaviors other than foraging are associated with variation in range size. Additionally, our measures of foraging range area post-brood size manipulation occurred one day after pre-manipulation measures. That said, neither brood enlargement nor reduction affected foraging range, suggesting that lack of response to brood size manipulation was not due solely to increase in nestling age.

In many prior studies, visitation rate alone was used as the sole measure of parent care, but we found that spatial foraging behavior was exceptionally variable across individuals, suggesting that visitation rate alone does not give a complete picture of parental investment. Because individuals varied in their foraging range area but did not adjust it with brood size, increased visitation rate with brood size might reflect much greater increases in energy expenditure for females with larger foraging ranges than those with smaller foraging ranges. Additionally, nestlings in enlarged broods gained less weight than those in reduced broods despite similar per-capita visitation rates, perhaps indicating that brood size manipulation affected some aspect of parent foraging behavior other than foraging range area. For example, parents of reduced broods may have increased their search time during foraging, allowing them to deliver larger or higher-quality prey but harder to obtain prey, while parents of enlarged broods may have decreased their search time during foraging, resulting in delivery of smaller or lower quality but easier to obtain prey, as has been observed in other studies (e.g., García-Navas and Sanz 2010; Mathot et al. 2017).

Contrary to our predictions (Fig. 1a, b) and some previous studies (barn swallows: Tajima and Nakamura 2003; but see Hasegawa et al. 2020), increasing parental energetic costs via GPS tagging did not significantly affect the visitation rate of female swallows. It is possible that tagging did not affect female visitation rate because tags did not substantially increase parental energetic costs. However, a concurrent study on costs of reproduction reported that GPS tagging had some physiological costs, including altered immune function (McDermott 2022). In addition, although tagging did not affect visitation rate, it may have affected unmeasured aspects of parental care or foraging behavior. We could not assess the effects of GPS tagging on spatial foraging behavior, leaving open the possibility that tagged females altered their foraging range area or other aspects of spatial foraging behavior relative to non-tagged females, allowing them to mitigate increased flight costs. Additionally, GPS-tagged females may have decreased their search time during foraging to avoid incurring flight costs. If tagged females had smaller foraging ranges or spent less time searching for food, they may have delivered smaller or lower quality prey to nestlings. In support of these ideas, a study of European starlings found that although increased parental costs did not affect female visitation rate, females with increased costs showed lower overall activity levels and brought back lower quality prey items (Serota and Williams 2019).

Despite a lack of measured female response, males with GPS-tagged mates had higher visitation rates than those with non-tagged mates (as we had predicted in the context of reduced visitation rate of GPS-tagged females; Fig. 1d–f). Thus, males apparently overcompensated for their tagged mates in terms of visitation rate, similar to some studies (e.g., Sanz et al. 2000), but in contrast to the most commonly observed response of partial compensation for decreased partner visitation rate (Harrison et al. 2009). Response to decreased mate parental care likely varies with the physical ability of the parent to respond and the certainty of information each parent has about brood need (e.g., Hinde and Kilner 2007). In addition, male response to mate GPS-tagging supports the idea that GPS-tagged females altered their behavior in some unmeasured way as discussed above, such as by decreasing their foraging range or search time, and thus delivering smaller or lower quality prey loads to nestlings. Males may then have responded to signals of increased nestling demand and signals from the female (e.g., Hinde and Kilner 2007). The lack of effect of GPS tagging on post-brood size manipulation nestling growth further suggests that males compensated for any female response to tagging. The dataset used to analyze treatment effects on post-manipulation nestling growth showed significantly higher pre-manipulation brood sizes in non-tagged nests than tagged nests (despite our randomized assignment of nests to treatment groups), which might suggest that non-tagged birds had higher individual condition or quality (Drent and Daan 1980). If non-tagged birds were of better condition or quality than tagged birds, however, we would have expected exaggerated effects of GPS tagging on nestling growth, which we did not find.

Only some measures of parental care and foraging behavior were affected by variation in environmental conditions. Total and per-capita visitation rate of both sexes significantly increased with temperature, indicating that barn swallow parents visit the nest more frequently when it is warmer. Temperature is the most important meteorological predictor of aerial insect abundance (e.g., Grüebler et al. 2008; Cinque et al. 2021), and barn swallow parents concentrate their foraging efforts during periods of good weather (Schifferli et al. 2014). Surprisingly, wind speed did not affect any measures of parental care or foraging behavior, in contrast to some previous work reporting significant effects of wind speed on aerial insect abundance (Grüebler et al. 2008; but see Cinque et al. 2021). Additionally, foraging range area and nestling growth were not significantly affected by any measured weather variables.

Our study provides a key test of the simultaneous effects of manipulated brood size and parental costs on multiple metrics of parental care, including foraging range, in a wild avian system. Future studies on spatial dimensions of parental care are needed to understand why and in what circumstances foraging range seems to be inflexible. The key challenge will be to relate GPS data to the actual behavior of the birds to determine when they are foraging instead of engaging in other behaviors away from the nest. Tri-axial accelerometers offer promising opportunities to infer foraging behavior and energy expenditure of larger birds without direct observation (e.g., Elliott et al. 2013; Hernández-Pliego et al. 2017), but a combined GPS and accelerometer attachment would likely be too heavy to safely deploy on most small songbirds at this time. Additionally, adding analyses of diet to studies of parental care is critical, particularly in combination with information about foraging sites and prey availability in the environment. Such studies could examine how manipulated brood size and parental costs influence travel distance, search time, and the size and quality of prey delivered to provide a comprehensive picture of how parents balance reproductive and self-maintenance costs when foraging to provision nestlings. Finally, future work should attempt to explicitly link measures of parental care and foraging behavior with metabolic energy expenditure to provide insight on how measures of parental care and foraging behavior relate to actual expenditure.

Conclusions

By simultaneously manipulating both brood size and parental costs and examining multiple metrics of parental care, including foraging behavior, we provide new insights into parental investment decisions during nestling rearing in a short-lived aerial insectivore. Contrary to our predictions, we did not find interactive effects of brood size manipulation and GPS tagging on parent behavior or nestling growth while controlling for measures of weather conditions, indicating that brood size and parental costs may have solely additive effects on parental care in our study system. Our results also suggest that investigation of foraging tactics alongside visitation rate is critical to understanding parental investment and the benefits and costs of reproduction. Barn swallow females with experimentally enlarged broods increased their visitation rate but did not adjust their foraging range area. Spatial foraging behavior was highly individually variable, which suggests that adjustments in visitation rate may be more costly for some individuals (those with larger foraging ranges) than others and indicates that visitation rate alone cannot fully capture parental investment. Additionally, GPS tagging did not affect female visitation rate, but males with tagged mates nonetheless had higher visitation rates. This finding suggests that GPS tagging may affect some unmeasured aspect of parental care or foraging behavior, such as prey delivery. Further work on of the effects of brood size manipulation and parental costs on multiple aspects of parental care and foraging behavior would be of great value.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s00265-022-03244-z.

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Author contribution SAM: conceptualization, methodology, validation, formal analysis, investigation, writing—original draft, writing—review and editing, visualization, funding acquisition.

MTM: conceptualization, methodology, validation, formal analysis, investigation, resources, writing—review and editing, supervision, funding acquisition.

RJS: conceptualization, methodology, validation, formal analysis, investigation, resources, writing—review and editing, supervision, funding acquisition.

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Data availability All datasets generated and analyzed during this study are included in this published article and its supplementary information files.

Code availability Code necessary to run and visualize the models used to analyze data in this study are included in this published article and its supplementary information files.

Declarations

Ethics approval All field methods used in this study adhered to the guidelines for the treatment of animals in behavioral research and teaching set forth by the Animal Behavior Society (ABS)/Association for the Study of Animal Behaviour (ASAB). Field methods were approved by the IACUC committee at the University of Colorado Boulder (protocol #2685), including consideration of all methods and sample sizes. All field researchers completed required animal care training prior to field work. Field work was conducted under federal (permit #23505) and state (permits #19TRb2005 and #20TRb2005) bird banding permits. No birds involved in this experiment were injured or died in our care, and no experimental nests were deserted following brood size manipulation or GPS tagging. Use of a paired experimental design for the brood size manipulation experiment allowed us to minimize the number of manipulated nests. The GPS tags in our study ranged from 5 to 8% of the birds' body mass, and all our experimental birds carried tags for only a short period—2 weeks or less (mean = 9.6 days, SD = 1.9). All tags were successfully recovered during the breeding season. GPS tags can increase energy expenditure and reduce productivity, but proportionally heavier devices do not have greater effects than lighter devices (Barron et al. 2010). We expected our tags to increase energy expenditure, but due to the short-term deployment, we did not expect effects on survival and reproduction. A concurrent study of the physiological and fitness costs of reproduction and GPS tagging reported that tags had some physiological effects, including altered immune function, but did not affect reproductive outcomes during second broods (McDermott 2022).

Conflict of interest The authors declare no competing interests.

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