- 1 **<u>Title:</u>** Automated tracking of avian parental care behavior
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27 Abstract:

28	1.	Parental care may be an important source of phenotypic variation for ecological and
29		evolutionary processes. However, it can be difficult to collect and interpret data on
30		parental care behaviors. To address these challenges, we developed a new hardware
31		and software platform for automated behavioral tracking called ABISSMAL (Automated
32		Behavioral Tracking by Integrating Sensors that Survey Movements Around a target
33		Location).
34	2.	ABISSMAL automatically collects data across low-cost sensors with built-in system
35		monitoring and error logging. ABISSMAL also generates behavioral inferences with
36		internal validation by integrating data across multiple movement sensors.
37	3.	We successfully used ABISSMAL to track nest attendance activities performed by
38		captive zebra finches (Taeniopygia guttata) that raised chicks through fledging. We
39		highlight the behavioral inferences that ABISSMAL can derive from integrated datasets
40		that represent discrete movement events, including types of behaviors, and the
41		direction and magnitude of movements.
42	4.	ABISSMAL streamlines the process of automated data collection, curation, and
43		interpretation for researchers studying parental care across many experimental
44		replicates and over long developmental timescales. ABISSMAL is a modular system
45		that can be deployed with different combinations of sensors to suit different research
46		questions and experimental setups. We made ABISSMAL open-access on GitHub with
47		detailed documentation to facilitate widespread use and modification.

<u>Data/Code for peer review statement:</u> Software and documentation for ABISSMAL are
publicly available on GitHub: https://github.com/lastralab/ABISSMAL. We uploaded the code
that we used to pre-process data, integrate data, and make figures to GitHub. We published
data associated with this manuscript on <u>figshare</u>.

- 52
- 53 Keywords: Automated behavioral tracking, Avian parental care behavior, Infrared beam
- 54 breakers, Integration across sensors, Motion-detection video recording, Movement detection,
- 55 Radio-frequency identification technology, Raspberry Pi

56 Introduction

Parental care can change offsprings' adult phenotypes. For instance, the diets that adult bees feed larvae can influence caste determination (Kamakura, 2011). In crocodilians, sex determination is impacted by incubation temperature (Lang & Andrews, 1994). Adults can also transmit behaviors to offspring through social learning that are important to survive, including foraging preferences (Slagsvold & Wiebe, 2011), and sequences of fine-scale motor movements to access specific foods (Zohar & Terkel, 1991). Parental care behaviors may therefore cause phenotypic variation in offspring that is critical for ecological and evolutionary processes (Klug & Bonsall, 2014; Laland et al., 2015; Uller, 2012).

However, in order to link variation in parental care behavior to ecologically and 65 evolutionarily relevant variation in offspring phenotypes, we need to be able to quantify fine-66 grained variation in parental care behaviors throughout the course of offspring development. 67 Collecting data on these behaviors is difficult because parental care can be infrequent, 68 cryptic, and performed by one or up to several individuals. The types of behaviors that adults 69 exhibit, and how often adults perform these behaviors, can also change as offspring develop. 70 To accurately capture variation in parental care behavior, we require non-invasive continuous 71 monitoring tools that can capture rare behavioral events (Iserbyt et al., 2018; Kalafut & Kinley, 72 2020). 73

There are few tools available for scientists interested in quantifying variation in parental care behaviors. The most commonly used tools often require costly resource investment and are largely limited to data collection, with little support for cleaning, checking, and interpreting data. Continuous video recordings are used to capture parental care behaviors (Bendesky et al., 2017; Gilby et al., 2011; Iserbyt et al., 2018; Ogino et al., 2021; Smiley & Adkins-Regan, 2016), but manually scoring videos over developmental trajectories and across many experimental replicates can become prohibitively time-consuming. Deep learning tools for
automated video scoring also require building large manually scored training datasets
(Ferreira et al., 2020; Mathis & Mathis, 2020).

83 Movement sensors are promising solutions for quantifying infrequent behaviors (Kalafut & Kinley, 2020; Smith & Pinter-Wollman, 2021), including parental care behavior. 84 These sensors provide continuous monitoring that is important to collect data on rare events 85 and can be programmed for automated data collection, which reduces the need for time-86 intensive manual scoring. Movement sensors are also financially accessible and can be 87 deployed in a high-throughput manner across many experimental replicates. While movement 88 sensors hold great potential, it can be difficult for biologists to apply these sensors to collect 89 empirical data from live animals. First, these sensors do not often come with "out-of-the-box" 90 91 software that can be easily deployed or modified to suit different practical applications. Second, using movement data collected by any one sensor to make inferences about 92 behavioral variation poses great challenges. 93

For example, radio frequency identification (RFID) systems are increasingly used to streamline data collection of animals' movements associated with parental care behaviors (Iserbyt et al., 2018; Maldonado-Chaparro et al., 2021; Prinz et al., 2016; Santema & Kempenaers, 2023). However, RFID systems alone do not contain built-in validation and can fail to detect passive integrated transponder (PIT) tags (Hughes et al., 2021; Iserbyt et al., 2018). RFID systems are also limited to collecting the timestamps when PIT tags were detected by an RFID antenna, and it can be very challenging to interpret patterns of behavioral variation from the timing of location-specific movement events.

In order to address these challenges associated with collecting and interpreting data
 on parental care behavior, we developed ABISSMAL, a unified hardware and software

platform for automated behavioral tracking. We named our tool "abysmal" as in "endless" to
highlight the many possibilities made available by this modular, open-access tracking system.
ABISSMAL automates data collection across multiple types of sensors with internal system
monitoring and error logging, and also derives behavioral inferences with built-in validation by
integrating data across sensors.

Below we describe the three main components of ABISSMAL: 1) a suite of sensors mounted around a nest container to track avian parental care behaviors, 2) software for automated data collection, system monitoring, and error logging, and 3) a set of computational analyses to derive behavioral inferences by integrating data across multiple movement sensors. We tested ABISSMAL with captive zebra finches to highlight how this tracking system helped us streamline the process of automated behavioral data collection, curation, and interpretation of movements associated with parental care behaviors. ABISSMAL is an accessible tool with estimated hardware costs around several hundred dollars (USD, Supplementary Table 1), and this tracking system is open-access through a public GitHub repository (https://github.com/lastralab/ABISSMAL).

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120 Materials and Methods: The core components of ABISSMAL

121 **Ethics statement:** Data collection and animal care for captive zebra finches was conducted 122 under an IACUC protocol approved by Rockefeller University (protocol no. 21063-H).

123

124 **1.** Custom hardware to track avian parental care

125 ABISSMAL can collect data across four different types of sensors: 1) infrared beam breakers,

126 2) a radio frequency identification (RFID) system, 3) an infrared camera triggered by motion

127 detection, and 4) a temperature probe. These sensors are mounted on a custom-built PVC

nest container in order to track activities associated with avian parental care behavior (Figure 129 1). The first three sensor types track movement around the entrance and inside of the nest container (Figure 1A-B). ABISSMAL later integrates data across these movement sensors in order to provide behavioral inferences. The infrared beam breakers sit on 3D-printed mounts to capture activity in front of the RFID antenna (the "outer" pair, which detects movement outside of the container) and behind the RFID antenna (the "inner" pair, which detects movement inside the container). The RFID antenna sits inside of the circular entrance of the nest container (Figure 1A). An infared camera and LEDs are mounted on a 3D-printed cap (Figure 1B). The camera captures activities that occur inside of the nest container. The fourth sensor, the temperature probe, can be mounted inside of the nest container to record ambient temperature, which can be a critical feature of the physical environment during development (Figure 1C).

These four types of sensors provide different types of information. The three types of movement sensors provide continuous monitoring of movements. Each sensor independently records the timing and location of movement. The outer and inner pairs of infrared beam breakers with 3mm LEDs and ranges of 25 cm (Adafruit Industries LLC, New York, NY, USA) detect the time at which their respective beams of infrared light are broken. The RFID antenna is connected to a CognIoT 125 kHz RFID reader (Bostin Technology Services Ltd, Lichfield, Staffordshire, UK) that detects when unique passive integrated transponder (PIT) tags attached to each individual are in close proximity (a few millimeters). The Waveshare H wide-angle infrared camera (Waveshare, Futian District, Shenzhen, China) is programmed to record short videos by motion detection in all three color channels, and we use the onset of video recording events as the timing of movement. Recording videos by motion detection also reduces the number of videos that need to be stored and scored to obtain finer-scale behavioral information (Prinz et al., 2016). The waterproof temperature probe (Low Voltage
Labs LLC, Vancouver, WA, USA) can be programmed to return temperature readings with
coarse or fine-grained temporal resolution. All sensors, including the temperature probe, are
connected to a Raspberry Pi computer (Raspberry Pi Ltd, Milton, Cambridge, UK
(Supplementary Figure 1). Raspberry Pi computers are increasingly used for behavioral
tracking (Alarcón-Nieto et al., 2018; Jolles, 2021; Maldonado-Chaparro et al., 2021; Prinz et
al., 2016; Youngblood, 2020) and facilitate long-term data collection as well as directly
comparing timestamps across multiple sensors. Supplementary sections 1-3 provide more
information about ABISSMAL hardware. Supplementary sections 4-5 contain more

162 Figure 1: The first component of ABISSMAL is a a suite of four sensor types mounted on a

163 custom-built nest container. Panels A and B show three types of sensors that capture

164 movement at the entrance and inside of the nest container. Panel C shows a temperature

165 probe mounted inside of the container.



168 2. Software for automated data collection, system monitoring, and error logging 169 The second component of ABISSMAL is software that provides automated data collection, 170 system monitoring, and error logging through Python version 3 (Van Rossum & Drake, 2009) 171 and the bash shell (GNU, 2007) (Figure 2). ABISSMAL's software facilitates data collection 172 across the four different sensor types, while the automated monitoring and logging can help 173 streamline long-term data collection and troubleshooting across parallel experimental 174 replicates. Movement events and temperature data recorded across the different sensors are 175 saved inside spreadsheets each day, and are also stored in log files to provide back-up data 176 and troubleshoot errors. Our system monitoring module automates the daily transfer of 177 spreadsheets (.csv format), videos (.mp4 format), and log files from the Raspberry Pi to an 178 external hard drive using cron (a utility for task scheduling). The data collection and system 179 monitoring modules are set up to automatically run in the background on different screens 180 once the tracking system initiates. We also include optional software for sending automated 181 text message alerts through Twilio when errors are encountered (users will need their own 182 Twilio account). Our software can be automatically set up using a script that installs software 183 dependencies and configures the Raspberry Pi for compatibility with ABISSMAL.

Figure 2: Here we highlight ABISSMAL's software for automated data collection across
different sensors (an RFID system, infrared beam breakers, a camera, and a temperature
probe), as well as automated system monitoring and error logging. The types of errors logged
by the system are described in documentation on GitHub.



190 3. Computational analyses to integrate data and make behavioral inferences

191 The use of multiple movement sensors in ABISSMAL increases the likelihood of detecting 192 movements associated with parental care behaviors and also provides redundant datasets 193 when a sensor fails (Figure 3). However, it can be challenging to link movements to 194 behavioral activities when using data from a single sensor alone. The third component of 195 ABISSMAL is a set of computational analyses to detect discrete movements and to make 196 behavioral inferences about different movement events. We detect movement events and link 197 these events with behavioral activities by using custom functions that pre-process and 198 integrate data collected across movement sensors (Figure 4). This integration across multiple 199 sensors provides higher confidence when linking movement events to behaviors, as well as 200 information about the direction of movement and the type of behavior that occurred (Figure 4). 201 The data pre-processing and integration functions are written using R and the tidyverse (R 202 Core Team, 2023; Wickham et al., 2019). Each function is unit-tested through a battery of 203 automated tests with simulated data and the package testthat to ensure that the functions 204 produce their expected outcomes (Wickham, 2011). Supplementary section 6 contains more 205 information about each function.

206 Figure 3: This plot shows raw data collected over 4 days (Days 4 through 7 out of 50 total)
 207 across three types of movement sensors for one pair of captive zebra finches (see Results).

207 across three types of movement sensors for one pair of captive zebra finch 208 Nocturnal periods are shaded in grey.



<u>Figure 4:</u> We provide a description of four ABISSMAL functions for data processing and
integration across movement sensors, as well as a graphical representation of the input and
output data per function. An additional function for combining raw data across dates per
sensor type (including the temperature probe) is not shown.



217 <u>Results: Testing ABISSMAL with captive zebra finches</u>

218 **1. Setting up the tracking system for data collection**

219 We used ABISSMAL to collect data from captive zebra finch pairs at the Rockefeller 220 University Field Research Center. Zebra finches are small Australian songbirds that readily 221 breed inside artificial containers in captivity. When bred in opposite-sex pairs, both parents 222 will contribute to parental care activities (Smiley & Adkins-Regan, 2016). In naturalistic aviary 223 settings, adults will allofeed unrelated fledglings (Ogino et al., 2021). We chose opposite-sex 224 pairs that had already raised chicks together, and fitted each adult with an EM4102 passive integrated transponder (PIT) tag leg band (2.3mm inner diameter, Eccel Technology, Groby, 225 226 Leicester, UK) to facilitate tracking individual identity through the RFID system. We placed each pair of birds in cages that were fitted with a custom-built nest container and placed 227 228 inside of sound attenuation chambers (Figure 1; supplementary section 2). We used ABISSMAL to monitor the birds' movements around each nest container, as well as ambient 229 230 temperature inside of the containers. All birds were kept on a 12:12 hour light:dark cycle with 231 ad libitum access to food and water in temperature-controlled rooms. We collected data from 232 5 different pairs over 7 rounds of breeding in all. Some of these rounds of data collection were 233 shorter (e.g. captured egg-laying only) and represented testing rounds with earlier versions of our hardware and software. Two pairs that were each bred twice raised 1 - 4 chicks through 234 235 fledging in each breeding round, which allowed us to ensure that our custom hardware in this 236 version of ABISSMAL did not compromise chick survival. Throughout our figures, we use data from one pair that laid 5 eggs and raised 4 chicks in their second round of breeding. 237 238 ABISSMAL captured movements associated with the nest container throughout the diurnal and nocturnal periods over 50 days of data collection (Figures 3, 5, 6). These birds laid 5 239

240 eggs over days 7 – 11 (Figures 5 and 6). Four of these eggs hatched over days 22 – 25, and

241 all four chicks fledged from days 40 - 41 (Figures 5 and 6). The adults started laying another 242 clutch of eggs shortly after their chicks fledged.

244 **2. Deriving behavioral inferences**

245 We used ABISSMAL's computational analyses to detect discrete movement events from the 246 raw data collected across sensors, and to generate behavioral inferences by integrating data 247 across sensors. We detected perching events in the raw data and pre-processed the raw data 248 collected by each movement sensor (Figure 4, Figure 5A). We integrated the pre-processed datasets across sensors by finding clusters of detections that occurred close together in time 249 (Figure 4). This integration was performed for 4 different combinations of sensors, in order to 250 251 highlight the built-in redundancy provided by using multiple sensors to track movements. The general pattern of how the number of daily activities changed over time was consistent across 252 253 sensor combinations, with the exception of the RFID and beam breaker dataset that did not 254 have video data (Figure 5B). We then focused on detection clusters from the integrated dataset across all sensors to make behavioral inferences. For each of these clusters we used 255 the order in which sensors triggered to score the direction of movements that occurred at the 256 container entrance (entrances and exits, Figure 4, Figure 5C). We integrated perching events 257 detected from the raw RFID data (another type of behavior at the container entrance), and 258 259 scored movements that were captured by video recordings only as movements that occurred 260 inside of the container (Figure 5C). We used information about perching events and 261 movement inside of the container to determine when these behaviors occurred together (Supplementary Figure 2). For detected clusters with video data, we also used the number of 262 263 pixels that changed across color channels to calculate the magnitude of movement. We 264 assessed how movements of different sizes changed over time (Supplementary Figure 3), 265 and how these movement categories mapped back onto behavioral inferences 266 (Supplementary Figure 4). Supplementary section 7 contains more information about 267 behavioral inferences.

Figure 5: We show data collected by ABISSMAL for 1 pair of birds over different stages of data processing. Panel A contains the pre-processed data from movement sensors prior to data integration. Panel B shows 4 datasets of inferred activities that were obtained by integrating pre-processed data across different sensor combinations. In panel C we show the fully integrated dataset (across all sensors) split by four different behavioral inferences. Earlylife events are shaded in grey across panels.



276 3. Assigning movements to individuals

277 We used the fully integrated dataset to assess how ABISSMAL captured movements 278 performed by each individual. When RFID data was present (e.g. movements that occurred at 279 the container entrance), we used the PIT tag(s) detected to assign the movement event to 280 one or both individuals (Figure 6), including which individual initiated or ended the movement 281 event. We found that more movement events through the nest container entrance were 282 assigned to the male than the female for this pair of birds, and this pattern was consistent 283 over time (Figure 6). This difference in the number of inferred activities assigned to each adult 284 does not mean that the female was performing fewer parental care activities, but rather that 285 this individual moved less often through the nest container entrance. Using multiple sensor 286 types through ABISSMAL also allowed us to capture movement events in the fully integrated 287 dataset that were not assigned to either adult (Figure 6). The greatest number of unassigned movements occurred for inferred movements inside of the container that were captured by 288 289 video recording events, which cannot resolve individual identity in the current version of 290 ABISSMAL.

292 Figure 6: Here we show how two types of inferred movements from the fully integrated
293 dataset were assigned back to individuals (the same dataset as Figure 5C). We show early294 life events in grey shading.



296 Discussion

How parents care for their offspring may be critically important for ecological and evolutionary processes (Klug & Bonsall, 2014; Laland et al., 2015; Uller, 2012), but parental care behaviors can be difficult to capture. We developed a new platform of unified hardware and software called ABISSMAL, which provides automated behavioral tracking with built-in system monitoring and error logging. ABISSMAL also provides the capacity to make behavioral inferences in order to streamline data collection, curation, and interpretation for researchers studying parental care. We successfully used ABISSMAL to highlight the process of data collection, integration, and making behavioral inferences for one pair of captive zebra finches that laid eggs and raised chicks over 50 days.

ABISSMAL provides a comprehensive overview of movements associated with parental care behavior by collecting and integrating data across multiple sensors. Collecting data across multiple sensors provides redundancy when any one sensor fails, and therefore higher confidence that the majority of movements around the entrance and inside of the nest container are recorded. Integrating data across multiple sensors also provides internal validation while drawing behavioral inferences from series of detections across sensors that represent movement events. The datasets of inferred behavioral activities returned by ABISSMAL can be used to assess general patterns of activities by adult birds around a nest container before and throughout offspring development.

ABISSMAL can be used to assign movement events to unique individuals in a breeding pair, which facilitates behavioral tracking in species that exhibit biparental care. However, questions about parental care behavior that rely on tracking individual identity and fine-scale behaviors with high confidence may require additional computational processing in later versions of ABISSMAL. The current version of ABISSMAL uses an RFID system to assign 320 activities to individuals, but this individual identity assignment is subject to the RFID antenna 321 failing to detect PIT tags, and is also currently limited to movements that occurred at the container entrance. Since we tracked birds' movements with multiple sensors, we were able 322 323 to capture how often birds moved through the entrance of the nest container without triggering 324 the RFID antenna (Figure 6), which could reflect the RFID antenna failing to detect PIT tags 325 due to individual variation in movements (Hughes et al., 2021). ABISSMAL also captured 326 movements that occurred inside of the nest container, which were captured by video recording events only and could not be assigned to individuals (Figure 6). These short videos 327 328 recorded by ABISSMAL could be used in image processing pipelines to assign behaviors that 329 occurred inside of the container back to individuals. In future work, validating datasets of 330 inferred behavioral activities and individual identity assignments generated by ABISSMAL 331 against behavioral datasets scored from videos by human observers will be important to 332 account for biases that can arise from automated data collection and processing (Smith & Pinter-Wollman, 2021), as well as to assess our confidence while using ABISSMAL for finer-333 334 grained behavioral inferences, such as calculating the duration of nest visits or incubation 335 events.

Quantifying variation in avian parental care behavior has traditionally relied on video scoring that can become prohibitively time-consuming when collecting data across many individuals and over long developmental timelines. ABISSMAL streamlines the process of automated data collection, curation, and interpretation for parental care behaviors. ABISSMAL makes it possible to deploy movement sensors for automated data collection in a highthroughput way, and also provides the capability to integrate movement data collected across these sensors in order to generate behavioral inferences. The built-in system monitoring and error logging, as well as the capacity for deriving behavioral inferences from large datasets, are features of ABISSMAL that will be particularly useful for capturing parental care and other
social behaviors across many experimental replicates and over long developmental
timescales. ABISSMAL is a unified platform but is also modular, and can be used with any
combination of the two pairs of infrared beam breakers, RFID system, infrared camera, and
temperature probe sensors. Our software for automated data collection, system monitoring,
and error logging will require the least amount of modification for different questions, study
species, and research settings. All core components of ABISSMAL will require modification
when adapting the tracking system to use more sensors across any of the four types listed
above, or when adding a new type of sensor for data collection. ABISSMAL is an open-access
tool that we made freely available through the GitHub repository *lastralab/Abissmal* with
extensive documentation to support widespread use and modification

355 (https://github.com/lastralab/ABISSMAL).

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374 contributed critically to the drafts and gave final approval for publication.

375

376 Data availability statement: We have made data publicly available on figshare
377 (https://figshare.com/articles/dataset/Smith-Vidaurre_et_al_2023_ABISSMALMethodsPaper/

378 24555883) to facilitate reproducing our results. We published the raw data used in this

379 manuscript that was collected for 1 pair of captive zebra finches over 50 days of data

380 collection. We also published the pre-processed and integrated versions of this data.

381 <u>References</u>

382

Alarcón-Nieto, G., Graving, J. M., Klarevas-Irby, J. A., Maldonado-Chaparro, A. A., Mueller, I.,
& Farine, D. R. (2018). An automated barcode tracking system for behavioural studies in
birds. *Methods in Ecology and Evolution*, 9(6), 1536–1547. https://doi.org/10.1111/2041210X.13005

Bendesky, A., Kwon, Y. M., Lassance, J. M., Lewarch, C. L., Yao, S., Peterson, B. K., He, M.
X., Dulac, C., & Hoekstra, H. E. (2017). The genetic basis of parental care evolution in
monogamous mice. *Nature*, 544(7651), 434–439. https://doi.org/10.1038/nature22074

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 in Ecology and Evolution*, *11*(9), 1072–1085. https://doi.org/10.1111/2041-

393 210X.13436

394 Gilby, A. J., Mainwaring, M. C., Rollins, L. A., & Griffith, S. C. (2011). Parental care in wild and

395 captive zebra finches: Measuring food delivery to quantify parental effort. *Animal*

396 *Behaviour*, *81*(1), 289–295. https://doi.org/10.1016/j.anbehav.2010.10.020

397 GNU, P. (2007). Free Software Foundation. Bash (3.2.48)[Unix shell program].

Hughes, E. J., Mady, R. P., & Bonter, D. N. (2021). Evaluating the accuracy and biological meaning of visits to RFID-enabled bird feeders using video. *Ecology and Evolution*, *11*,

400 17132–17141. https://doi.org/10.1002/ece3.8352

401 Iserbyt, A., Griffioen, M., Borremans, B., Eens, M., & Müller, W. (2018). How to quantify

402 animal activity from radio-frequency identification (RFID) recordings. *Ecology and* 403 *Evolution*, 8(20), 10166–10174. https://doi.org/10.1002/ece3.4491

404 Jolles, J. W. (2021). Broad-scale applications of the Raspberry Pi: A review and guide for

405 biologists. *Methods in Ecology and Evolution*, *12*(9), 1562–1579.

406 https://doi.org/10.1111/2041-210X.13652

407 Kalafut, K. L., & Kinley, R. (2020). Using radio frequency identification for behavioral

408 monitoring in little blue penguins. Journal of Applied Animal Welfare Science, 23(1), 62–

- 409 73. https://doi.org/10.1080/10888705.2019.1571922
- 410 Kamakura, M. (2011). Royalactin induces queen differentiation in honeybees. Nature,
- 411 473(7348), 478–483. https://doi.org/10.1038/nature10093
- 412 Klug, H., & Bonsall, M. B. (2014). What are the benefits of parental care? The importance of

413 parental effects on developmental rate. *Ecology and Evolution*, *4*(12), 2330–2351. https://

414 doi.org/10.1002/ece3.1083

415 Laland, K. N., Uller, T., Feldman, M. W., Sterelny, K., Muller, G. B., Moczek, A., Jablonka, E.,

- 416 & Odling-Smee, J. (2015). The extended evolutionary synthesis: Its structure,
- 417 assumptions and predictions. *Proceedings of the Royal Society B: Biological Sciences*,
- 418 282(1813), 20151019. https://doi.org/10.1098/rspb.2015.1019

419 Lang, J. W., & Andrews, H. V. (1994). Temperature-dependent sex determination in

420 crocodilians. *Journal of Experimental Zoology*, 270(1), 28–44.

421 https://doi.org/10.1002/jez.1402700105

422 Maldonado-Chaparro, A. A., Forstmeier, W., & Farine, D. R. (2021). Relationship quality

423 underpins pair bond formation and subsequent reproductive performance. *Animal*424 *Behaviour*, *182*, 43–58. https://doi.org/10.1016/j.anbehav.2021.09.009

425 Mathis, M. W., & Mathis, A. (2020). Deep learning tools for the measurement of animal

426 behavior in neuroscience. *Current Opinion in Neurobiology*, 60, 1–11.

427 https://doi.org/10.1016/j.conb.2019.10.008

428 Ogino, M., Maldonado-Chaparro, A. A., & Farine, D. R. (2021). Drivers of alloparental

429 provisioning of fledglings in a colonially breeding bird. *Behavioral Ecology*, *32*(2), 316–
430 326. https://doi.org/10.1093/beheco/araa137

431 Prinz, A. C. B., Taank, V. K., Voegeli, V., & Walters, E. L. (2016). A novel nest-monitoring

- 432 camera system using a Raspberry Pi micro-computer. *Journal of Field Ornithology*, 87(4),
- 433 427–435. https://doi.org/10.1111/jofo.12182

434 R Core Team. (2023). *R: A Language and Environment for Statistical Computing*.

435 https://www.r-project.org/

436 Santema, P., & Kempenaers, B. (2023). Patterns of extra-territorial nest-box visits in a

- 437 songbird suggest a role in extrapair mating. *Behavioral Ecology*, *34*(1), 150–159.
- 438 https://doi.org/10.1093/beheco/arac111

439 Slagsvold, T., & Wiebe, K. L. (2011). Social learning in birds and its role in shaping a foraging

440 niche. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 366(1567),

441 969–977. https://doi.org/10.1098/rstb.2010.0343

442 Smiley, K. O., & Adkins-Regan, E. (2016). Prolactin is related to individual differences in

443 parental behavior and reproductive success in a biparental passerine, the zebra finch

- 444 (Taeniopygia guttata). General and Comparative Endocrinology, 234, 88–94.
- 445 https://doi.org/10.1016/j.ygcen.2016.03.006

446 Smith, J. E., & Pinter-Wollman, N. (2021). Observing the unwatchable: Integrating automated

sensing, naturalistic observations and animal social network analysis in the age of big

448 data. Journal of Animal Ecology, 90(1), 62–75. https://doi.org/10.1111/1365-2656.13362

Uller, T. (2012). Parental effects in development and evolution. In N. J. Royle, P. T. Smiseth, &
M. Kölliker (Eds.), *The evolution of parental care* (pp. 247–266). Oxford University Press.

451 Van Rossum, G., & Drake, F. L. (2009). Python 3 Reference Manual. CreateSpace.

452 Wickham, H. (2011). testthat: Get started with testing. *The R Journal*, 3(1), 5.

453 Wickham, H., Averick, M., Bryan, J., Chang, W., McGowan, L. D., François, R., Grolemund,

- 454 G., Hayes, A., Henry, L., Hester, J., Kuhn, M., Pedersen, T. L., Miller, E., Bache, S. M.,
- 455 Müller, K., Ooms, J., Robinson, D., Seidel, D. P., Spinu, V., ... Yutani, H. (2019).
- 456 Welcome to the Tidyverse. *Journal of Open Source Software*, *4*(43), 1686. https://doi.org/
- 457 **10.21105/joss.01686**
- 458 Youngblood, M. (2020). A Raspberry Pi-based, RFID-equipped birdfeeder for the remote
- 459 monitoring of wild bird populations. *Ringing and Migration*, *34*(1), 25–32.
- 460 https://doi.org/10.1080/03078698.2019.1759908
- 461 Zohar, O., & Terkel, J. (1991). Acquistion of pine cone stripping behaviour in black rats
- 462 (Rattus rattus). International Journal of Comparative Psychology, 5(1), 1–6.

463 https://doi.org/10.46867/c4kw2h