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## Article

### Using artificial intelligence classification of videos to examine the environmental, evolutionary and physiological constraints on provisioning behavior

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The use of artificial intelligence (AI) technologies can revolutionize how we approach data collection and analysis in behavioral ecology. One such example is in provisioning behavior. Parents of altricial species are selected to provide parental care (such as food provisioning) for their offspring, but there is substantial variation in the level of this care. Provisioning rate may be determined environmentally, by the physiological ability of parents and needs of nestlings, or by evolutionary incentives. We quantified provisioning rate in 20 purple martin *Progne subis* nests in the context of an experimental reduction of nest ectoparasites. 10 nests had a parasite reduction treatment, and 10 nests were controls. By using AI to automate the analysis of nest camera videos we were able to obtain nearly-continuous provisioning rate information at a high temporal resolution for the first half of the nestling period. We used random forest modeling to assess the factors determining provisioning rate and found evidence for environmental, evolutionary and physiological constraints and incentives on provisioning. Birds appeared to be environmentally limited in their provisioning in cool, wet conditions, especially later in the breeding season; but adjusted their provisioning according to the changing physiological needs of nestlings. We found evidence for a compensatory response to increased parasite load, in which parents increased provisioning to more heavily parasitized nests.

Keywords: artificial intelligence, parasite compensation hypothesis, parent-offspring conflict, parental care, provisioning, purple martin

## Introduction

Parents of altricial young are under selection to provide care for their offspring. However, this relationship has limits which are imposed by the environment, physiology and natural selection (at least for iteroparous species) (Santos and Nakagawa 2012). This implies the existence of an ever-changing dynamic of costs and benefits of parental care over the provisioning period. Most previous studies were not able to consider dynamics in provisioning rate in response to varied weather conditions, changed nestling requirements and adult physiological states, as they did not have access to



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continuous provisioning rate information with a high temporal resolution (Smith et al. 2015). Early studies of provisioning were limited by how long a researcher could observe with binoculars (Simmons 1986, Conrad and Robertson 1992) or the use of proxy data such as the number of times an LED light beam at a nest box entrance was broken (Nur 1984). Although many studies now use in-nest video cameras (Cox et al. 2012), researchers are still often forced to limit the duration of their study due to the time-consuming nature of watching and categorizing these videos (Davis and Holmes 2012). The use of deep learning technology to automate analysis of nest camera videos and provide estimates of the number of provisioning events has recently been tested (Williams et al. 2019). Automated image classification of nest camera analysis of provisioning results in a much more complete dataset than manual sampling methods and can provide an opportunity to look at changes throughout the life stage rather than focus on a small subset of sampled points (Williams and DeLeon 2020).

Considering the provisioning of nestlings in birds, parents might be environmentally limited in their ability to provision when challenging weather conditions reduce prey availability (Johnson and Best 1982, Tinbergen and Verhulst 2000, Barba et al. 2009), or force them to modify their time budgets to spend more time brooding offspring in inclement weather and less time foraging (Barba et al. 2009). Low habitat quality may also reduce the ability of parents to provision young by reducing prey availability (Wilkin et al. 2009). Parents might be physiologically limited in their provisioning efforts in their first breeding attempt due to a lack of experience (Goosen and Sealy 1982, Davidar and Morton 1993, Wagner et al. 1997) or when their own health declines due, for example, to the effects of parasitism (Wagner et al. 1997). The nestlings own physiological requirements are also predicted to impact provisioning rate. For example, nestling food requirements increase with nestling age (Bolton 1995) and, while increased brood size clearly increases the required per-nest provisioning, nestlings in small broods may require more food per nestling than those in larger broods due to higher heat loss and increased metabolic rate (Royama 1966, O'Connor 1975). Natural selection may also act more directly on provisioning through trade-offs between the relative value of offspring to a parent's lifetime reproductive output, versus the potential reduction in survival and future reproduction associated with the physiological costs of parental care (Nur 1984, Winkler 1987, Tinbergen and Verhulst 2000). Adults may, for example, reduce effort in provisioning offspring hatched later in the season not only due to limitation from declining environmental conditions (O'Neill Goodbred and Holmes 1996, Naef-Daenzer et al. 2000, Barba et al. 2009), but because they are selected to do so given their own increasing chance of survival to the next breeding season with time (Winkler 1987).

Many of these and other effects are occurring simultaneously and the various costs and benefits of parental care will interact with each other. One potential interaction between

physiological, environmental and evolutionary limits to parental care which has been a particular focus of research, is the effect of nest ectoparasites on provisioning (Hund et al. 2015). High levels of parasitism in the nest can degrade parental condition and their physiological ability to adequately provision their offspring (Wagner et al. 1997, Tomas et al. 2007). The same ectoparasites can simultaneously reduce the quality and potential future reproductive output of nestlings (Moss and Camin 1970, Merino and Potti 1995, Fitze et al. 2004, Edworthy et al. 2018) thus diminishing the selective value of these parasitized offspring and leading to a reduced evolutionary incentive for provisioning (Darolova et al. 1997, Stoehr et al. 2000, Aviles et al. 2009). Parents might, conversely, be selected to increase parental care to parasitized offspring if this will increase offspring quality in a compensatory response (Johnson and Albrecht 1993, Christie et al. 1996, Tripet and Richner 1997, Bouslama et al. 2002, Tripet et al. 2002, Bañbura et al. 2004).

There are clearly many additive and opposing forces acting on provisioning rate, and the lack of agreement between studies in the direction and significance of the effect of ectoparasites on provisioning is likely due to nuances between studies and a lack of continuous, high resolution data. For example, different results may have been obtained when birds were already at/near environmental or physiological limits of provisioning, for different brood sizes, at different stages of the breeding season or for differing severities of parasite infestations (Hund et al. 2015). Additionally, important aspects in the changing dynamics of provisioning rate may have been missed by only recording data for a small portion of the nestling period.

Purple martins *Progne subis* are single brooded cavity nesters with bi-parental provisioning. The eastern breeding subspecies *P. subis subis* is unusual in that it breeds colonially, and exclusively in man-made nest boxes (Brown and Tarof 2017), making this species relatively easy to observe at the nest. They are commonly associated with a high abundance of nest ectoparasites (Moss and Camin 1970, Hill 1994) presumably due to their relatively long nestling period (ca 28 days), the microclimate of the nest cavity and their colonial habit (Møller et al. 1990). Their high parasite load has led to the leading conservation group for the species (the Purple Martin Conservation Association) recommending that managers of purple martin nest boxes undertake nest material replacements at regular intervals during the nestling phase to reduce the load of nest ectoparasites (Kostka and Hill 1994). The efficacy of this policy is currently under investigation as part of a wider study at our field site in terms of its effect on parasite abundance and on nestling survival and condition (Williams et al. unpubl.).

Here we provide the first example of the use of deep learning image classification for provisioning analysis using near continuous nest camera footage from these nests in the first half of the provisioning stage (days 0–13). We pair this high coverage provisioning data with weather data and nest level metrics as we aim to explain variation in provisioning rate



in the context of a parasite abundance manipulation experiment. We discuss the implications of our results in terms of the likely interactions between environmental, physiological and evolutionary limits on provisioning.

## Material and methods

### Field site and field protocol

12 purple martin artificial gourds (Troyer horizontal gourd Conley II with tunnel entrance, Part THGC) were fitted with in-nest cameras (CCTV HD-TVI Mini Security Camera 1080P 2.0MP 15 mm lens) and video recordings were made in 2017 and in 2018 as part of a purple martin monitoring study at our field site at Iroquois National Wildlife Refuge in Western New York State (43.111°N, 78.409°W). Cameras were set to record continuously in each nest from 6 am until 9 pm from egg hatching until the last nestling fledged the nest. Full details of data collection are available in (Williams et al. 2019). The species typically lays 3–6 eggs, although clutches of 1–2 and 7–8 are not unusual (Brown and Tarof 2017). Purple martins are aerial insectivores, and nestlings are fed exclusively on invertebrates – mostly Odonata, Lepidoptera and small Coleoptera at our field location.

Nests were manually checked every week between nest initiation and fledging. Nestlings were counted and aged and any dead nestlings removed from the nest. All nestlings were banded between 12 and 18 days old with federal bird bands. We weighed nestlings at banding. Our field site hosts a weather station less than 100 m from the nest boxes. We collected hourly temperature, precipitation and wind speed data from the weather station for the duration of the provisioning period.

Nest boxes were arranged in a circular configuration on two freestanding poles within 10 m of each other. Nests were assigned to a parasite reduction treatment ( $n = 12$ ) or a control treatment ( $n = 12$ ) in an alternating pattern on each structure as part of a wider study (2017:  $n_{\text{parasite reduction treatment}} = 5$ ,  $n_{\text{control}} = 6$ ; 2018:  $n_{\text{parasite reduction treatment}} = 5$ ,  $n_{\text{control}} = 4$ ). Nests in the parasite reduction treatment had all nesting materials (with associated nest ectoparasites) removed and replaced at each weekly nest check when nestlings were between 5 and 20 days old resulting in either 2 or 3 replacements per nest depending on nestling age at the first nest check. After we removed the loose material, we brushed any remaining residue out of the nests, but we did not use any chemicals or cleaning products on the nest boxes. We replaced the original nest material with dried pine needles (a sample of which had been previously checked and found to be free of arthropods) and returned the nestlings to the nest. Nest boxes in the control treatment did not have any parasites or materials removed during the provisioning phase, but nestlings were disturbed and prevented from feeding for the same durations as for the nestlings in the parasite reduction treatment. Nests from both control and parasite reduction treatments were collected after the last nestling fledged each nest.

### Quantifying parasite load

We placed the nest materials that were collected into Berlese funnels for 2–3 h to separate the ectoparasites from the nesting material. Preliminary work showed that the three most prevalent and abundant ectoparasites in this system were a hematophagous mite *Dermanyssus prognepphilus*, a flea *Ceratophyllus idius* and a bird blowfly larva *Protocalliphora sialia* (hereafter, ‘mites’, ‘fleas’ and ‘blowfly’). Parasites were identified via morphology following (Moss 1968, Traub et al. 1983, Sabrosky et al. 1989) using a Zeiss microscope. Using a dissecting microscope, we counted all mites, fleas and blowfly larvae found in the material collected in the ethanol from the Berlese funnels. We kept accurate counts for abundances under 200 individuals, but made estimates for abundances over 200 individuals based on the proportion of the material sampled when we reached a count of 200. Preliminary work showed that mites and fleas were accurately sampled by looking only at the material which passed through the Berlese funnels into the ethanol, but we also sorted through the nesting material to collect any blowfly pupae or pupal cases which were not collected in the ethanol. Final blowfly counts include larvae, pupae and pupal cases.

Given the established positive relationship between a parasite’s body size and the volume of blood they draw from their host (Gold and Dahlsten 1983), we scaled the abundance of parasites by their body volume, so as to allow an analysis of a combined ‘parasite effect’. We observed little heterogeneity in body size of fleas and mites, and so estimated volume based on mean upper surface area and depth measurements of a subset of individuals measured in ImageJ (Rueden et al. 2017). This resulted in an estimated volume of  $2.40 \text{ mm}^3$  for fleas, and  $0.44 \text{ mm}^3$  for mites. Blowfly body size varied greatly by stage of development (Sabrosky et al. 1989), so we measured the length and width of each individual larva, pupa or pupal case and estimated volume based on a cylindrical body shape. Resulting volumes varied between  $3.14 \text{ mm}^3$  and  $275 \text{ mm}^3$ . We harnessed information on blowfly, flea and mite lifecycles (Sabrosky et al. 1989), population growth (Maurer and Baumgartner 1992, Tripet and Richner 1999, Dawson et al. 2005, Donovan et al. 2006) and our abundance data to estimate daily nest volumes for each parasite species. Full details of our approach are available in Supplementary material Appendix 1.

Unlike the blowfly, which leave pupal cases after emergence, there is no way to tell how many fleas or mites may have left the nests after the birds have fledged, making abundance estimates of mites and fleas inherently less reliable. Given their much smaller body size, fleas and mites also contribute very little to total parasite volume, adding an average of just 6% to daily estimated parasite volumes where blowfly larvae were present. To maintain a conservative analysis, we include only blowfly volumes for the main analysis, but present total parasite volume in Supplementary material Appendix 1.

We split mean daily blowfly volumes into four groupings: 1) pre-treatment experimental, reflecting blowfly load in parasite reduction treatment nests prior to the first reduction



treatment, 2) post-treatment experimental, reflecting blowfly load in parasite reduction treatment nests after the first reduction treatment, 3) pre-treatment control, reflecting blowfly load in control nests at approximately the same nestling ages (0–7 days) as in the pre-treatment experimental nests, 4) post-treatment control, reflecting blowfly load in control nests at approximately the same nestling ages (8–13 days) as in the post-treatment experimental nests. We used an ANOVA and post-hoc Tukey HSD test to test for significant differences in blowfly volume between these groups with alpha set to  $p < 0.05$ .

We weighed nestlings when they were banded between the ages of 11 and 18 days. As nestling mass is obviously affected by age, we first conducted a linear regression of age (11–18 days) on mass. The residuals of this regression can then be considered as an age-corrected mass index, where positive values indicate a nestling which was relatively heavy for its age and negative values imply a nestling which was relatively light for its age. We then used these residual values as the dependent variable in a t-test to check for a significant difference in mass by experimental condition and in an ANOVA and post hoc Tukey HSD test to check for a significant difference in mass by brood size. Finally, we used a t-test to check for a difference in the within-nest range of age-mass residuals between experimental condition, as smaller nestlings sometimes pay a higher cost of parasitism than their larger siblings (Christie et al. 1998).

### Artificial intelligence analysis of video footage

We used a convolutional neural network model to automate the analysis of video footage to determine provisioning rate for each nest. Full details of this procedure are available in (Williams et al. 2019), but briefly, we used the Keras API for Tensor Flow to train the neural network to count the number of adult birds present in a nest. We provided the model with pre-classified still frames showing representative examples of 0, 1 or 2 adults in the nest. Once trained the neural network then provides a frame by frame classification of the number of adults in videos. When the number of birds increased (either from 0 to 1, or from 1 to 2) we counted that as a provisioning event. Although this is an overestimate of provisioning (as adult birds occasionally returned to the nest without food), when a subset of data was manually viewed, these non-provisioning visits were found to account for less than 2% of visits (below). As the nestlings change in their appearance and behavior with age, we trained three separate models based on nestling age categories (hatch day–day 5; day 6–10; day 11–13). We concluded our analysis when nestlings were 14 days old as nestlings would frequently crowd the entrance to the nest box, meaning adults could provision without entering the nest box and our counts became inaccurate. We validated our models on a manually viewed 69.3 h of footage which was spread evenly across all 20 nests in the study with approximate equal representation of both the nestling ages represented in our dataset and hours of the day. For the hatch day–day 5 model we viewed 25.3 h of footage, which

resulted in 258 nest visits (3 of which did not result in provisioning). For the day 6–10 model we viewed 22 h of footage, which resulted in 330 nest visits (4 of which did not result in provisioning). For the day 11–15 model we viewed 22 h of footage, which resulted in 308 nest visits (6 of which did not result in provisioning). After post classification filtering, our final deep learning models achieved a 99, 93 and 86% accuracy when compared to these manual classifications for the three age classes modeled (Williams et al. 2019). We aggregated the data for each nest to provide an hourly provisioning rate for each nest during the recording hours of 6 am to 9 pm.

### Statistical analyses of provisioning rate

Data were analyzed by random forest models using the randomForest package (Liaw and Wiener 2002) in R version 3.5.2 (<[www.r-project.org](http://www.r-project.org)>) with hourly provisioning per nest as the dependent variable. Random forest analysis is a machine learning method which is based on selection trees, such that the result for a given data point is determined by following down the decision levels in a selection tree process. Unlike a simple decision tree, each tree in random forest utilizes only a portion of the attribute decision rules and is only applied to a subset of the data. This allows for model averaging over hundreds of selection trees in the forest which is the basis for random forest's success. Due to this methodology, random forest does not a priori choose an arbitrary functional form for the fit as is required for many models nor is it required to sort variables into random and fixed categories as is done in general linear mixed models (GLMM). This makes the random forest model generally suitable for many of the complex modeling challenges in biological processes (Cutler et al. 2007) and specifically for the challenges that arise in modeling our present provisioning process. We specifically chose to use a random forest model, rather than the more common GLMM method as preliminary analysis of data trends showed several likely non-linear relationships which would be better fit by a random forest model than a GLMM. The dataset was split 80:20 into training and validation groups. We used conditional inference forests (Hothorn et al. 2006, Strobl et al. 2007, 2008) for variable selection where the most parsimonious set of predictors was selected using the Akaike information criterion for small sample sizes (AICc). Errors on training and test data were examined; out-of-bag and validation performance was compared; predictor variables were ranked by importance; biological relationships were examined using partial plots and the variance explained was examined.

The dataset was analyzed by a random forest model with nestling age; hour of day, daily blowfly larval volume; mean daily temperature, rainfall and wind speed; brood size; hatch date, male and female age class; and nest ID as candidate predictors (Table 1). We account for annual variability in provisioning rate (which is presumed to be caused by changes in food availability) through inclusion of temperature and precipitation variables which directly determine food availability. As parasite load was variable within experimental conditions,



Table 1. Description of variables used in candidate models as predictors of daily provisioning rate.

Predictor	Details	Hypothesized effect
Nestling age	Measured in days (0–13)	Provisioning will increase with age until nestlings near their fledging weight (Grundel 1987, O'Neill Goodbred and Holmes 1996, Huin et al. 2000, Barba et al. 2009)
Hour of day	Provisioning events were counted per hour for each nest.	Provisioning will rate will be higher in the morning than the evening (Berrow and Croxall 2001), but will peak in the afternoon as a function of temperature (Barba et al. 2009).
Daily blowfly volume	Blowfly larval volume is estimated based on life cycle constraints and larval growth estimates (mm <sup>3</sup> per day)	Provisioning will increase with blowfly load as parents attempt to compensate offspring for the effects of parasitism (Christie et al. 1996, Tripet and Richner 1997, Bouslama et al. 2002, Tripet et al. 2002, Bañbura et al. 2004). But see (Rogers et al. 1991, Darolova et al. 1997, Stoehr et al. 2000, Cantarero et al. 2013).
Temperature	Mean ambient temperature during the hours of data collection (6 am–9 pm) (°C)	Provisioning will increase with increased temperature, likely due to increased food availability and/or decreased time brooding young offspring (Barba et al. 2009, Arbeiter et al. 2015).
Rainfall	Total rainfall during the hours of data collection (6 am–9 pm) (mm)	Provisioning will decrease with increased rainfall, likely due to decreased food availability and/or increased time brooding young offspring (Johnson and Best 1982, Arbeiter et al. 2015).
Wind speed	Mean wind speed during the hours of data collection (6 am–9 pm) (km <sup>h</sup> )	Provisioning will decrease with increased wind speed, likely due to decreased food availability (Arbeiter et al. 2015, Irons et al. 2017).
Brood size	Number of live nestlings in the brood at the start of the day of recording	Provisioning per nest will increase with increased brood size, although per nestling provisioning may still decrease with brood size (Biermann and Sealy 1982, Johnson and Best 1982, Moreno et al. 1995, Ryttonen et al. 1996, Sanz and Tinbergen 1999, Robinson and Hamer 2000, Tinbergen and Verhulst 2000, Barba et al. 2009) but see (Knapp 1984).
Hatch date	Ordinal date that the first egg hatched in the nest	Provisioning will decrease later in the breeding season due to a decline in environmental conditions and due to a decreased reproductive value of offspring through the season (Winkler 1987, O'Neill Goodbred and Holmes 1996, Naef-Daenzer et al. 2000, Barba et al. 2009).
Adult male and female age classes	After second year (ASY) or second year (SY) based on plumage	Provisioning rate will be decreased in SY parents due to a lack of experience in provisioning a nest (Goosen and Sealy 1982, Davidar and Morton 1993, Wagner et al. 1997) but see (O'Neill Goodbred and Holmes 1996, Wagner et al. 1996).
Nest ID	Nest identity	There will be some repeatability of relative provisioning rates over time within nests.

we include a continuous predictor of parasite load (daily blowfly larval volume) rather than simply account for experimental condition as a categorical variable. An alternative model which included volumes of all three parasite species combined (blowfly larvae, mites and fleas) was analyzed using the same procedure. Finally, we conducted a GLMM analysis with the same predictor variables (with nest ID as a random factor) and AICc model selection procedure as used in the random forest model to provide a methodological comparison. Continuous predictors were centered and rescaled prior to analysis, and one data point was removed as an outlier for clutch size (caused by one day of provisioning in one nest to one surviving nestling after the death of its siblings).

## Results

Of the 24 nest boxes fitted with cameras across the two years of the study, 20 attracted purple martins (11 in 2017 and 9 in 2018). 10 nests were in the control group and 10 nests were in the parasite reduction treatment. The mean clutch size was 5.05 eggs per nest (min = 4, max = 6), and the mean brood size was 4.9 nestlings per nest (min = 3, max = 6) at the

start of provisioning. There was low nestling mortality during the study (hatch day–day 13), with a 93% survival rate (5 of 6 nestlings died on day 12 in one nest, and 1 of 3 nestlings died on day 6 in a second nest). Survival to fledging was 83%. Nests were provisioned a mean of 186 times per recording day (6 am–9 pm) during the study period with substantial variation (min = 43, max = 295 visits per day). Hourly provisioning rate was 12.38 visits per hour, again with high variation (min = 0, max = 39).

There were significant differences between the four experimental groups (pre-treatment control, post-treatment control, pre-treatment parasite reduction and post-treatment parasite reduction) in terms of their daily blowfly larval volume ( $F_{(3,35)} = 9.42$ ,  $p < 0.001$ ). Post-hoc comparisons showed that the post-treatment control group had a significantly higher blowfly load than any other group (Fig. 1, Table 2). This result was mirrored in the alternate model which included volumes of all three parasite species (Supplementary material Appendix 1 Fig. A1).

Unsurprisingly, older nestlings were heavier than younger nestlings ( $F_{(1,86)} = 6.134$ ,  $p = 0.02$ ,  $R^2 = 0.07$ , estimate = 0.65). When the residuals of this regression were used as an age-corrected mass index in a t-test, there was no evidence for



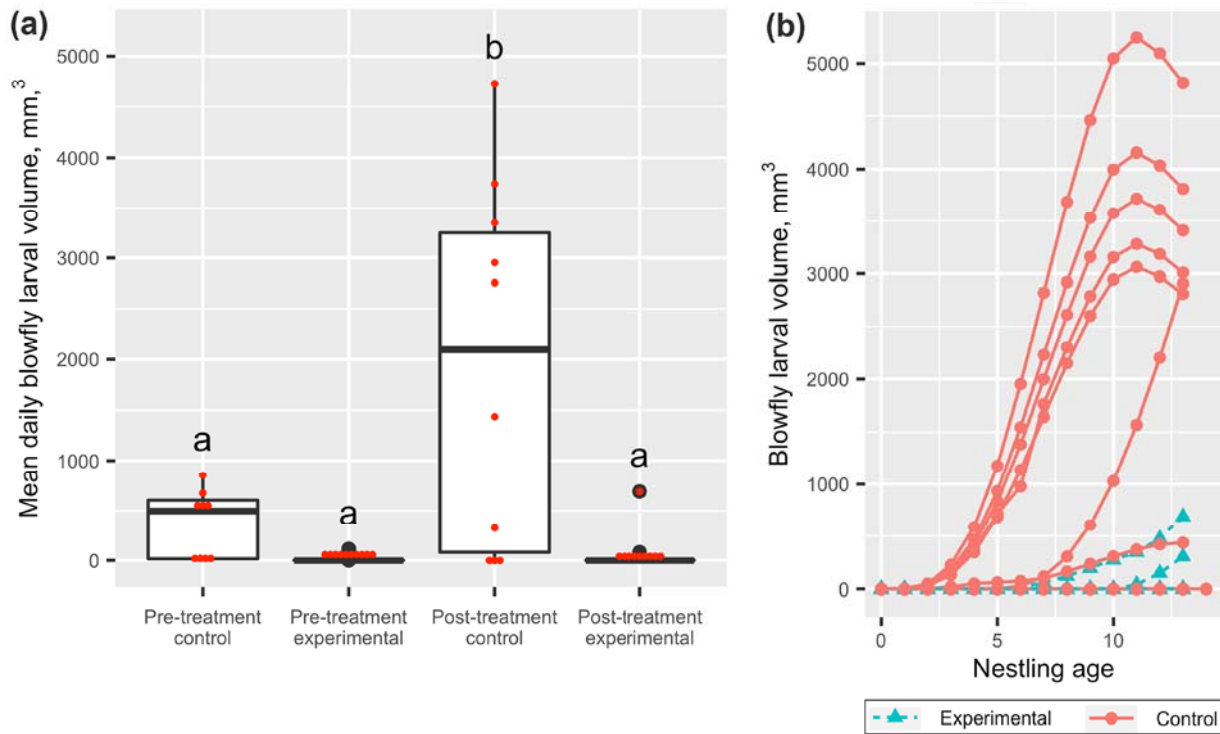


Figure 1. (A) Box and whisker plot showing mean daily blowfly volume per nest in each of the experimental conditions. Red points show actual data. Groups with statistically different blowfly volumes are shown with different letters (a and b) above bars. Parasite load is significantly higher in the post-treatment control group than in any other group. (B) Plot showing growth in blowfly larval load over the first half of nestling development. Each line shows a single nest.

a difference in nestling mass between control and parasite reduction treatment nests ( $T_{(85,73)} = 0.67$ ,  $p = 0.51$ ,  $\text{mean}_{\text{control}} = -0.37$ ,  $\text{mean}_{\text{parasite reduction}} = 0.40$ ) or by brood size in an ANOVA ( $F_{(3,84)} = 1.93$ ,  $p = 0.13$ ). There was also no significant difference in the within-nest range of age-mass residuals by experimental condition ( $T_{(12)} = 0.15$ ,  $p = 0.88$ ,  $\text{mean}_{\text{control}} = 7.41$ ,  $\text{mean}_{\text{parasite reduction}} = 7.11$ ).

### Random forest analyses to determine factors affecting provisioning rate

Model selection procedures with AICc showed the most parsimonious model to describe hourly provisioning visits included nestling age, temperature, nest ID, time of day, wind speed and daily blowfly larval volume (Supplementary material Appendix 1 Table A1). Provisioning rate in the alternate model, which included the combined effects of all three parasite species, was parsimoniously explained by

the same variables (with blowfly larval volume exchanged for parasite volume) (Supplementary material Appendix 1 Table A1).

Daily provisioning increased by around 5 items per hour between hatch day and day 13, in a roughly sigmoidal relationship (Fig. 2a), and varied somewhat within each nest (Fig. 2c). Provisioning decreased by 6 visits per hour in cool weather under 17°C compared with the value at 25°C (Fig. 2b). Provisioning was slightly suppressed early in the day (Fig. 2d) and increasing blowfly volume resulted in a modest increase in provisioning of around 1 visit per hour, following an apparent step function where provisioning is increased in response to thresholds of parasitism (Fig. 2f). Although wind speed was maintained in the final model its effect was minor, with an addition of less than one provisioning visit at moderate wind speeds (Fig. 2e). After tuning the mtry parameter and number of trees, the final model explained 42% of the variation and had a mean absolute error of 3.46 provisioning visits per hour.

Table 2. Results of Tukey HSD test comparisons of blowfly volume by experimental group. Numbers in tables are p-values. Significant contrasts are shown in bold. The post-treatment control group had a higher parasite load than any other group.

	Pre-treatment control	Pre-treatment parasite reduction	Post-treatment control	Post-treatment parasite reduction
Pre-treatment control	NA			
Pre-treatment parasite reduction	0.85	NA		
Post-treatment control	<b>0.004</b>	<b>&lt;0.001</b>	NA	
Post-treatment parasite reduction	0.92	0.99	<b>&lt;0.002</b>	NA



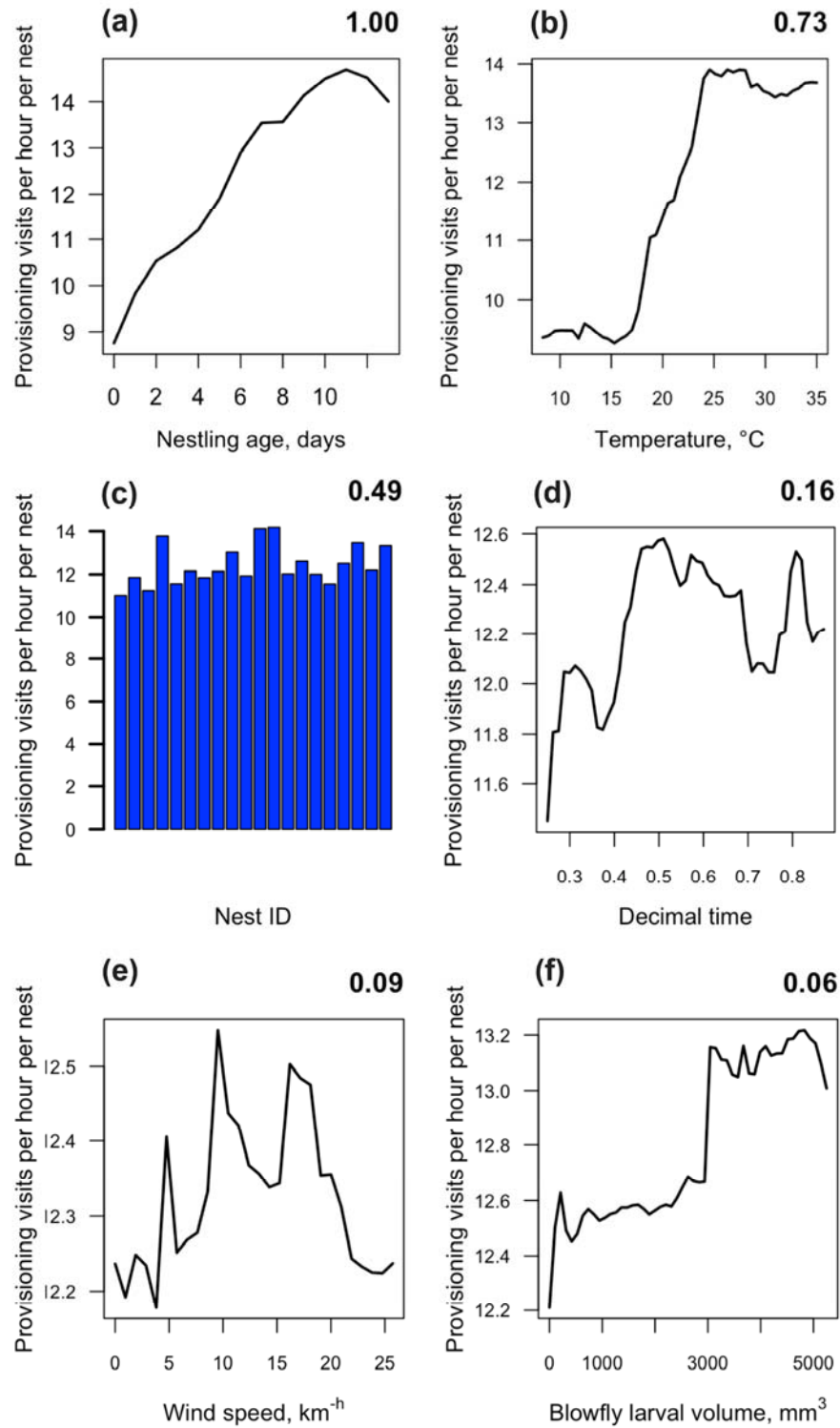


Figure 2. Partial plots showing the predicted relationships between provisioning rate and the predictor variables supported by AICc model selection in a random forest model. Plots show the isolated predicted effect of each variable on provisioning rate. Note that y-axes have different ranges in different plots. Variable importance of each predictor, defined by normalized increase in mean squared error when its effect is permuted, is in the top-right of each plot.



The alternate model including the combined effect of all three parasite species explained a similar amount of variation (42%) with a similar error rate (mean absolute error of 3.46 provisioning visits) and near identical relationships with all predictors except for parasite/blowfly volume (Supplementary material Appendix 1 Table A1, Fig. A2). The parasite/blowfly volume plots differ in that the parasite volume plot shows a much sharper increase in provisioning rate at very low parasite levels – likely due to more data points being situated in this part of the plot. The shape and effect size of parasite load and blowfly load at medium to high volumes is almost identical, likely as these larger volumes are only achieved by having blowfly in the nest. Both models (main and alternate) support an increase in provisioning rate with increased parasite load.

### Comparison of random forest model with GLMM

Model selection procedures with AICc showed the most parsimonious GLMM to describe hourly provisioning visits included nestling age, temperature, rainfall, blowfly larval volume, time of day and hatch date as predictors, while accounting for nest ID as a random factor (Supplementary material Appendix 1 Table A1, Fig. A3). The random forest model explained more variation than the GLMM (random forest: Variation explained = 0.42; GLMM:  $R^2_{\text{marginal}} = 0.25$ ,  $R^2_{\text{conditional}} = 0.28$ ) but overall directions of relationships (positive or negative) were the same in both model structures for all shared variables. Both model structures found a similar set predictors to be the most parsimonious, with the support for nestling age, temperature, time of day and blowfly volume as predictors. Whereas the random forest additionally included wind speed, the GLMM found more support for the inclusion of rainfall and hatch date (Supplementary material Appendix 1 Table A2).

### Discussion

The use of artificial intelligence (AI) technology to analyze nest camera video footage from purple martin nests provided us with a nearly-continuous estimate of the number of provisioning trips in 20 nests.

The use of AI for image classification tasks is becoming ubiquitous in society. Its uptake in wildlife research has been somewhat slower, with just the first few examples of using AI to identify species from camera trap images now in the literature (Tabak et al. 2018, Willi et al. 2018, Williams and DeLeon 2020). However, the increased speed with which AI systems can analyze data, and the lack of ‘fatigue related deterioration’ of classification quality give ecologists the power to work with much more comprehensive image datasets than were previously available (Kwok 2019). Here, using an AI approach to analysis helped us improve on an analysis of determinants of provisioning rate at a snapshot in time and enabled a nearly-continuous assessment at a fine scale of temporal resolution, of how the changing dynamics of environmental and

physiological limitation interact with evolutionary incentives to determine the level of parental care.

Our results showed that nestling age was one of the most influential predictors of provisioning rate. Provisioning rate was found to increase steadily with age between hatch day and 4 days, then increase more rapidly between day 4 and day 8, before stabilizing after day 8. This pattern is familiar from many other studies (Grundel 1987, O’Neill Goodbred and Holmes 1996, Huin et al. 2000, Barba et al. 2009) and most likely reflects the changing physiological needs of the nestlings as they grow (Barba et al. 2009). Indeed, the pattern quite closely mirrors the nestling mass growth curve for purple martins (Finlay 1971, Walsh 1978, Poulin and Brigham 2001) and passerines more generally (Remes and Martin 2002). As well as a physiological need, there is also a case for an evolutionary incentive to increase provisioning to older nestlings. With every day that passes, a nestling is more likely to survive to reproductive age, meaning that the potential selective benefit of provisioning an older nestling is greater than that of provisioning a younger nestling (Winkler 1987). Both of these incentives may work synchronously to produce the observed pattern of increased provisioning with increased nestling age.

After nestling age, the next most powerful determinant of provisioning was ambient temperature. Provisioning was relatively low below 17°C, increased between 17°C and 25°C beyond which it plateaued. This pattern matches both our hypothesis and results found in previous work (Barba et al. 2009, Arbeiter et al. 2015). Indeed, given the strength of the effect of temperature on provisioning, we expect that the slight suppression of provisioning we found in the early morning (when temperatures are cooler) is driven largely by underlying correlations with temperature. Winkler et al. (2013) measured temperature at their field site (approximately 100 miles south-east from our own) and found that flying insect abundance formed a very similar pattern with steep increases at moderate temperatures (around 15–23°C) and a plateau after around 25°C. This makes it likely that the increase in provisioning with temperature is due to changes in food availability where parents may be environmentally limited in their ability to provision at low temperatures, but be able to increase provisioning at high temperatures with relatively low costs. The temperature response could also be explained by a reallocation of parental care to increase nestling brooding and decrease foraging (Johnson and Best 1982), especially in young nestlings which have not yet developed homeothermic responses (Ricklefs and Hainsworth 1968). In either case, it seems that the environment has a significant role to play in determining the ability of purple martins to provision their young.

Adult birds slightly increased their provisioning rate with increased parasitism, offering some support for the parental compensation hypothesis (Johnson and Albrecht 1993) (albeit with a small effect size) and implying that parents may be selected to increase their investment in parasitized offspring to avoid fitness costs to the nestlings. Indeed, we did not find any evidence for a difference in nestling mass



between control and parasite reduction treatment nests, which is consistent with an effective parental compensatory strategy. While previous evidence for the parental compensation hypothesis has examined a linear response (Johnson and Albrecht 1993, Christie et al. 1996, Tripet and Richner 1997, Bouslama et al. 2002, Tripet et al. 2002, Bañbura et al. 2004), our predicted relationship was different and more characterized by a step function, where provisioning was increased once certain thresholds of parasitism were reached. This step function may reflect imperfect detection of parasite load, or it may be adaptive in that further increases of provisioning beyond a threshold may reduce individual fitness more than they may benefit inclusive fitness.

Surprisingly, we did not find evidence that nest provisioning was increased in response to increased brood sizes. While studies do frequently find that parent birds respond positively to increased brood size in terms of their provisioning, it is also common to find a simultaneous decrease in the per-nestling provisioning rate (Johnson and Best 1982, Grundel 1987, Rytönen et al. 1996, Sanz and Tinbergen 1999, Robinson and Hamer 2000, Tinbergen and Verhulst 2000, Barba et al. 2009). There are three principal explanations for this effect in the literature. Classically this effect was attributed to environmental and parental physiological limitation, where parents were unable to increase per nestling provisioning beyond the population mean brood size (Lack 1947, Gibb 1955, Tinbergen and Verhulst 2000). Royama (1966), meanwhile suggested that per nestling provisioning could safely be reduced with increasing brood size because huddling of larger broods decreased nestling metabolism as they were able to thermoregulate more efficiently. Finally, (Nur 1984), suggested an evolutionary explanation for the phenomenon where parents seek to minimize their own provisioning costs and maximize their offspring's benefits, resulting in an optimal per nestling provisioning rate which reduces with increasing clutch size. The lack of a well-supported increase in nest level provisioning with brood size found here, combined with our finding of no mass reduction in larger broods, is perhaps most congruent with increased thermoregulatory efficiency in larger broods.

Contrary to our hypothesis, adult age class was not a supported predictor of provisioning rate. This is surprising given the number of studies in other avian species which have found a substantial effect of parental age (Goosen and Sealy 1982, Davidar and Morton 1993, Wagner et al. 1997). We should note, however, that our dataset is dominated by older parents (with 13 nests where both parents are after second year compared with just 6 nests including one second year parent, and just one where both parents are in their second year), meaning we have low power to detect a difference. Furthermore, second-year purple martins at our field site were more likely to breed later in the season, and have smaller brood sizes than older parents. This suggests the possibility that age class of adults is somewhat confounded by these variables. Our finding is however, supported by Wagner et al. (1996) who also did not find a difference in provisioning rate between purple martins of different age classes.

Despite no clear role for adult age in determining provisioning, a large proportion of variation was still explained by 'nest identity' i.e. some sets of parents consistently offered a higher provisioning rate than others under the same conditions. This points to some unmeasured element of parental quality, or physiological ability. Infection with the protozoan parasite *Hemoproteus* spp. has been shown to decrease provisioning rate in female second year purple martins (Wagner et al. 1997) and female blue tits *Cyanistes caeruleus* given anti-malarials increased their provisioning rate (Tomas et al. 2007), implying a role for adult endoparasite load in modifying parental care. Adult provisioning potential may also differ depending on other aspects of their own body condition unmeasured in this study such as body size and mass (Tveraa et al. 1998) or corticosterone levels (Doody et al. 2008).

We compared the results of random forest and GLMM at explaining variation in hourly provisioning rate. We found broad agreement between the two methods in terms of which variables had the greatest explanatory power, and overall directions of relationships. We did, however, find that the random forest model explained a greater proportion of the variation in our dataset, and, thus, achieved a better fit. This is likely because the random forest was able to more closely fit non-linear patterns observed in our data (e.g. the plateau of the provisioning ~ nestling age response), whereas the GLMM was constrained to a single slope for the entire span of the data (Conway and Martin 2000, Williams and DeLeon 2020).

Although our data clearly showed interesting variation in provisioning rate, it is limited by a relatively small sample size and by only considering one form of parental care. Our approach did not allow us to account for the provisioning of different prey items, although martins are known to use multiple prey species of different energetic values (Helms et al. 2016). Secondly, males and females may show different responses to environmental costs and evolutionary incentives for provisioning (Tripet et al. 2002, Hund et al. 2015). Although preliminary studies showed a roughly equal investment by each parent, as is supported in the literature (Allen and Nice 1952, Helms et al. 2016, Brown and Tarof 2017), as we did not account for them separately we cannot exclude differential responses over time. Considering the parasite response specifically, parents may increase parental care in response to parasitism in ways beyond altering provisioning rates. For example, in heavily parasitized nests, adult pied flycatchers *Ficedula hypoleuca* spent increased time on nest sanitation and grooming of nestlings (Cantarero et al. 2013), and nestling great tits *Parus major* showed delayed fledging (Fitze et al. 2004). Conversely, there are other ways in which parents can reduce their investment in parasitized broods, for example in great tits *Parus major*, Oppliger et al. (1994) showed increased nest desertion rates with an experimentally increased flea load and Gallizzi et al. (2008) showed reductions in brooding time, as parents presumably aim to minimize their own contact with ectoparasites.

Provisioning behavior in birds is ultimately determined by natural selection. Parents must seek to minimize the costs to



their individual fitness incurred by provisioning, while maximizing the benefit of healthy offspring to their inclusive fitness. The exact position of that selective peak is condition dependent. For example, environmental conditions may alter the cost of provisioning, with low investment in foraging needed to provide a high feeding rate in times of high food abundance, but much higher effort required in more challenging environmental conditions. Nest ectoparasites, by definition, reduce the fitness of nestlings, and thus the inclusive fitness of parents. Parents may counter this by increasing provisioning to fight the effects of parasites, or by reducing provisioning to reduce their investment in a potentially low quality brood. Which of these options are selected may depend on the parents own body condition and the nestlings' physiology in terms of their current body condition, age and brood size.

Use of deep learning to categorize video footage provided us with near continuous provisioning information at a high temporal resolution, without which it would have been challenging to unpick the effects of these parameters. We suggest that similar methodology could be usefully employed to quantify provisioning and other in-nest behaviors in other avian species.

## Transparent Peer Review

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## Data availability statement

Data available from the Dryad Digital Repository: <<http://dx.doi.org/10.5061/dryad.02424>> (Williams and DeLeon 2020).

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**Author contributions** – HMW planned and conducted experimental data collection. RLD led the artificial intelligence video classification. Both authors contributed to analysis of provisioning rate. HMW wrote the manuscript and both authors edited it.

**Conflicts of interest** – None to declare.

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## References

- Allen, R. W. and Nice, M. M. 1952. A study of the breeding biology of the purple martin (*Progne subis*). – *Am. Midl. Nat.* 47: 606–665.
- Arbeiter, S., Schulze, M., Tamm, P. and Hahn, S. 2015. Strong cascading effect of weather conditions on prey availability and annual breeding performance in European bee-eaters *Merops apiaster*. – *J. Ornithol.* 157: 155–163.
- Aviles, J. M., Perez-Contreras, T., Navarro, C. and Soler, J. J. 2009. Male spotless starlings adjust feeding effort based on egg spots revealing ectoparasite load. – *Anim. Behav.* 78: 993–999.
- Bañbura, J., Perret, P., Blondel, J., Thomas, D. W., Cartan-Son, M. and Lambrechts, M. M. 2004. Effects of *Protocalliphora* parasites on nestling food composition in Corsican blue tits *Parus caeruleus*: consequences for nestling performance. – *Acta Ornithol.* 39: 93–103.
- Barba, E., Atiénzar, F., Marín, M., Monrós, J. S. and Gil-Delgado, J. A. 2009. Patterns of nestling provisioning by a single-prey loader bird, great tit *Parus major*. – *Bird Study* 56: 187–197.
- Berrow, S. D. and Croxall, J. P. 2001. Provisioning rate and attendance patterns of wandering albatrosses at Bird Island, South Georgia. – *Condor* 103: 230–239.
- Biermann, G. C. and Sealy, S. G. 1982. Parental feeding of nestling yellow warblers in relation to brood size and prey availability. – *Auk* 99: 332–341.
- Bolton, M. 1995. Food delivery to nestling storm-petrels – limitation or regulation. – *Funct. Ecol.* 9: 161–170.
- Bouslama, Z., Lambrechts, M. M., Ziane, N., Djenidi, R. D. and Chabi, Y. 2002. The effect of nest ectoparasites on parental provisioning in a north-African population of the blue tit *Parus caeruleus*. – *Ibis* 144: E73–E78.
- Brown, C. R. and Tarof, S. A. 2017. Purple martin (*Progne subis*). Account 287. – In: Poole, A. (ed.), *The birds of North America online*. Cornell Lab of Ornithology, Ithaca, NY, Account 287.
- Cantarero, A., López-Arrabé, J., Redondo, A. J. and Moreno, J. 2013. Behavioural responses to ectoparasites in pied flycatchers *Ficedula hypoleuca*: an experimental study. – *J. Avian Biol.* 44: 591–599.
- Christie, P., Richner, H. and Oppliger, A. 1996. Begging, food provisioning and nestling competition in great tit broods infested with ectoparasites. – *Behav. Ecol.* 7: 127–131.
- Christie, P., Møller, A. P. and De Lope, F. 1998. Immunocompetence and nestling survival in the house martin: the tasty chick hypothesis. – *Oikos* 83: 175–179.
- Conrad, K. F. and Robertson, R. J. 1992. Intraseasonal effects of clutch manipulation on parental provisioning and residual reproductive value of eastern phoebes (*Sayornis phoebe*). – *Oecologia* 89: 356–364.



- Conway, C. J. and Martin, T. E. 2000. Effects of ambient temperature on avian incubation behavior. – *Behav. Ecol.* 11: 178–188.
- Cox, W., Pruett, M. S., Benson, T. J., Chiavacci, S. J. and Thompson, F. R. I. 2012. Development of camera technology for monitoring nests. – In: Ribic, C. A., Thompson, F. R. I. and Pietz, P. J. (eds), *Video surveillance of nesting birds*. Univ. of California Press, Berkeley, CA.
- Cutler, D. R., Edwards Jr., T. C., Beard, K. H., Cutler, A., Hess, K. T., Gibson, J. and Lawler, J. J. 2007. Random forests for classification in ecology. – *Ecology* 88: 2783–2792.
- Darolova, A., Hoi, H. and Schleicher, B. 1997. The effect of ectoparasite nest load on the breeding biology of the penuline tit *Remiz pendulinus*. – *Ibis* 139: 115–120.
- Davidar, P. and Morton, E. S. 1993. Living with parasites – prevalence of a blood parasite and its effect on survivorship in the purple martin. – *Auk* 110: 109–116.
- Davis, S. and Holmes, T. G. 2012. Sprague's pipit incubation behavior. – In: Ribic, C. A., Thompson, F. R. I. and Pietz, P. J. (eds), *Video surveillance of nesting birds*. Univ. of California Press, Berkeley, CA, pp. 67–76.
- Dawson, R. D., Hillen, K. K. and Whitworth, T. L. 2005. Effects of experimental variation in temperature on larval densities of parasitic *Protocalliphora* (Diptera: Calliphoridae) in nests of tree swallows (Passeriformes: Hirundinidae). – *Environ. Entomol.* 34: 563–568.
- Donovan, S. E., Hall, M. J., Turner, B. D. and Moncrieff, C. B. 2006. Larval growth rates of the blowfly, *Calliphora vicina*, over a range of temperatures. – *Med. Vet. Entomol.* 20: 106–114.
- Doody, L. M., Wilhelm, S. I., McKay, D. W., Walsh, C. J. and Storey, A. E. 2008. The effects of variable foraging conditions on common murre (*Uria aalge*) corticosterone concentrations and parental provisioning. – *Horm. Behav.* 53: 140–148.
- Edworthy, A. B., Langmore, N. E. and Heinsohn, R. 2018. Native fly parasites are the principal cause of nestling mortality in endangered Tasmanian pardalotes. – *Anim. Conserv.* 22: 96–103.
- Finlay, J. C. 1971. Breeding biology of purple martins at the northern limit of their range. – *Wilson Bull.* 83: 255–269.
- Fitz, P. S., Tschirren, B. and Richner, H. 2004. Life history and fitness consequences of ectoparasites. – *J. Anim. Ecol.* 73: 216–226.
- Gallizzi, K., Alloitteau, O., Harrang, E. and Richner, H. 2008. Fleas, parental care and transgenerational effects on tick load in the great tit. – *Behav. Ecol.* 19: 1225–1234.
- Gibb, J. A. 1955. Feeding rates of great tits. – *Brit. Birds* 48: 49–58.
- Gold, C. S. and Dahlsten, D. L. 1983. Effects of parasitic flies (*Protocalliphora* spp.) on nestlings on mountain and chestnut-backed chickadees. – *Wilson Bull.* 95: 560–572.
- Goosen, J. P. and Sealy, S. G. 1982. Production of young in a dense nesting population of yellow warblers, *Dendroica petechia* in Manitoba. – *Can. Field Nat.* 96: 189–199.
- Grundel, R. 1987. Determinants of nestling feeding rates and parental investment in the mountain chickadee. – *Condor* 89: 319–328.
- Helms, J. A., Godfrey, A. P., Ames, T. and Bridge, E. S. 2016. Predator foraging altitudes reveal the structure of aerial insect communities. – *Sci. Rep.* 6: 28670.
- Hill, J. R. I. 1994. What's bugging your birds? An introduction to the ectoparasites of purple martins. – Purple martin update. Purple Martin Conservation Association, Erie, PA, USA.
- Hothorn, T., Buehlmann, P., Dudoit, S., Molinaro, A. and Van Der Laan, M. 2006. Survival ensembles. – *Biostatistics* 7: 355–373.
- Huin, N., Prince, P. A. and Briggs, D. R. 2000. Chick provisioning rates and growth in black-browed albatross *Diomedea melanophrys* and grey-headed albatross *D. chrysostoma* at Bird Island, South Georgia. – *Ibis* 142: 550–565.
- Hund, A. K., Aberle, M. A. and Safran, R. J. 2015. Parents respond in sex-specific and dynamic ways to nestling ectoparasites. – *Anim. Behav.* 110: 187–196.
- Irons, R. D., Harding Scurr, A., Rose, A. P., Hagelin, J. C., Blake, T. and Doak, D. F. 2017. Wind and rain are the primary climate factors driving changing phenology of an aerial insectivore. – *Proc. Biol. Sci.* 284: 20170412.
- Johnson, E. J. and Best, L. B. 1982. Factors affecting feeding and brooding of gray catbird nestlings. – *Auk* 99: 148–156.
- Johnson, L. S. and Albrecht, D. J. 1993. Effects of hematophagous ectoparasites on nestling house wrens, *Troglodytes aedon* – who pays the cost of parasitism. – *Oikos* 66: 255–262.
- Knapton, R. W. 1984. Parental feeding of nestling Nashville warblers – the effects of food type, brood-size, nestling age and time of day. – *Wilson Bull.* 96: 594–602.
- Kostka, K. and Hill, J. R. I. 1994. How and why do nest replacements for purple martins. – Purple martin update. Purple Martin Conservation Association, Erie, PA.
- Kwok, R. 2019. AI empowers conservation biology. – *Nature* 567: 133–134.
- Lack, D. 1947. The significance of clutch-size. – *Ibis* 89: 302–252.
- Liaw, A. and Wiener, M. 2002. Classification and regression by randomForest. – *R News* 2: 18–22.
- Maurer, V. and Baumgartner, J. 1992. Temperature influence on life table statistics of the chicken mite *Dermanyssus gallinae* (Acari: Dermanyssidae). – *Exp. Appl. Acarol.* 15: 27–40.
- Merino, S. and Potti, J. 1995. Pied flycatchers prefer to nest in clean nest boxes in an area with detrimental nest ectoparasites. – *Condor* 97: 828–831.
- Møller, A. P., Allander, K. and Dufva, R. 1990. Fitness effects of parasites on passerine birds: a review. – In: Blondel, J., Gosler, A., Lebreton, J. D. and McCleery, R. (eds), *Population biology of passerine birds*. Springer, pp. 269–280.
- Moreno, J., Cowie, R. J., Sanz, J. J. and Williams, R. S. R. 1995. Differential response by males and females to brood manipulations in the pied flycatcher – energy-expenditure and nestling diet. – *J. Anim. Ecol.* 64: 721–732.
- Moss, W. W. 1968. An illustrated key to the species of the acarine genus *Dermanyssus* (Mesostigmata: Laelapoidea: Dermanyssidae). – *J. Med. Entomol.* 5: 67–84.
- Moss, W. W. and Camin, J. H. 1970. Nest parasitism, productivity and clutch size in purple martins. – *Science* 168: 1000–1003.
- Naef-Daenzer, L., Naef-Daenzer, B. and Nager, R. G. 2000. Prey selection and foraging performance of breeding great tits *Parus major* in relation to food availability. – *J. Avian Biol.* 31: 206–214.
- Nur, N. 1984. Feeding frequencies of nestling blue tits (*Parus caeruleus*): costs, benefits and a model of optimal feeding frequency. – *Oecologia* 65: 125–137.
- O'Connor, R. J. 1975. The influence of brood size upon metabolic rate and body temperature in nestling blue tits *Parus caeruleus* and house sparrows *Passer domesticus*. – *J. Zool.* 175: 391–403.
- O'Neill Goodbred, C. and Holmes, R. T. 1996. Factors affecting food provisioning of nestling black-throated blue warblers. – *Wilson Bull.* 108: 467–479.
- Oppliger, A., Richner, H. and Christe, P. 1994. Effect of an ectoparasite on lay date, nest-site choice, desertion and hatching success in the great tit (*Parus major*). – *Behav. Ecol.* 5: 130–134.



- Poulin, R. and Brigham, R. M. 2001. Effects of supplemental calcium on the growth rate of insectivorous bird, the purple martin (*Progne subis*). – *Ecoscience* 8: 151–156.
- Remes, V. and Martin, T. E. 2002. Environmental influences on the evolution of growth and developmental rates in passerines. – *Evolution* 56: 2505–2518.
- Ricklefs, R. E. and Hainsworth, F. R. 1968. Temperature regulation in nestling cactus wrens: the development of homeothermy. – *Condor* 70: 121–127.
- Robinson, J. A. and Hamer, K. C. 2000. Brood size and food provisioning in common terns *Sterna hirundo* and arctic terns *S. paradisaea*: consequences for chick growth. – *Ardea* 88: 51–60.
- Rogers, C. A., Robertson, R. J. and Stutchbury, B. J. 1991. Patterns and effects of parasitism by *Protocalliphora sialia* on tree swallow nestlings. – In: Loye, J. E. and Zuk, M. (eds), Bird–parasite interactions: ecology, evolution and behaviour. Oxford Ornithology Series, Oxford, UK, pp. 123–139.
- Royama, T. 1966. Factors governing feeding rate, food requirements and brood size of nestling great tits *Parus major*. – *Ibis* 108: 313–347.
- Rueden, C. T., Schindelin, J., Hiner, M. C., DeZonia, B. E., Walter, A. E., Arena, E. T. and Eliceiri, K. W. 2017. ImageJ2: ImageJ for the next generation of scientific image data. – *BMC Bioinformatics* 18: 529.
- Rytönen, S., Koivula, K. and Orell, M. 1996. Patterns of per-brood and per-offspring provisioning efforts in the willow tit, *Parus montanus*. – *J. Avian Biol.* 27: 21–30.
- Sabrosky, C. W., Bennett, G. F. and Whitworth, T. L. 1989. Bird blow flies (Protocalliphora) in North America (Diptera: Calliphoridae), with notes on the palearctic species. – Smithsonian Institution Press, Washington D.C, USA.
- Santos, E. S. and Nakagawa, S. 2012. The costs of parental care: a meta-analysis of the trade-off between parental effort and survival in birds. – *J. Evol. Biol.* 25: 1911–1917.
- Sanz, J. J. and Tinbergen, J. M. 1999. Energy expenditure, nestling age and brood size: an experimental study of parental behavior in the great tit *Parus major*. – *Behav. Ecol.* 10: 598–606.
- Simmons, R. 1986. Food provisioning, nestling growth and experimental manipulation of brood size in the African red-breasted sparrowhawk, *Accipiter rufiventris*. – *Ornis Scand.* 17: 31–40.
- Smith, J. A., Cooper, C. B. and Reynolds, S. J. 2015. Advances in techniques to study incubation. – In: Deeming, D. C. and Reynolds, S. J. (eds), Nests, eggs and incubation. Oxford Univ. Press, Oxford, UK, pp. 179–195.
- Stoehr, A. M., Nolan, P. M., Hill, G. E. and McGraw, K. J. 2000. Nest mites (*Pellonyssus reedi*) and the reproductive biology of the house finch (*Carpodacus mexicanus*). – *Can. J. Zool.* 78: 2126–2133.
- Strobl, C., Boulesteix, A. L., Zeileis, A. and Hothorn, T. 2007. Bias in random forest variable importance measures: illustrations, sources and a solution. – *BMC Bioinformatics* 8: 25.
- Strobl, C., Boulesteix, A. L., Kneib, T., Augustin, T. and Zeileis, A. 2008. Conditional variable importance for random forests. – *BMC Bioinformatics* 9: 307.
- Tabak, M. A., Norouzzadeh, M. S., Wolfson, D. W. and Al, E. 2018. Machine learning to classify animal species in camera trap images: applications in ecology. – *Methods Ecol. Evol.* 10: 585–590.
- Tinbergen, J. M. and Verhulst, S. 2000. A fixed energetic ceiling to parental effort in the great tit? – *J. Anim. Ecol.* 69: 323–334.
- Tomas, G., Merino, S., Moreno, J., Morales, J. and Martínez-De La Puente, J. 2007. Impact of blood parasites on immunoglobulin level and parental effort: a medication field experiment on a wild passerine. – *Funct. Ecol.* 21: 125–133.
- Traub, R., Rothschild, M. and Haddow, J. F. 1983. The Ceratophyllidae: key to the genera and host relationships. – Academic Press, Cambridge, England.
- Tripet, F., Glaser, M. and Richner, H. 2002. Behavioural responses to ectoparasites: time-budget adjustments and what matters to blue tits *Parus caeruleus* infested by fleas. – *Ibis* 144: 461–469.
- Tripet, F. and Richner, H. 1997. Host responses to ectoparasites: food compensation by parent blue tits. – *Oikos* 78: 557–561.
- Tripet, F. and Richner, H. 1999. Dynamics of hen flea *Ceratophyllus gallinae* subpopulations in blue tit nests. – *J. Insect Behav.* 12: 159–174.
- Tveraa, T., Saether, B. E., Aanes, R. and Erikstad, K. E. 1998. Regulation of food provisioning in the Antarctic petrel; the importance of parental body condition and chick body mass. – *J. Anim. Ecol.* 67: 699–704.
- Wagner, R. H., Davidar, P., Schug, M. D. and Morton, E. S. 1997. Do blood parasites affect paternity, provisioning and mate-guarding in purple martins? – *Condor* 99: 520–523.
- Wagner, R. H., Schug, M. D. and Morton, E. S. 1996. Confidence of paternity, actual paternity and parental effort by purple martins. – *Anim. Behav.* 52: 123–132.
- Walsh, H. 1978. Food of nestling purple martins. – *Wilson Bull.* 90: 248–260.
- Wilkin, T. A., King, L. E. and Sheldon, B. C. 2009. Habitat quality, nestling diet and provisioning behaviour in great tits *Parus major*. – *J. Avian Biol.* 40: 135–145.
- Willi, M., Pitman, R. T., Cardoso, A. W., Locke, C., Swanson, A., Boyer, A., Veldthuis, M., Fortson, L. and Gaggiotti, O. 2018. Identifying animal species in camera trap images using deep learning and citizen science. – *Methods Ecol. Evol.* 10: 80–91.
- Williams, H. M. and DeLeon, R. L. 2020. Deep learning analysis of nest camera video recordings reveals temperature sensitive incubation behavior in the purple martin (*Progne subis*) – *Behav. Ecol. Sociobiol.* 74: 7.
- Williams, H. M., Dittmar, K. and Pagano S.. In review. A parasite reduction conservation intervention does not improve fledging success or most condition metrics for purple martins. – *The Condor: Ornithological Applications*.
- Williams, H. M., Matott, L. S. and DeLeon, R. L. 2019. Automated deep learning analysis of purple martin videos depicting incubation and provisioning. Practice and experience in advanced research computing. – ACM, Chicago, IL, pp. 64.
- Winkler, D. W. 1987. A general model for parental care. – *Am. Nat.* 130: 526–543.
- Winkler, D. W., Luo, M. K. and Rakhimberdiev, E. 2013. Temperature effects on food supply and chick mortality in tree swallows (*Tachycineta bicolor*). – *Oecologia* 173: 129–138.

Supplementary material (available online as Appendix jav-02424 at <[www.avianbiology/appendix/jav-02424](http://www.avianbiology/appendix/jav-02424)>). Appendix 1.