1 **Temperature loggers capture intraregional variation of inundation timing for**

2 **intermittent ponds**

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10 **ABSTRACT**

11   Hydroperiod, or the amount of time a lentic waterbody contains water, shapes

12 communities of aquatic organisms. Precise measurement of hydroperiod features such as

13 inundation timing and duration can help predict community dynamics and ecosystem stability. In

14 areas defined by high spatial and temporal variability, fine-scale temporal variation in inundation

15 timing and duration may drive community structure, but that variation may not be captured using

16 common approaches including remote sensing technology. Here, we provide methods to

17 accurately capture inundation timing by fitting hidden Markov models to measurements of daily

18 temperature standard deviation collected from temperature loggers. We describe a rugged

19 housing design to protect loggers from physical damage and apply our methods to a group of

20 intermittent ponds in southeastern Arizona, showing that initial pond inundation timing is highly

21 variable across a small geographic scale ($\sim$50km^2). We also compare a 1-logger (pond only) and

22 2-logger (pond + control) design and show that, although a single logger may be sufficient to

23 capture inundation timing in most cases, a 2-logger design can increase confidence in results.

24 These methods are cost-effective and show promise in capturing variation in intraregional

25 inundation timing that may have profound effects on aquatic communities, with implications for

26 how these communities may respond to hydroperiod alteration from a changing climate.

27 **Key Words: temporary ponds, hydroperiod, HOBO Pendant logger, temperature sensor,**
28 **hidden Markov models, American Southwest, aquatic, desert**
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1. Introduction

For water-dependent organisms, hydroperiod – or the amount of time a lentic waterbody holds water – plays a critical role in population and community dynamics (De Meester et al., 2005). Dispersal decisions (Tournier et al., 2017), fitness (Johnson et al., 2013; Rogers & Chalcraft, 2008), reproductive success (Ryan & Winne, 2001), survival (Acosta & Perry, 2001), and source-sink dynamics (Ruetz III et al., 2005; Werner et al., 2007) are all influenced by hydroperiod. Hydroperiod is also an important predictor of community composition (Razgour et al., 2010; Skelly, 1997; Waterkeyn et al., 2008) and diversity (Schriever et al., 2015; Schriever & Williams, 2013; Stendera et al., 2012), and thus may influence ecosystem stability. Specific components of hydroperiod, such as inundation timing or stability, influence species density and richness (Florencio et al., 2020; Kneitel, 2014) may play a key role in determining reproductive success of amphibians (Paton & Crouch III, 2002).

The wide-ranging effects of hydroperiod on individual organisms, populations, and ecological communities necessitate tools to enable fine-scale measurement and monitoring of the timing, frequency, and duration of hydroperiod events in temporary lentic waters. Such tools will play an important role in predicting how hydroperiods may change in response to future water use and climate scenarios – and how organisms that rely on these habitats will fare. Satellite remote sensing tools such as Synthetic Aperture Radar (Bourgeau-Chavez et al., 2005; Hong et al., 2010) and Landsat imagery (DeVries et al., 2017; Díaz-Delgado et al., 2016; Murray-Hudson et al., 2015) enable wetland hydroperiod assessment over multi-year or multi-decade periods and covering 10s to 1000s km^2. The accuracy of these methods continues to improve with advances in image analytical techniques that provide information on surface water presence and area at a sub-pixel level (Halabisky et al., 2018). Despite these promising advances, the temporal grain of

60   remotely sensed data remains coarse for most remotely sensed datasets. For example, Landsat

61   captures images at a spatial resolution of 30 meters every 16 days (Irons et al., 2012; Ozesmi &

62   Bauer, 2002). Remotely-sensed images can be obscured by cloud cover, further decreasing

63   temporal resolution. In many regions, inundation of intermittent lentic habitat may occur over

64   hours or days. Temporal resolution on the order of 2-4 weeks may miss important fine-scale

65   differences in pond inundation timing, particularly in regions with unpredictable spatial patterns

66   of precipitation that drive a patchwork of inundation dates.

67   Temperature and conductivity sensors are used increasingly in both lotic and lentic

68   systems to provide fine-scale spatial and temporal hydroperiod measurements (Anderson et al.,

69   2015; Arismendi et al., 2017; Jaeger & Olden, 2012). Daily temperature variance is typically

70   lower in water than in air, and comparison of daily temperature variance provides a reliable

71   proxy for inundation state (Sowder & Steel, 2012). A rapid drop in daily temperature variance

72   can reliably measure the precise timing of an inundation event (Anderson et al., 2015; Arismendi

73   et al., 2017). For example, Anderson et al. (2015) tested the ability of temperature sensors to

74   accurately predict inundation states both in natural wetlands and in controlled mesocosms. The

75   authors deployed temperature sensors for two six-month periods in ponds over a 7140 ha area

76   that varied in size and depth. They demonstrated that daily temperature variance reflected pond

77   filling and drying events, with higher variance in dry ponds and in control sensors placed on the

78   ground outside of ponds, and they determined an approximate variance threshold to predict

79   inundation states. Arismendi et al. (2017) placed paired temperature sensors and electrical

80   resistors in temporary streams. They found that using daily temperature standard deviation more

81   accurately predicted inundation states than mean hourly or daily temperature measurements, and

82   they applied 2-state hidden Markov models, which account for autocorrelation of time series

83 data, to the daily temperature standard deviations measured from the streams in order to predict

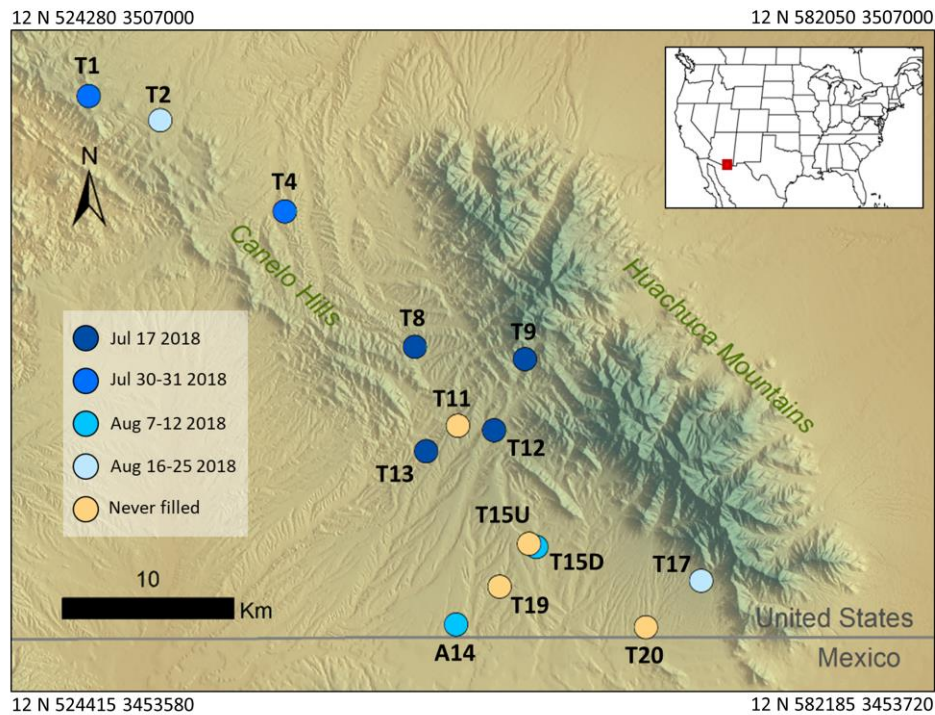84 shifts from wet to dry states.

85   Here, we describe methods for deployment and data analysis of an array of temperature

86 loggers to monitor inundation state of intermittent ponds in the San Rafael Valley of Arizona,

87 USA. The objectives of this study were: 1) design a sturdy, low cost, and low maintenance

88 housing unit for temperature sensor deployment in remote and rugged terrain; 2) deploy paired

89 sensors (one within the target pond and one outside the pond) to monitor hydroperiod inundation

90 states in temporary ponds; 3) evaluate inundation states using hidden Markov models, comparing

91 inundation date inference between 1-logger (pond only) and 2-logger (pond + control)

92 experimental design; 4) compare observed and inferred inundation state recorded during in-

93 person visits to ponds. Overall, our findings point to the utility of temperature loggers as a cost-

94 effective, low profile tool in uncovering ecologically relevant spatiotemporal differences in

95 intraregional inundation timing. This is particularly useful in regions with highly localized

96 precipitation events that drive small-scale differences in spatiotemporal hydroperiod dynamics.

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98 **2. Methods**

99 **2.1 Study area**

100 We deployed paired temperature loggers (one within and one outside a pond) in 16 intermittent

101 ponds in the Coronado National Forest, located within the Huachuca Mountains Canelo Hills

102 (HMCH) region and San Rafael Valley of southeastern Arizona, USA in June and July 2018

103 (Figure 1). The HMCH region is part of the Madrean Sky Islands, with an elevation range of

104 approximately 1150 m to 2880 m. Habitat composition includes cienega wetlands, semi-arid

105 grasslands and thorn-scrub, and evergreen and coniferous woodlands. The climate of this region

106 is semi-arid, with up to half of the annual rainfall occurring during the summer monsoon season

107 (Sheppard et al., 2002). Rain events during the monsoon season are typically short in duration,

108 high in intensity, and seasonally predictable but spatially variable (Goodrich et al., 2008). Ponds

109 in the region were originally constructed to provide water for livestock and are often called

110 "stock tanks"; these ponds are now surrogating for aquatic habitat lost to human activities and

111 support a range of aquatic species (Rosen & Schwalbe 1998; Storfer et al. 2014; Mims et al.

112 2016). We selected ponds based on historical hydroperiod data that indicated they were generally

113 intermittent and tended to have longer (>1 month) duration wetted phases (Parsley et al., 2020).

114 **Figure 1.** Study ponds (N=14) in the Huachuca Mountains-Canelo Hills region of southeastern
115 Arizona (reference map inset). Colors indicate pond initial fill dates, ranging from 17 July 2018
116 (T8, 9, 12, and 13) to 25 August 2018 (T2). Initial fill dates were calculated from paired pond-
117 control Hidden Markov models, where inundation was defined as a period of 5 or more
118 consecutive days with the daily temperature standard deviation measured by the pond logger was
119 at least 2°C less than that of the control logger. UTM coordinates (NAD 83) indicate position of
120 each corner of the map.

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2.2 Sensors, housing units, and deployment

We selected a waterproof temperature logger with the capacity for battery replacement by the

user for longevity (company: Onset, Bourne, MA, USA; model: HOBO Pendant, MX2201;

diameter: 3.35 cm; temperature range: -20 ˚C to 50˚C; temperature precision: ± 0.5˚C; cost:

$54.00 USD; data retrieval: Bluetooth, battery: user replaceable CR2032 3V lithium). Our study

region is remote with rugged terrain, and deployed equipment is exposed to variable weather,

UV exposure, and potential tampering from humans, wildlife, or livestock. The intermittent

ponds in our study region are visited frequently by cattle, and equipment must be able to

withstand trampling or tampering. With this in mind, we designed a rugged housing unit to

protect temperature loggers from damage and ensure long-term durability (Figure S1). We

placed a logger inside a PVC junction box (hereafter called the housing unit) with two nuts

between the box and the lid for increased air or water flow. The logger moved freely inside the

housing unit to increase the chance that it remained submerged (i.e., fell to the lowest point

within the housing unit) if disturbed after deployment. The housing unit was connected to a

concrete tie or other secure post (e.g., a metal fence post marking edges of allotments) via a

3/32" (2.381 mm) galvanized, uncoated steel cable strung through the holes of the junction box.

We fastened the cable by swaging a crimping sleeve. We provide a complete list of

specifications for tools and materials in Table S1.

At each of the 16 ponds, we deployed one logger at the approximate deepest point of fill

within the tank (the pond logger) and one logger approximately 10 m outside of the high-water

mark for the pond (the control logger). Where possible, we placed control loggers in sunny,

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144   shade-free areas in order to most closely match conditions and exposure of the pond logger. If

145   the pond basin consisted of fine clay or silt, we placed the housing unit on a flat rock partially

146   buried to sit flush with the ground and to avoid it becoming buried in silt upon pond inundation.

147   We then secured the housing unit to an existing fence post (typically a metal T post) or to a

148   concrete tie using steel cable looped through the housing. We used a mallet to drive concrete ties

149   completely into the ground for protection of livestock. Finally, we covered units with loosely

150   stacked rocks to minimize livestock tripping risk and to help camouflage units to avoid

151   tampering (Figure S2). Loggers recorded temperature at 15-minute intervals with Bluetooth set

152   to manual (i.e., not continuously seeking a signal), resulting in an estimated 3.2-year battery life

153   for each logger. We visited ponds three times after sensor deployment: 31 Jul – 2 Aug 2018, 31

154   Mar - 3 April 2019, and 21 – 27 June 2019 (time of data retrieval).

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156   **2.3 Prediction of pond inundation states using Hidden Markov models**

157   We used a custom script in R v3.6.1 (R Development Core Team, 2018) to calculate the daily

158   temperature standard deviations (tSDs) measured by each temperature logger. We then used the

159   package depmixS4 v1.4.0 (Visser & Speekenbrink, 2010) in R to fit hidden Markov models

160   (HMMs) to detect temporal shifts in tSD, representing pond filling and drying events. HMMs

161   can be used to identify shifting trends in time series data (e.g. high tSDs associated with dry

162   states and low tSDs associated with wet states) while accounting for temporal autocorrelation.

163   Therefore, they are useful tools for modeling climatic data (reviewed in Srikanthan & McMahon,

164   2001). We initially fit both 2-state and 3-state HMMs to both of our datasets, with the former

165   modeling a simple scenario of distinct dry and wet states, and the latter factoring in the potential

166   effects of seasonal differences, which may cause daily tSD readings to differ due to varying

167 water depths above the sensors (Anderson et al., 2015) or as a result of seasonal environmental

168 variation (Campbell & Diebold, 2005). We compared two different datasets for each study site:

169 one using temperature data from the paired pond and control loggers at each site, calculated by

170 subtracting the tSDs of the pond loggers from the tSDs of control loggers (wherein a value of 0

171 indicates no difference in daily tSD between the pond and air temperatures), and another using

172 tSDs from pond loggers only.

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174 **3. Results and Discussion**

175 **3.1 Assessment of housing unit performance**

176 We retrieved data from 30 (n = 14 pond loggers, n = 16 control loggers) of the 32 loggers

177 deployed, with two pond loggers underwater at the time of collection. We downloaded

178 temperature data for the entire study period (between 1 July 2018 and 21 June 2019) for 26

179 loggers. Four pond loggers at sites T1, T2, T8, and T13 failed due to a potentially faulty logger

180 backing design that was addressed by the manufacturer during the time between initial

181 deployment and site visits in June 2019; all pond loggers were replaced by the manufacturer, and

182 replacements were deployed following data retrieval in June 2019. No subsequent issues

183 emerged (0% failures) using loggers with the updated backing for other experiments during

184 which loggers were submerged in water for months at a time (M.C. Mims, unpublished data).

185 During each site visit, we evaluated logger function, cleared any mud or sediment in the rugged

186 housing units, and replaced disturbed rock piles (Figure S3).

187   Overall, we found that the logger design accomplished our goals, but there were some

188 considerations and limitations. Our logger housing design successfully protected the loggers

189 from physical damage, even when disturbed by cattle. Careful placement of loggers in the

190   deepest point in the pond is also imperative for accurate hydroperiod estimation. At site T11, we

191   observed that the pond logger did not appear to be placed at the lowest point within the pond, as

192   was intended. We observed very shallow water pooled in another location near the logger in

193   summer 2019 that dried a few days later. Therefore, the data collected from this logger may not

194   accurately reflect the pond inundation state. The other issue with our physical design was the

195   accumulation of sediment or other debris within the rugged housing unit that contain the logger

196   and interfered with temperature readings from the pond loggers at sites A14, T4, T9, and T17

197   (see Figure S3 for example). We occasionally observed animals inside housing units, including

198   several salamanders inside the housing for the pond logger at site T9 (Figure 2). Additionally,

199   rock piles placed on top of the rugged housing likely affected absolute temperature readings.

200   Though rock color or density may have had differential effects among loggers, we suspect the

201   variation among loggers was likely low overall. Furthermore, because this method considers tSD

202   rather than absolute temperature, we do not anticipate these differences had substantial effects on
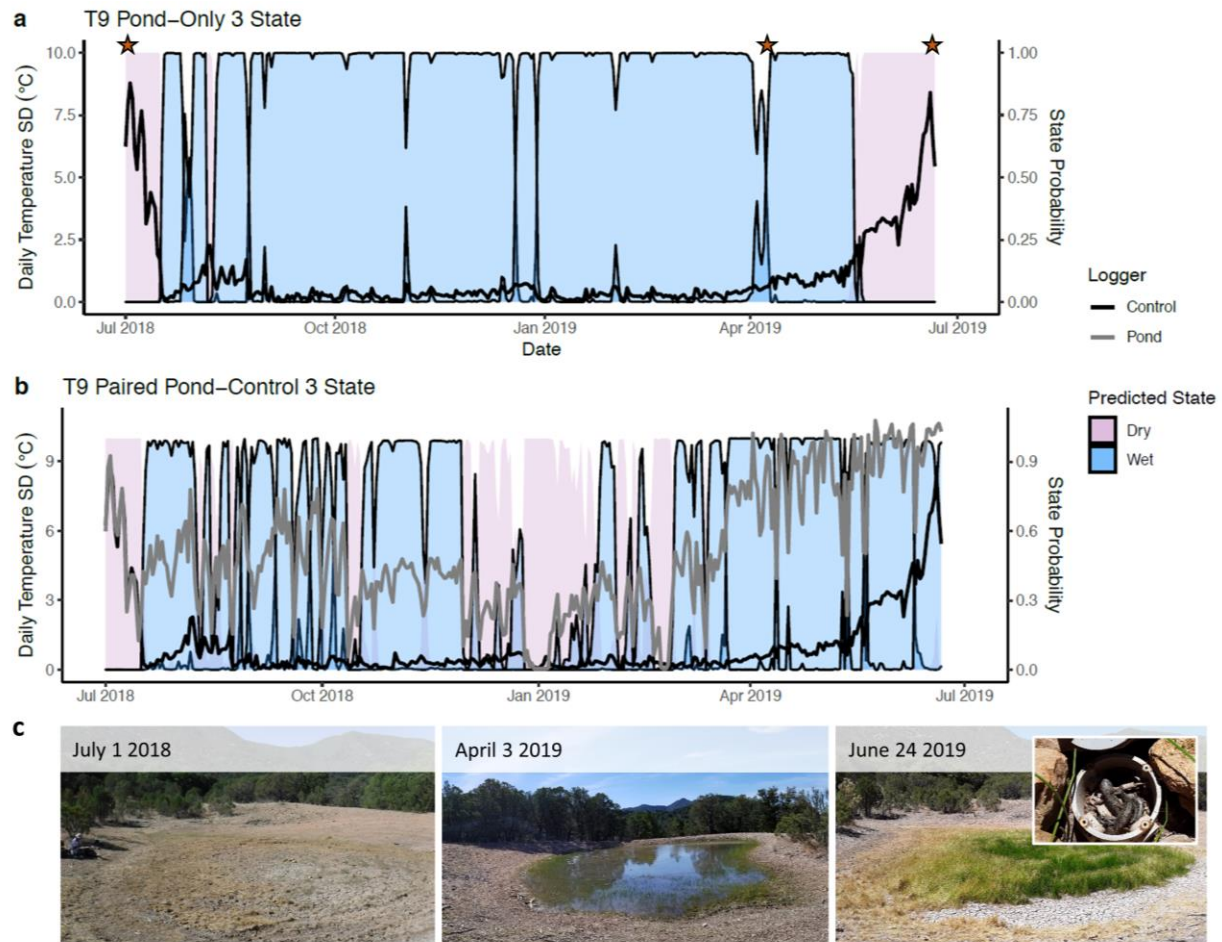
203   results.

Figure 2. Three-state hidden Markov model predictions for pond T9 using (a) pond-only dataset, and (b) paired pond-control dataset. (c) Photos from site visits (dates correspond with stars in (a)), in which observed pond inundation state was dry at the time of sensor deployment (1 July 2018), wet during a return visit the following spring (3 April 2019), and dry at the time of sensor retrieval (24 June 2019). Though we observed no standing water on 24 June 2019, the pond supported vegetation, and we found salamanders in the sensor housing unit (inset photo; possibly contributing to different predicted states on 24 June 2019). Colors indicate temporal state predictions for each pond (pink=dry, blue=wet) and lines represent daily temperature standard deviation (tSD) measurements from pond logger (black lines) and control logger (grey lines).

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3.2 Comparison of 2- versus 3-state Hidden Markov models and determination of wet state threshold values

Because the fit() function in depmixS4 will force each dataset into the designated number of states, even in the absence of a true wet state, we used the HMM parameter estimates to determine appropriate tSD thresholds to designate each state as "wet" or "dry" for both datasets, comparing the predicted states to the known states of the ponds during our four site visits (Tables S2 and S3). For the paired pond-control dataset, we used a wet state threshold of -2.0°C, meaning that the daily tSDs measured by the pond sensors were at least 2.0°C lower on average than those measured by the control sensors. This -2.0°C threshold minimized the number of false dry state predictions. It did result in a false wet prediction for T17, but this was likely due to sediment in the pond sensor housing that may have affected the reading. A more conservative threshold of -2.2°C falsely predicted T12 as dry (Table S3).

Use of HMMs with >2 states can help resolve variation among dry-wet states, improving classifications. Although 2-state HMMs have been applied in past work (Arismendi et al., 2017), we found that 2-state HMMs appeared to over- or underestimate inundation duration for several ponds or predict additional wet states when we were confident that the ponds were dry (Figure S4). Using 3-state HMMs and subsequently combining multiple wet or dry states provided more accurate and consistent state predictions between pond only and paired pond-control datasets (Tables S2, S3). Anderson et al. (2015) showed that seasonal fluctuation, canopy cover, pond vegetation, and water depth can influence temperature variance readings from temperature loggers placed in wetland basins, and that loggers in relatively deeper water have lower variance than those in shallower water. Therefore, we focused our analyses on results from the 3-state HMMs, which allow for the potential for seasonal variation in daily tSDs and intermittent wet-

240   dry states (e.g., damp), accounting for potential uncertainty due to wet sediment or other factors

241   (see Figure 3 for examples).

242   Upon fitting 3-state HMMs to the pond-only dataset, we found that a threshold between

243   2.9°C to 3.3°C minimized the number of false dry states for most ponds (Table S2, Table S3).

244   This threshold is slightly lower than that proposed by Anderson et al. (2015), who determined

245   that using daily temperature variances cutoffs between 13 and 15 (corresponding to tSDs

246   between 3.6°C and 3.9°C) for the wet state provided the most accurate predictions of pond

247   inundation states in their field experiments. Within our pond-only dataset, using a less

248   conservative tSD threshold of 3.5°C decreased the accuracy leading to a false wet state

249   prediction for pond T15U. For pond T8, the state with the highest average temperature standard

250   deviation (~2.8°C) fell below our wet state cutoff of 3.0°C (Table S5). Because we knew that the

251   pond was dry at two timepoints in this state (during logger deployment and logger retrieval), we

252   decreased the wet state threshold to 2.7°C for this particular pond and considered the average

253   tSD of 2.8°C to reflect a dry state.

254   To further define a "reliable" wet state prediction from our HMMs, we also required that

255   the pond remain in a given state for a minimum of 5 consecutive days. We chose this cutoff

256   based on site observations in early August 2018, during which ponds T17 and T20, which had

257   short predicted wet states of 7 and 5 days in July respectively, both showed evidence of prior

258   inundation despite being dry at the time of our visit, and pond A14, which had a predicted wet

259   state of 4 days in mid-July but showed no evidence of earlier inundation in early August (Table
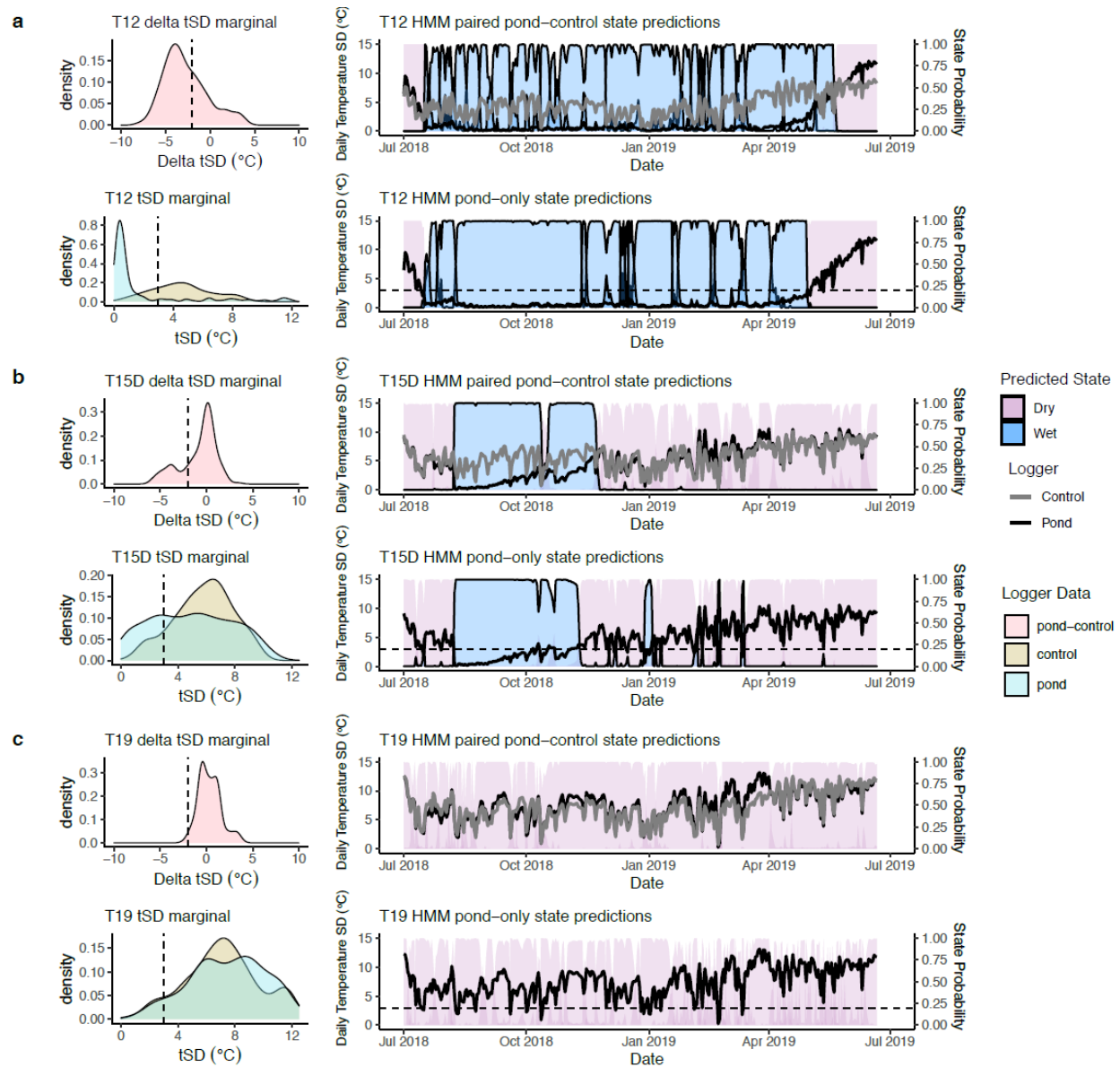
260   S2, Table S3).

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Figure 3. Inundation state predictions by 3-state hidden Markov models (HMMs). Shown are marginal distributions and predicted inundation timing for select ponds that (a) became inundated for long durations during the study period, (b) filled for relatively shorter durations, and (c) had no predicted wet state. Left panels represent marginal distributions and right panels represent HMM estimates from paired pond-control models (top) and pond-only models (bottom). Shading on HMM graphs indicate temporal state predictions for each pond (pink=dry, blue=wet) and lines represent temperature standard deviation (tSD) measurements from control loggers (grey lines) and pond loggers (black lines). Dashed lines indicate wet state thresholds (3.0°C for the pond only dataset and -2.0°C difference for the paired dataset).

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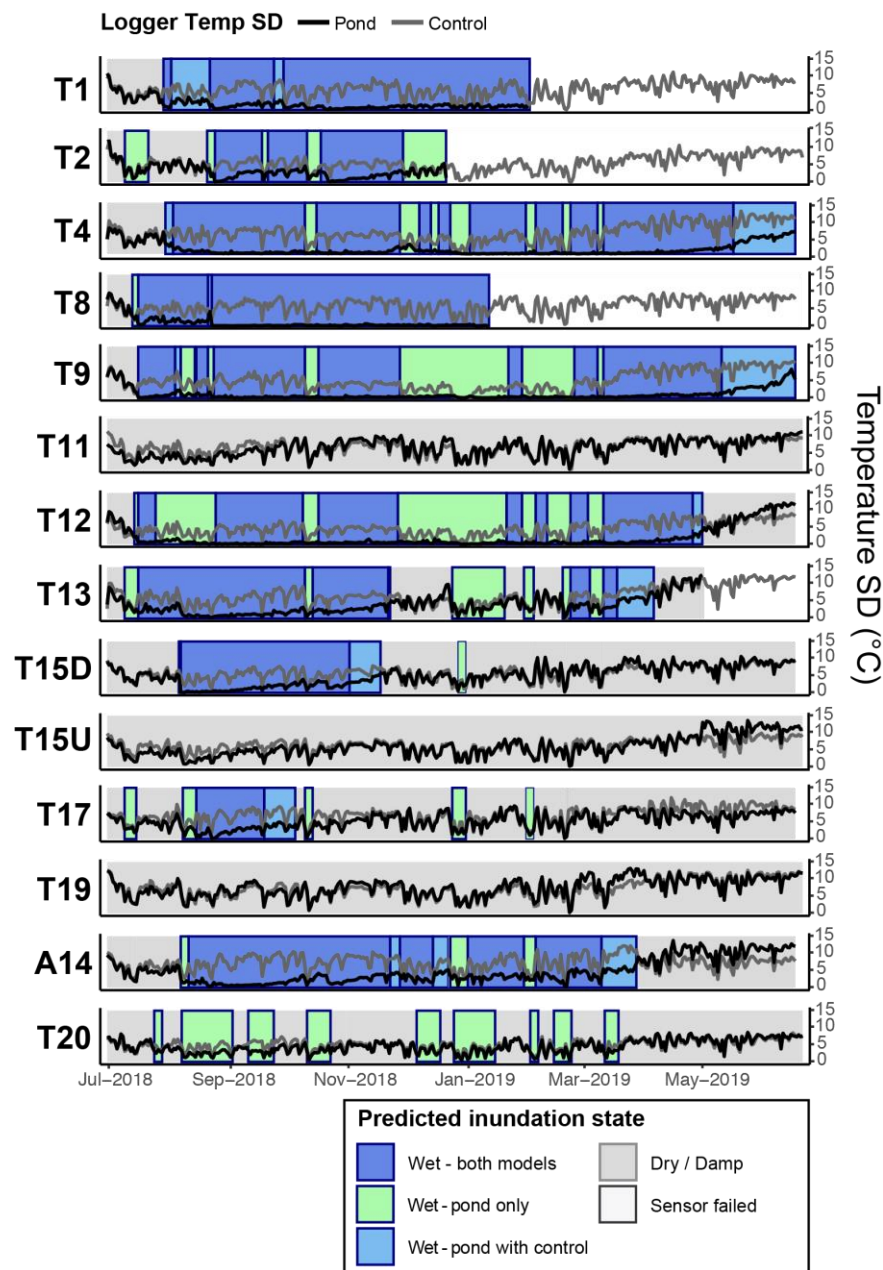**3.3 Pond inundation regimes**

Under the wet state criteria defined above, 3-state HMMs for the pond-only model accurately predicted inundation states for 92% of site visits for the 14 ponds. The paired pond-control model accurately predicted inundation states for 90% of sites visits. Most of the incorrect state predictions were likely due to sediment or additional debris accumulating within the rugged housing units, which was more likely to affect precision of drying dates rather than initial inundation timing.

Based on HMM estimates, ponds varied in both initial timing and duration of inundation (Figure 4), with initial inundation dates ranging from 10 July 2018 to 7 August 2018, over a small geographic area (Figure 1). Eleven of the fourteen ponds in our study had at least one predicted wet state during our monitoring period. Ten of these ponds had wet states predicted from both datasets. Based on the state predictions by both models, ponds in the central range of our study area filled first, with ponds T8, T9, T12, and T13 all inundated between 10 - 17 July 2018. Ponds in the northern and southern portions of the study area had more variation in their initial inundation dates, which were predicted to occur between late July and mid-August (Table S6, Figure 1, Figure 4).

Disagreement between pond-only and pond-control models regarding whether or not a pond filled was rare. Only pond T20 was predicted to have a wet state by one model (the pond-only model) and not the other. The presence of vegetation at the perimeter of the pond and mud inside the housing of the T20 pond logger during our visit in April 2019 suggest that the pond may have been inundated with water at some point during logger deployment. Visual inspection of the T20 temperature standard deviation readings revealed a slight difference between August and October 2018. Ponds T11 and T15U, which had no predicted inundation dates, also showed

296   slightly lower readings from the pond loggers relative to the control loggers at certain points in

297   the monsoon season and had mean state values close to but slightly above our wet state

298   thresholds. It is possible that some water accumulated in these ponds and that our wet state

299   threshold for the HMMs lacked the sensitivity to capture these low signals. The tSD threshold

300   may need to be adjusted to increase precision in cases where small amounts of water accumulate

301   for durations shorter than 5 days.

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304 **Figure 4.** Hidden Markov model (HMM) pond inundation predictions. Lines show daily tSDs
305 measured by pond loggers (black) and control loggers (grey). Rectangles represent wet days
306 predicted by HMMs from single pond loggers (light green), by paired pond-control loggers (light
307 blue), and by both models (dark blue). Grey shading indicates a predicted dry/damp state and
308 lack of shading indicates no data due to logger failure.

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311 **3.4 Comparison of 1 (pond-only) versus 2 (paired pond-control) logger design**

312 Models using temperature data from pond loggers alone predict inundation states that closely

313 aligned with those using paired pond-control logger data, indicating that a single logger design

314 may be sufficient to capture inundation timing of longer-duration events (Table S5, Figure 4).

315 However, control logger data may help alleviate some of the wet state false-positives,

316 particularly when the standard deviation of daily air temperature is relatively low or issues such

317 as sediment in rugged housing units occur. For example, earlier inundation dates are predicted

318 for several ponds by the pond-only model relative to the paired pond-control model. This may be

319 a true wet state, or the coincident low temperature standard deviations measured by the control

320 loggers may have simply resulted in lower variance in the temperature on those days. For site

321 T13, the state was correctly predicted as wet by the paired pond-control model, but not by the

322 pond-only model in April 2019. While we did observe water in the pond at this time, the water

323 level was just at the base of the rock pile covering the logger housing, which may explain the

324 discrepancies between the models. In cases such as this when shallow water is present, the 2-

325 logger design may help to increase the probability of detecting inundation. Predicting pond

326 drying may require an array of pond loggers situated at different heights within in the pond to

327 capture this fine-scale variation. But considerations exist for the pond-control logger model as

328 well. For example, pond-only models predicted wet states for most ponds in the winter months

329 (between December and February) that were not predicted by the paired pond-control models.

330 The relatively low tSDs of the loggers in the winter months may be due to snow accumulation on

331 top of the control loggers.

332 Although we have relatively high confidence in inundation timing, drying dates were less

333 precise largely due to the accumulation of sediment in the housing unit. Paired pond-control

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334 models also predicted later drying states for ponds T4, T9, and A14. At site A14, mud was

335 discovered in the logger housing on 31 March 2019 and was cleared. In the days preceding 31

336 March 2019, the temperature standard deviations from the pond logger were considerably lower

337 than those from the control logger at this site, despite a lack of water in the pond, resulting in the

338 paired pond-control model falsely predicting that the pond was in a wet state. After the sediment

339 was cleared, the difference in these tSDs decreased to nearly zero, and the paired pond-control

340 model correctly designated the pond state as dry. Mud and debris found inside the rugged

341 housing of the pond loggers at sites T4 and T9 in late June likely caused the tSDs of these pond

342 loggers to remain low relative to those of the control loggers even after drying, leading to false

343 wet predictions.

344   To improve drying date precision, the housing unit design would likely need to exclude

345 sediment, which is difficult to do without making other compromises. Solutions for avoiding the

346 issue of sediment packing in rugged housing units, and the subsequent decoupling of pond and

347 control data, include packing the housing unit with insulation or other material that would not

348 allow sediment to enter. However, this can lead to issues such as a buoyant housing unit and may

349 affect the temperature readings if the material is a good insulator. Conductivity sensors offer an

350 alternative to temperature loggers. However, custom modifications required to create

351 conductivity sensors can be time-consuming or, if outsourced, may result in units that are >2

352 times the cost of temperature loggers. Additionally, conductivity sensors may suffer from the

353 same issues related to poor or imprecise detection of drying patterns due to water trapped in

354 sediments. Temperature measurements offer data that are biologically meaningful (temperature

355 as well as presence/absence of water) and that may address multiple needs depending on the

356 objectives of a study.

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4. Conclusions

359 Precise measurement of pond inundation timing can be essential for studies of ecological and

360 hydrological dynamics, particularly in areas with fine-scale variation in climate, where limited

361 water supply may be crucial in shaping population and community dynamics. In this study, we

362 observed an approximate 4-week difference in initial inundation timing between ponds within a

363 small geographic range ($\sim$50km^2), which is a substantial portion of the aquatic stage for many

364 aquatic organisms that rely on these ponds to complete their life cycle (e.g., amphibians: Mims et

365 al., 2020; Moore et al., 2020); these intraseasonal differences in inundation timing may thus have

366 major implications for community composition and species turnover in these habitats. Fine-scale

367 hydrological data such as those presented herein provide valuable information about dynamic

368 water regimes that can improve conservation strategies by identifying potential refugees for

369 plants and wildlife and can also aid in planning for human adaptation in response to the changing

370 climate.

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