- 1 Machine learning pipeline extracts biologically significant data automatically from wildlife
- 2 monitoring videos

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**Abstract** 

- Measuring parental care behaviour in the wild is central to the study of animal life-history trade-offs, but is often labour and time-intensive. More efficient machine learning-based video processing tools have recently emerged that allow parental nest visit rates to be measured using video cameras and computer processing. Here, we used open-source software to detect movement events from videos taken at the nest box of a wild passerine bird population. We show that visit numbers from our automatic data collection pipeline strongly correlate with human observations, and predicts an increase in fledglings and recruits in a brood. We further tested other annotation methods on a subset of videos, showing that a machine learning assisted annotation approach can largely increase the accuracy of the obtained measures and cut annotation time significantly compared to a cohort of undergraduate students. Since our automatic pipeline collected biological-meaningful data that would have taken approximately 800 days by human observers, we encourage more researchers to apply existing open-source tools to assist data collection in animal behaviour studies.
- **Keywords:** Parental Care, Computer Vision, Deep Meerkat, House Sparrow, Machine Learning,

# Introduction

Parental care behaviour is a life history trait that is commonly studied in a wide range of animals (Royle et al., 2012). Parental care is defined as any behaviour that increases the fitness of offspring (Clutton-Brock, 1991; Royle et al., 2012), but often decreases the survival probability of parents (Trivers, 1972) presenting as a life history trade-off (Stearns, 1992). While there are many forms of parental care (*e.g.*, nest building, predator defence, incubation, and feeding; see Royle et al., 2012), parental care in the form of feeding of the young is traditionally considered as very costly for parents (Owens and Bennett, 1994; Winkler and Wilkinson, 1988). As such, a large body of literature focuses on how the frequency with which parents visit their nest with dependent young is associated with aspects of an animal's life history, especially in birds, where 90% of species engage in parental care (Cockburn, 2006). For example, work on life history trade-off in terms of parent and offspring fitness (Schroeder et al., 2013), parent coordination (see Ihle et al., 2019; Wojczulanis-Jakubas et al., 2018), parent-offspring conflict (Estramil et al., 2013), or ageing (Wilcoxen et al., 2010) all used the frequency of parental visits to nests (or provisioning) as a proxy of parental investment.

However, measuring parental visitation rates in the wild is labour intensive and time-consuming. Data is traditionally collected by direct observations (*e.g.* Dunn and Cockburn, 1996), which can be invasive by disturbing animals in the vicinity of their nest (Rose, 2009). Less invasive methods include video recording (*e.g.*, García-Navas and Sanz, 2010; Nakagawa et al., 2007), radio tracking (see Mitchell et al., 2012), and the use of radio-frequency tags and antennas at the nest (RFID; Mariette et al., 2011; Ringsby et al., 2009). While automatic methods allow visitation rates to be quantified over long periods of time, the technology is prone to error (up to 20%; see Mariette et al., 2011). On the other hand, video analysis is more flexible and allows for other behaviours to be quantified, like nest defence, copulations or feeding load (Lendvai et al., 2015). Maybe most importantly, using video cameras also allows for visual confirmation of individual identity if colour rings are used. However, manual

annotation of video data is time-consuming and error-prone (Tuyttens et al., 2014), calling for more effective ways to extract data from videos (Conway et al., 2021; Weinstein, 2018a).

Recent advances in deep learning (Borowiec et al., 2021) and computer vision (Weinstein, 2018a) allow quick and reliable information to be extracted from field data (Valletta et al., 2017). For example, machine learning methods have been successfully applied to solve problems with species identification (see Wäldchen and Mäder, 2018), bird song complexity measurement (see Pearse et al., 2018; Priyadarshani et al., 2018), social behaviour measurement (see Robie et al., 2017), and individual identification (Bogucki et al., 2019; Ferreira et al., 2020; Körschens et al., 2018; Schofield et al., 2019). Since computing resources are much cheaper than human-labour, such approaches have immense potential in reducing the financial and time costs of data collection, evidenced by a recent increase in popularity for ecological applications (Borowiec et al., 2021; Tuia et al., 2022).

Simultaneously, open-source tools were developed to aid data collection from video data. Examples include software on tracking animals and behaviours in captive settings (Harmer and Thomas, 2019; Pennington et al., 2019; Sridhar et al., 2019; Walter and Couzin, 2021), pose estimation (Graving et al., 2019; Lauer et al., 2021; Pereira et al., 2019), or species identification (Falzon et al., 2020; Van Horn et al., 2015). Particularly, Weinstein (2018b) developed an open-source tool named Deep Meerkat which uses convolutional neural networks (CNNs) to capture movement events from wildlife monitoring videos. Despite the name, the software was initially designed for use with a hummingbird population (Marcot et al., 2019; Weinstein, 2018b), but the software has been adapted for use in marine (Sheehan et al., 2020) and insect (Mertens et al., 2021; Pegoraro et al., 2020) systems. To the best of our knowledge, the software has not been used in avian systems other than the original hummingbird population.

Here, we applied Deep Meerkat (Weinstein, 2018b) to automatically process and extract visitation rates from parental provisioning videos collected in the house sparrow (*Passer domesticus*) population on Lundy Island, UK since 2004 (see Nakagawa et al., 2007). We first compared the results to manually-collected data by trained individuals in the past. Next, we compared the outputs from the automatic processing with other methods of annotation, including crowdsourced annotation by a cohort of undergraduate students, as well as a machine learning-assisted approach. Lastly, we determined the biological relevance of the extracted data by testing the hypothesis that increased rates of feeding would lead to increased annual reproductive fitness of the parents — a classic life-history theory hypothesis from behavioural ecology (Trivers, 1972).

# **Materials and Methods**

# Study System

Data were collected from a population of house sparrows (*Passer domesticus*) on Lundy Island (51° 10′ N, 4°40′ W) located on the Bristol Channel, UK. The population is part of a long-term study and is monitored systematically since 2000, with >99% of individuals marked with a unique combination of colour rings, metal ring by the British Trust for Ornithology (Cleasby et al., 2011), and unique PIT transponders (Schroeder et al., 2011). Since house sparrows rarely fly over large bodies of water (Magnussen and Jensen, 2017) very little immigration or emigration has taken place in the population (Schroeder et al., 2015). As a result, the population has high recapture rates with no trapping bias (Simons et al. 2015) and reliable life history data for every individual (Schroeder et al., 2015).

#### Parental provisioning videos

The Lundy sparrow population is situated within a 0.2km² area around a small village, since that is the only viable habitat on the island (Schroeder et al., 2011). Nest boxes were put up for the sparrows, and every box is checked systematically to detect all breeding attempts throughout the summer breeding season (Cleasby et al., 2011). After eggs were found and the identity of the parents confirmed by video, 90-minute videos were recorded on the 7th and 11th day after egg hatching, with a video camera 2-5m away from the nest box and a field of view of 30cm radius (see Nakagawa et al., 2007a for detailed procedure) to measure parental visitations.

When annotating the videos, birds were considered as feeding the young when entering and exiting the nest box, and when feeding behaviour could be seen through the nest box hole without entering the nest box. We recorded when birds are perching outside the nest box but as a separate behaviour such that it did not count towards feeding rate estimates. Feeding rates were then calculated from the first visit of either parent until the end of the video, or until 90 minutes had elapsed from the first visit, whichever came first. We started counting from the first visit, and not the beginning of the video,

to allow time for the birds to adjust to the disturbance possibly caused by the camera setup. The resulting time during which visits were scored was termed the effective observational time (Nakagawa et al., 2007a). The total number of visits by both parents was divided by the effective observational time to obtain the manual feed rate (feeds per hour) as a measure of parental provision rate.

Between 2004 and 2015, videos (N=2112) were manually annotated by postgraduate students and researchers, which contributed to multiple publications (see Ihle et al., 2019; Nakagawa et al., 2007; Schroeder et al., 2019, 2016, 2013, 2012). We used these data as a baseline – the 'manual feed rate' – to be compared against the automatically-collected data ('automatic feed rate') outlined below.

#### **Automatic Video Processing Pipeline**

We processed videos collected between 2011 and 2019 (N=2629) through the open-source programme Deep Meerkat, which uses convolution neural networks (CNNs) to classify moving frames and identify moving objects in wildlife monitoring videos (Weinstein, 2018b). Since the performance of the default model was satisfactory from initial tests, we did not further fine-tune the model using video frames from our study. We post-processed the output from Deep Meerkat to merge movement events detected fewer than 40 frames apart and more than 2 frames in length into the same event. We then further grouped the events into 7-second video clips, to allow effective post-processing annotation and matching with manually-generated data. We then tallied the number of events for each video, then divided the tally by the total time of the video recording to obtain the automatic feed rate (in events per hour; Figure 1). Since the majority of the feeding events on Lundy sparrows were done by parents entering the nest box, we assume each feeding event broadly corresponds to 2 detected movement events by the pipeline (entering and exiting the nest box), hence the automatic feed rate was further divided by 2.



Figure 1: Automatic data collection pipeline for processing parental provisioning videos of house sparrows on Lundy Island.

Parental investment videos were collected on Lundy Island UK, on days 7 and 11 post egg hatching. Videos were processed using open source software Deep Meerkat (Weinstein, 2018b), which applied convolutional neural networks to detect movement from wildlife monitoring videos, outputting frames with movement detected. Events were then defined by grouping movement frames that were less than 40 frames apart and at least 2 frames long. Lastly, events for each provisioning video were tallied to obtain an automatic feed rate as a proxy of parental provisioning.

#### Validation

After processing all videos using the automatic pipeline, we first tested for differences between the automatic and manual feed rates using Pearson's correlation test. To further compare different methods of video annotation, we randomly chose 8 videos to be used a test dataset. Using manual feed rates from previous annotation as the baseline value, we calculated three separate return rate measures by dividing the number of events detected using each method over the baseline number of events (e.g. if previous baseline found 10 feeding events and an alternative method found 7, the method has a return rate of 0.7). Firstly, we calculated the automatic pipeline return rate using the automatic feed rate obtained from the pipeline. Next, the machine learning (ML) assisted return rate

was calculated by manually reviewing the video clips extracted from the pipeline (Figure 1), to manually filter out irrelevant non-feeding events. Lastly, we organized an undergraduate practical session to annotate the same full-length videos to obtain an undergraduate return rate.

To test whether the extracted return rates were comparable to the baseline, we first did one sampled t-tests to see whether each return rate was significantly different from 1 by setting the theoretical mean  $(\mu)$  to 1. We then compared the collected return rates with each other using pairwise t-tests between each annotation method.

# Case study

Finally, we used the automatic feed rate in a case study to test for the first part of the life-history trade-off predicted by Trivers (1972). We tested whether broods whose parents visited the nest more often had a higher fledgling and recruitment success, using the automatic feed rate. Since each brood was measured on the 7<sup>th</sup> and 11<sup>th</sup> day after hatching, we averaged both values to obtain an average feed rate for each brood. However, since feeding rates increases as a brood age (see Schroeder et al., 2019), we also ran the models separately using Day 7 and 11 rates to ensure results are consistent.

To test the prediction that increased automatic feed rate was associated with higher chick survival in a brood, we fitted generalised linear mixed models with the number of fledglings and the number of recruits for each brood as respective response variables, against automatic feed rates (events per hour) as explanatory variables, using a Poisson link function. A fledgling was defined as a sparrow chick that did not die in the nest and successfully fledged, while recruits were defined as fledglings that produced at least one genetic offspring in their lifetime. To allow effect sizes to be compared, we z-transformed the feed rates. To control for other effects that might affect the fitness metrics, we added the age of the mother and father (see Wiebe, 2018), and hatch date (Days after April 1st) as fixed effects. Since breeding success usually corresponds to peak food abundance (see Cresswell and Mccleery, 2003;

Lack, 1968), we also added a quadratic fixed-effect term for hatch date. Next, the population has undergone routine cross-fostering, which is associated with increased survival (see Winney et al., 2015), hence we added a fixed factor for fostered status (yes/no) in all models, however, note that the feed rate we used were always from the social parent (parent that did the actual feeding). We added the social parent IDs and the year as random effects to control for environmental effects (see Rose et al., 1998) and repeatable feeding rates by individual parents (Nakagawa et al., 2007). The location of the nest box was also added as a random effect to control for known environmental effects (Schroeder et al., 2012).

We ran all models specified above using the R packages MCMCglmm (Hadfield, 2010) on R version 3.6.1 (R Core Team, 2013). The posterior distributions and autocorrelations were checked following Hadfield (2014) to ensure all fixed and random effects converged without violating any model assumptions. We defined a parameter as statistically significant if the 95% credible interval did not overlap with zero.

# Results

# **Qualitative Data**

Using the automatic pipeline, we processed a total of 2629 videos and so approximately 3900 hours (160 days) of recordings. We compared the extracted provisioning rates using a correlation (Figure 2), revealing a significant positive correlation of 0.62 between automatic feed rates and manual feed rates (Pearson's rank correlation;  $t_{781}$ =22.6, 95%CI: 0.58-0.66, p < 0.001).

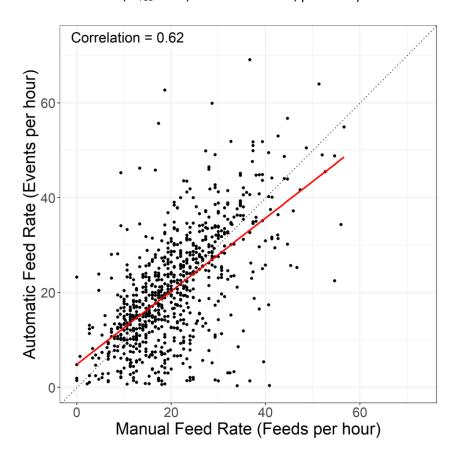


Figure 2: Positive correlation between two measures of parental provisioning of house sparrows on Lundy Island, UK.

Manual feed rate refers to the number of feeding visits by both parents of a brood, measured manually through video annotation. Automatic feed rate refers to the number of movement events detected using the automatic video analysis pipeline divided by 2. The red line shows a significant positive correlation between both measures and the dotted line shows a 1:1 line if both rates were equal.

# **Validation**

Automatic pipeline return rate was significantly larger than 1 (Table 1) and significantly inflated compared to other methods (Figure 3). However, once the extracted clips were manually reviewed to eliminate non-feeding events to calculate the ML-assisted return rate, the rate is comparable with the baseline (Table 1). The ML-assisted return rate is also not significantly different from undergraduate annotation (Figure 3), both not significantly different from 1 (Table 1), comparable to the baseline measure. On average, the ML-assisted approach took an average of 11.5 minutes per video (min 6.1 minutes, max 14.5 minutes).

Table 1: Comparing event return rates of three data collection methods using a test dataset of 8 provisioning videos from house sparrows (*Passer domesticus*) on Lundy Island, UK.

The return rate for each video was calculated by dividing the number of detected events obtained using each method by the number obtained from previously annotated data. Test statistics were obtained from a one-sampled t-test, with the theoretical mean ( $\mu$ ) set to 1. A) Videos were processed by the pipeline to obtain an automatic feed rate. B) Videos were first processed by the pipeline, with extracted clips further manually reviewed to filter out non-feeding events C) A cohort of undergraduates annotated the same test videos, and the average number of annotated events for each video were determined

Metrics	Mean	95% Confidence Interval	t	p-value
A) Automatic pipeline return rate	1.45	1.13-1.78	3.31	0.01
B) Machine learning assisted	0.93	0.78 – 1.03	-1.86	0.10
return rate				
C) Undergraduate return rate	1.03	0.96 – 1.11	1.13	0.30

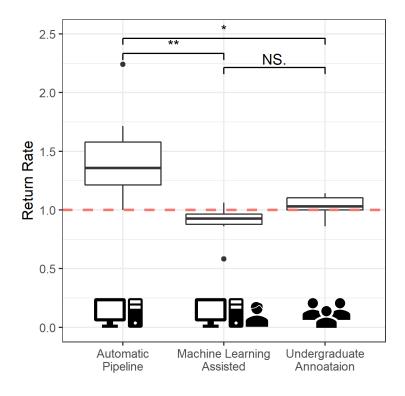


Figure 3: Comparison of return rates for three separate data collection methods on 8 parental provisioning videos of house sparrows (*Passer domesticus*) on Lundy Island, UK.

Return rates were calculated by dividing the number of feeding events each method detected over the number of events detected by manual annotation completed by past trained researchers. Automatic pipeline return rates were computed using the automatic feed rate collected from the video processing pipeline. Machine learning-assisted return rates were calculated by manually reviewing the short clips generated by the pipeline to remove non-feeding events. Undergraduate annotation return rates were collected by a cohort of undergraduate students annotating the original full-length videos. Red dotted line represents the reference level of 1, and brackets and labels represent the significance of t-test between all groups (N.S: not significant, \*: p<0.05, \*\*: p<0.01, \*\*\*: p<0.001).

# Case study

The data that we used contained 658 unique broods, of 2116 individual chicks, of which 728 (34%) fledged and 328 (16%) were recruited. Automatic feed rates significantly predict an increase in the number of fledgelings and recruits for all models fitted (Figure 4; Supporting Information 1). We found

a noticeable change in brood survival over the breeding season, with a significant negative quadratic effect for hatch date, showing that fitness is the highest in mid-breeding season (Supporting Table S1).



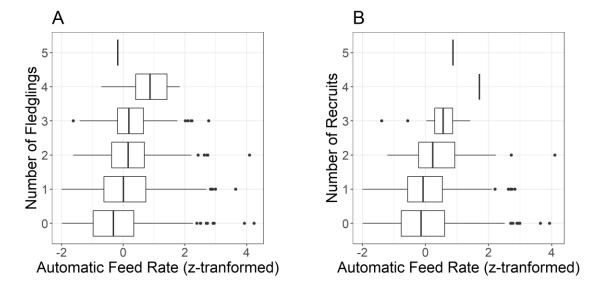


Figure 4: Increase in the number of (A) fledglings and (B) recruits as average automatic feed rates increase in house sparrows (*Passer domesticus*) on Lundy Island, UK

Automatic feed rates were obtained by processing provisioning videos using a machine learning assisted pipeline and tallying the number of movement events detected then dividing by 2. Provision rates were further z\_tranformed to allow effect sizes to be comparable, with 0 representing the mean and each unit representing one standard deviation away from the mean.

# Discussion

Using an automatic data collection pipeline based on Deep Meerkat (Weinstein, 2018b), we extracted visitation rates from parental provisioning videos of house sparrows and found that automatic feed rates positively correlated with manual annotation, and can reproduce biological results, equivalent to ~800 hours (~100 8-hour workdays) of human labour work. Even though the computational time for Deep Meerkat is 1:1 (1 hour video takes ~1 hour to process; see Marcot et al., 2019), computing time is much cheaper than human labour time, especially when techniques like parallel computing were used. As such, we managed to process a huge backlog of unprocessed videos from the Lundy sparrow system that would have been infeasible without the use of machine learning methods.

When applying machine learning methods, there is often a trade-off between the variance and bias of a trained model (Geman et al., 1992; but see Neal, 2019). Here, the 8 test videos showed that the pipeline produced biased results, since the obtained automatic feed rate produced overinflated estimates compared to the baseline, likely due to over-detection of non-feeding events when birds are present within the video frame. However, the high bias was complemented with low variance (or high consistency), with automatic feed rate correlating well with manual feed rates and predicting an increase in fledgelings and recruits within broods in our case study. Although not comparable with manual feed rates, the automatic feed rate can hence be considered as another proxy of parental investment (see Schroeder et al., 2013; Trivers, 1972) allowing more biological hypotheses to be tested with increased sample size and statistical power. Moreover, the motion detection algorithm of Deep Meerkat is not species-specific, allowing the same method to be applied to other study systems or species, opening a new avenue of research for newly established systems or large video datasets.

In this study, we also tested other methods for data collection, including crowdsourcing undergraduate students and adopting a ML-assisted approach. Manual annotation by undergraduate students was accurate, with mean event return rates higher than the reference baseline, possibly due

to the multiple observer effect (*e.g.* Guay et al., 2013), but can also be due to inflation in detected events due to misidentifications. We also showed that there were no significant difference between the undergraduate and ML-assisted return rates, highlighting the value of using an ML-assisted approach. Given sex-specific hypotheses on parental investment are often tested in the population (*e.g.* Schroeder et al., 2016), using the pipeline as a pre-processing step can be useful for collecting additional sex or behavioural data within the feeding events. Further development using deep learning and computer vision techniques can also classify the sex (see Ferreira et al., 2020) and behaviour (see Conway et al., 2021; Ditria et al., 2021) automatically, which has potential to fully replace human annotation in the future.

Machine learning approaches are becoming widely used in ecology in recent years (Borowiec et al., 2021). Here, we presented an excellent case study of machine learning assisted data collection that can obtain biologically meaningful results in existing datasets without further manual intervention. With the increase in open-source tools that are being developed in the field to reduce manual annotation efforts (e.g. Van Horn et al., 2015; Walter and Couzin, 2021; Weinstein, 2018b), and the increase in computing literacy of ecology graduates (Farrell and Carey, 2018), we encourage researchers to make use of such tools to be adapted to their own existing datasets. This would not only unlock the bottleneck of unanalysed data that would otherwise go to waste, but also allow more interesting hypotheses to be tested.

#### Conclusion

In this study, we used a data collection pipeline based on Deep Meerkat to automatically process parental provisioning videos on Lundy sparrows. Automatic feed rates collected from the machine learning pipeline correlated well with manual annotation, as well as predicting recruitment and fledging success in broods. The pipeline also acts as an effective pre-processing step to allow annotation time to be largely reduced, as we encourage researchers to adopt similar methods in their

study systems. Machine learning techniques and open-source tools are becoming widespread in ecology, we provide here a successful case study of the use of such tools to eliminate the bottleneck of laborious manual data collection. **Significance Statement** Collecting data on avian parental provisioning rates are often time and labour intensive. Recent advancements in open-source machine learning software allow such data to be effectively collected without human annotation. This paper provides a case-study of the validity and potential of such software to easily collect parental provisioning data in the wild. **Conflict of Interest Statement** None **Funding Statement** This research was supported by Imperial College, a fellowship from the Volkswagen Foundation (JS), a grant from the German Research Foundation: Deutsche Forschungsgemeinschaft (JS), CIG PCIG12-GA-2012-333096 from the European Research Council (JS), and by grant NE/J024597/1 (TB). WDP and the Pearse lab are also funded by NSF. Grant ABI-1759965 and UKRI/NERC NE/V009710/1. Acknowledgements We would like to thank the Lundy Landmark trust and the Lundy Field Society for their ongoing support for our field work. **Author's Contributions** 

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- Bogucki, R., Cygan, M., Khan, C.B., Klimek, M., Milczek, J.K., Mucha, M., 2019. Applying deep learning to right whale photo identification. Conserv. Biol. 33, 676–684.
- Borowiec, M.L., Frandsen, P., Dikow, R., McKeeken, A., Valentini, G., White, A.E., 2021. Deep learning as a tool for ecology and evolution.
- Cleasby, I.R., Burke, T., Schroeder, J., Nakagawa, S., 2011. Food supplements increase adult tarsus length, but not growth rate, in an island population of house sparrows (Passer domesticus).

  BMC Res. Notes 4, 431.
- 345 Clutton-Brock, T.H., 1991. The evolution of parental care. Princeton University Press.
- Cockburn, A., 2006. Prevalence of different modes of parental care in birds. Proc. R. Soc. B Biol. Sci. 273, 1375–1383.
- Conway, A.M., Durbach, I.N., McInnes, A., Harris, R.N., 2021. Frame-by-frame annotation of video recordings using deep neural networks. Ecosphere 12, e03384.
- 350 Cresswell, W., Mccleery, R., 2003. How great tits maintain synchronization of their hatch date with 351 food supply in response to long-term variability in temperature. J. Anim. Ecol. 72, 356–366.
- Ditria, E.M., Jinks, E.L., Connolly, R.M., 2021. Automating the analysis of fish grazing behaviour from videos using image classification and optical flow. Anim. Behav. 177, 31–37.
- Dunn, P.O., Cockburn, A., 1996. Evolution of male parental care in a bird with almost complete cuckoldry. Evolution 2542–2548.
- Estramil, N., Eens, M., Müller, W., 2013. Coadaptation of offspring begging and parental provisioning-an evolutionary ecological perspective on avian family life. PloS One 8, e70463.
- Falzon, G., Lawson, C., Cheung, K.-W., Vernes, K., Ballard, G.A., Fleming, P.J., Glen, A.S., Milne, H.,
  Mather-Zardain, A., Meek, P.D., 2020. ClassifyMe: a field-scouting software for the
  identification of wildlife in camera trap images. Animals 10, 58.
- Farrell, K.J., Carey, C.C., 2018. Power, pitfalls, and potential for integrating computational literacy into undergraduate ecology courses. Ecol. Evol. 8, 7744–7751.
- Ferreira, A.C., Silva, L.R., Renna, F., Brandl, H.B., Renoult, J.P., Farine, D.R., Covas, R., Doutrelant, C., 2020. Deep learning-based methods for individual recognition in small birds. Methods Ecol. Evol. 11, 1072–1085.
- García-Navas, V., Sanz, J.J., 2010. Flexibility in the foraging behavior of blue tits in response to shortterm manipulations of brood size. Ethology 116, 744–754.
- 368 Geman, S., Bienenstock, E., Doursat, R., 1992. Neural networks and the bias/variance dilemma. 369 Neural Comput. 4, 1–58.
- 370 Graving, J.M., Chae, D., Naik, H., Li, L., Koger, B., Costelloe, B.R., Couzin, I.D., 2019. DeepPoseKit, a 371 software toolkit for fast and robust animal pose estimation using deep learning. Elife 8, 372 e47994.
- Guay, P.-J., McLeod, E.M., Cross, R., Formby, A.J., Maldonado, S.P., Stafford-Bell, R.E., St-James Turner, Z.N., Robinson, R.W., Mulder, R.A., Weston, M.A., 2013. Observer effects occur
   when estimating alert but not flight-initiation distances. Wildl. Res. 40, 289–293.
- Hadfield, J., 2014. MCMCglmm course notes. Available Cran R-Proj.OrgwebpackagesMCMCglmmvignettesCourseNotes Pdf.
- Hadfield, J.D., 2010. MCMC methods for multi-response generalized linear mixed models: the MCMCglmm R package. J. Stat. Softw. 33, 1–22.
- Harmer, A.M., Thomas, D.B., 2019. pathtrackr: An r package for video tracking and analysing animal movement. Methods Ecol. Evol. 10, 1196–1202.
- 382 Ihle, M., Pick, J.L., Winney, I.S., Nakagawa, S., Schroeder, J., Burke, T., 2019. Rearing success does not 383 improve with apparent pair coordination in offspring provisioning. Front. Ecol. Evol. 7, 405.
- Körschens, M., Barz, B., Denzler, J., 2018. Towards automatic identification of elephants in the wild.

  ArXiv Prepr. ArXiv181204418.
- Lack, D.L., 1968. Ecological adaptations for breeding in birds.

- Lauer, J., Zhou, M., Ye, S., Menegas, W., Nath, T., Rahman, M.M., Santo, V.D., Soberanes, D., Feng, G., Murthy, V., Lauder, G., Dulac, C., Mathis, M., Mathis, A., 2021. Multi-animal pose estimation and tracking with DeepLabCut. bioRxiv.
- Lendvai, A.Z., Akçay, Ç., Ouyang, J.Q., Dakin, R., Domalik, A.D., St John, P.S., Stanback, M., Moore,
   I.T., Bonier, F., 2015. Analysis of the optimal duration of behavioral observations based on an
   automated continuous monitoring system in tree swallows (Tachycineta bicolor): is one hour
   good enough? PLoS One 10, e0141194.
- 394 Magnussen, E., Jensen, J.-K., 2017. Ringing recoveries of house sparrow (Passer domesticus) in the 395 Faroe Islands during the years 1963-2007/Ringmerkingar av føroyskum gráspurvum (Passer 396 domesticus) árini 1963-2007. Fróðskaparrit-Faroese Sci. J. 57, 182–189.
- Marcot, B.G., Lorenz, T.J., Fischer, P., Weinstein, B.G., Cowell, S., 2019. Efficacy of automated detection of motion in wildlife monitoring videos. Wildl. Soc. Bull. 43, 726–736.
- Mariette, M.M., Pariser, E.C., Gilby, A.J., Magrath, M.J., Pryke, S.R., Griffith, S.C., 2011. Using an electronic monitoring system to link offspring provisioning and foraging behavior of a wild passerine. The Auk 128, 26–35.
- Mertens, J.E., Brisson, L., Janeček, Š., Klomberg, Y., Maicher, V., Sáfián, S., Delabye, S., Potocký, P.,
   Kobe, I.N., Pyrcz, T., 2021. Elevational and seasonal patterns of butterflies and hawkmoths in plant-pollinator networks in tropical rainforests of Mount Cameroon. Sci. Rep. 11, 1–12.
- Mitchell, G.W., Newman, A.E., Wikelski, M., Ryan Norris, D., 2012. Timing of breeding carries over to influence migratory departure in a songbird: an automated radiotracking study. J. Anim. Ecol. 81, 1024–1033.
- Nakagawa, S., Gillespie, D.O.S., Hatchwell, B.J., Burke, T., 2007. Predictable males and unpredictable
   females: sex difference in repeatability of parental care in a wild bird population. J. Evol.
   Biol. 20, 1674–1681.
- Neal, B., 2019. On the bias-variance tradeoff: Textbooks need an update. ArXiv Prepr.
   ArXiv191208286.
- Owens, I.P., Bennett, P.M., 1994. Mortality costs of parental care and sexual dimorphism in birds.

  Proc. R. Soc. Lond. B Biol. Sci. 257, 1–8.
- Pearse, W.D., Morales-Castilla, I., James, L.S., Farrell, M., Boivin, F., Davies, T.J., 2018. Global macroevolution and macroecology of passerine song. Evolution 72, 944–960.
- Pegoraro, L., Hidalgo, O., Leitch, I.J., Pellicer, J., Barlow, S.E., 2020. Automated video monitoring of insect pollinators in the field. Emerg. Top. Life Sci. 4, 87–97.
- Pennington, Z.T., Dong, Z., Feng, Y., Vetere, L.M., Page-Harley, L., Shuman, T., Cai, D.J., 2019.
   ezTrack: An open-source video analysis pipeline for the investigation of animal behavior. Sci.
   Rep. 9, 1–11.
- Pereira, T.D., Aldarondo, D.E., Willmore, L., Kislin, M., Wang, S.S.-H., Murthy, M., Shaevitz, J.W.,
   2019. Fast animal pose estimation using deep neural networks. Nat. Methods 16, 117–125.
- 424 Priyadarshani, N., Marsland, S., Castro, I., 2018. Automated birdsong recognition in complex acoustic 425 environments: a review. J. Avian Biol. 49, jav-01447.
- 426 R Core Team, 2013. R: A language and environment for statistical computing.
- Ringsby, T.H., Berge, T., Saether, B.-E., Jensen, H., 2009. Reproductive success and individual variation in feeding frequency of House Sparrows (Passer domesticus). J. Ornithol. 150, 469–429 481.
- 430 Robie, A.A., Seagraves, K.M., Egnor, S.R., Branson, K., 2017. Machine vision methods for analyzing social interactions. J. Exp. Biol. 220, 25–34.
- 432 Rose, A.P., 2009. Temporal and individual variation in offspring provisioning by tree swallows: a new 433 method of automated nest attendance monitoring. Plos One 4, e4111.
- Rose, K.E., Clutton-Brock, T.H., Guinness, F.E., 1998. Cohort variation in male survival and lifetime breeding success in red deer. J. Anim. Ecol. 979–986.
- Royle, Nick J, Smiseth, P.T., Kölliker, M., 2012. The evolution of parental care. Oxford University Press.

- Royle, Nick J., Smiseth, P.T., Mathias, K., 2012. The evolution of parental care, The evolution of parental care. Oxford University Press, Oxford.
- Schofield, D., Nagrani, A., Zisserman, A., Hayashi, M., Matsuzawa, T., Biro, D., Carvalho, S., 2019.
   Chimpanzee face recognition from videos in the wild using deep learning. Sci. Adv. 5,
   eaaw0736.
- Schroeder, J., Cleasby, I., Dugdale, H.L., Nakagawa, S., Burke, T., 2013. Social and genetic benefits of parental investment suggest sex differences in selection pressures. J. Avian Biol. 44, 133–140.
- Schroeder, J., Cleasby, I.R., Nakagawa, S., Ockendon, N., Burke, T., 2011. No evidence for adverse effects on fitness of fitting passive integrated transponders (PITs) in wild house sparrows Passer domesticus. J. Avian Biol. 42, 271–275.
- Schroeder, J., Dugdale, H., Nakagawa, S., Sparks, A., Burke, T., 2019. Social genetic effects (IGE) and genetic intra-and intersexual genetic correlation contribute to the total heritable variance in parental care.
- Schroeder, J., Hsu, Y.-H., Winney, I., Simons, M., Nakagawa, S., Burke, T., 2016. Predictably philandering females prompt poor paternal provisioning. Am. Nat. 188, 219–230.
- Schroeder, J., Nakagawa, S., Cleasby, I.R., Burke, T., 2012. Passerine birds breeding under chronic noise experience reduced fitness. PLoS One 7, e39200.
- Schroeder, J., Nakagawa, S., Rees, M., Mannarelli, M.-E., Burke, T., 2015. Reduced fitness in progeny from old parents in a natural population. Proc. Natl. Acad. Sci. 112, 4021–4025.
  - Sheehan, E.V., Bridger, D., Nancollas, S.J., Pittman, S.J., 2020. PelagiCam: A novel underwater imaging system with computer vision for semi-automated monitoring of mobile marine fauna at offshore structures. Environ. Monit. Assess. 192, 1–13.
- Sridhar, V.H., Roche, D.G., Gingins, S., 2019. Tracktor: image-based automated tracking of animal movement and behaviour. Methods Ecol. Evol. 10, 815–820.
- Stearns, S., 1992. The evolution of life histories. Oxford University Press, Oxford.

459

- Trivers, R., 1972. Parental investment and sexual selection. Sex. Sel. Descent Man Aldine Gruyter N. 465 Y. 136–179.
- Tuia, D., Kellenberger, B., Beery, S., Costelloe, B.R., Zuffi, S., Risse, B., Mathis, A., Mathis, M.W., van
   Langevelde, F., Burghardt, T., 2022. Perspectives in machine learning for wildlife
   conservation. Nat. Commun. 13, 1–15.
- Tuyttens, F.A.M., de Graaf, S., Heerkens, J.L., Jacobs, L., Nalon, E., Ott, S., Stadig, L., Van Laer, E.,
  Ampe, B., 2014. Observer bias in animal behaviour research: can we believe what we score,
  if we score what we believe? Anim. Behav. 90, 273–280.
- Valletta, J.J., Torney, C., Kings, M., Thornton, A., Madden, J., 2017. Applications of machine learning in animal behaviour studies. Anim. Behav. 124, 203–220.
- Van Horn, G., Branson, S., Farrell, R., Haber, S., Barry, J., Ipeirotis, P., Perona, P., Belongie, S., 2015.
   Building a bird recognition app and large scale dataset with citizen scientists: The fine print in fine-grained dataset collection, in: Proceedings of the IEEE Conference on Computer
   Vision and Pattern Recognition. pp. 595–604.
- Wäldchen, J., Mäder, P., 2018. Machine learning for image based species identification. Methods Ecol. Evol. 9, 2216–2225.
- Walter, T., Couzin, I.D., 2021. TRex, a fast multi-animal tracking system with markerless identification, and 2D estimation of posture and visual fields. Elife 10, e64000.
- 482 Weinstein, B.G., 2018a. A computer vision for animal ecology. J. Anim. Ecol. 87, 533–545.
- Weinstein, B.G., 2018b. Scene-specific convolutional neural networks for video-based biodiversity detection. Methods Ecol. Evol. 9, 1435–1441.
- Wiebe, K.L., 2018. Age-related improvements in fecundity are driven by the male in a bird with partially reversed sex roles in parental care. Oecologia 188, 1095–1104.
- Wilcoxen, T.E., Boughton, R.K., Schoech, S.J., 2010. Older can be better: physiological costs of paternal investment in the Florida scrub-jay. Behav. Ecol. Sociobiol. 64, 1527–1535.

489	Winkler, D.W., Wilkinson, G.S., 1988. Parental effort in birds and mammals: theory and
490	measurement. Oxf. Surv. Evol. Biol.
491	Winney, I., Nakagawa, S., Hsu, YH., Burke, T., Schroeder, J., 2015. Troubleshooting the potential
492	pitfalls of cross-fostering. Methods Ecol. Evol. 6, 584–592.
493	Wojczulanis-Jakubas, K., Araya-Salas, M., Jakubas, D., 2018. Seabird parents provision their chick in a
494	coordinated manner. PloS One 13, e0189969.
495	