DOI: 10.1002/ece3.4097

REPLY TO LETTER TO THE EDITOR

WILEY Ecology and Evolution Open Access

Reproductive ecology of interior least tern and piping plover in relation to Platte river hydrology and sandbar dynamics: Response to the letter to the editor

1 | INTRODUCTION

We appreciate the opportunity to respond to Alexander, Jorgensen, and Bomberger-Brown's (hereafter AJB's) letter to the editor of Ecology and Evolution (Alexander et al. 2018). We begin by restating the principal findings of our study to correct AJBs' mischaracterization of our work beginning in the abstract where they attribute to us a principal assertion that "interior least tern and piping plovers are not adapted to occupying and nesting on river sandbars on the Platte River system." We made no such assertion. These species do occupy Platte River sandbars. Our research focused on the potential for on-channel reproductive success in the contemporary lower Platte River (LPR) and historical and contemporary central Platte River (CPR) finding that: (1) there is no evidence that interior least terns (*Sternula antillarum athalassos*; hereafter, least tern) and piping plovers (*Charadrius melodus*) are physiologically adapted to begin nesting concurrent with the recession of spring floods in the Platte River basin; (2) there are many years when no successful on-channel reproduction is possible because emergent sandbar habitat is inundated after most nests have been initiated; (3) the limited potential for reproductive success thus limits the potential for maintenance of stable subpopulations via on-channel nesting habitat alone; and (4) the availability and use of off-channel habitats, like sandpits, may have allowed for these species to develop stable subpopulations in a river basin where hydrology is not ideally suited to their nesting ecology.

The remainder of this response addresses AJB's major points of criticism under their topic subheadings in the order that the subjects were addressed in our original manuscript. In instances where we have included figures or tables that expand upon our emergent sandbar habitat model results, we focus on the contemporary LPR segment as it is the segment with the highest potential for reproductive success and is cited by AJB as an example of a resilient and dynamic natural system (along with the historical AHR) that benefits these species.

2 | THE HISTORICAL RECORD

AJB assert that we "overlooked portions of the historical record which demonstrate terns and plovers were regularly present and successfully nested along the central Platte River (CPR) and lower Platte River (LPR)." They support this assertion by summarizing early historical references to the occurrence of least terns and piping plovers in Nebraska. Anecdotal observations such as the Bruner, Wolcott, and Swenk (1904) assessment that least terns were "not a rare breeder" in Nebraska are neither evidence for or against AJB's assertion that the species successfully nested along the CPR and LPR. Neither do they speak to the purpose of our study, which was to evaluate the reproductive ecology of these species in relation to historical and contemporary AHR and contemporary LPR hydrology and sandbar dynamics.

Simply put, the first observation of on-channel least tern nesting in the AHR occurred in 1942 when a colony was discovered nesting on the river near Lexington, Nebraska by Dr. Ray S. Wycoff (Wycoff, 1960). That colony was observed nesting on a low sandbar in the channel, a high in-channel island created by sand mining, and at adjacent sandpits. The first observations of piping plovers in the AHR are more general in nature, but indicate that some on-channel nesting may have occurred in the early 1950s (Pitts, 1988). The first observation of least tern and piping plover nesting in the LPR occurred in 1941 when both species were observed nesting on a sandbar near Columbus (Ducey, 1985).

These observations occurred near the end of large-scale surface water development in the Platte Basin when the channel was actively adjusting to hydrologic alteration (Murphy, Randle, Fotherby, & Daraio, 2004; Simons & Associates Inc. and URS Greiner Woodward Clyde, 2000, Williams, 1978). The various authors (Currier, Lingle, & VanDerwalker, 1985; National Research Council 2005, USFWS 2006) that concluded the AHR supported populations of both species prior to water development inferred a decline in species use and productivity from (1) the reduction in AHR channel width from the predevelopment period, (2) a reduction in the magnitude of the spring rise resulting in unsuitably low sandbar habitat likely to be inundated during the nesting season, (3) a lack of on-channel nesting in the contemporary AHR, and (4) species use of the contemporary LPR. This inference assumes physical conditions in the historical AHR were similar to the contemporary LPR and the LPR currently supports viable species subpopulations. We examined the first assumption in Section 4 of our original manuscript, finding that the potential for successful nesting in the historical AHR was likely much lower than the contemporary LPR due to important differences in-channel width and discharge magnitude. The second assumption is addressed in following sections of this response.

In their discussion of the historical records, AJB also state the presence of species populations on other Great Plains rivers like the Niobrara that lack off-channel habitats provide additional evidence “contradicting the notion that adjacent that off-channel habitats are a prerequisite for these species to colonize and breed within a river segment.” We consider this a straw man argument (Talisse & Aikin, 2006). Our findings were specific to the Platte River study segments we evaluated, and we did not generalize to other segments or river systems. We concur with AJB that the Niobrara supports stable species subpopulations in the absence of off-channel habitats (Adolf, Higgins, Kruse, & Pavelka, 2001). As such, it provides a valuable contrast to the AHR that has been explored by the PRRIP as part of a larger peer-reviewed data synthesis project (PRRIP 2015, Chapter 6).

3 | COMPARISONS OF PLATTE RIVER HYDROGRAPH WITH NEST INITIATION DATE DISTRIBUTIONS

In this portion of their critique, AJB criticizes our comparison of species nest initiation periods to the annual hydrograph of the historical and contemporary Platte. They conclude that it would have been more informative to plot the timing and magnitude of instantaneous annual peak discharges in relation to nesting periods. AJB's focus on the instantaneous annual peak discharge assumes that it is the only discharge relevant to species reproductive potential. This is a flawed assumption. As discussed in our study, AJB's critique, and in subsequent section of this response, sandbars do not build to the peak stage of formative events making them vulnerable to inundation at discharges lower than the instantaneous annual peak. Consequently, the timing of the instantaneous annual peak does not speak to the presence or absence of habitat-inundating flow events during the species' nesting periods. Our emergent sandbar habitat model was developed to explicitly assess the frequency and timing of such events in relation to species nesting periods.

Emergent sandbar habitat model results for the contemporary LPR Reach are presented in Figure 1 along with the period necessary for successful nesting and brood rearing for each species. We also present a summary of annual inundation events as well as the number of days sandbar habitat was inundated (Table 1). Model results indicate that sandbar habitat is inundated at least one time during the nesting season (1-May to 30-August) in most years with a median duration of 6 days. Inundation occurs most frequently in June with the highest potential for inundation in mid-June (44% of years; Figure 1).

As illustrated in Figure 1 and Table 1, LPR emergent sandbar habitat is inundated in >75% of years during the nesting period (1-May to 30-Aug) with the highest proportion of inundation events occurring during the latter half of June. Due to the greater availability of emergent sandbar habitat in the early portion of the nesting period, both species often initiate many nests prior to inundating events in mid- to late June resulting in high levels of renesting in early to mid-July. In order for these species to routinely avoid June inundation events, they would need to begin initiating nests in either early April to fledge prior to mid-June or begin initiating nests in early July after the June peak. We are unaware of any evidence from any regional river system indicating that this is currently or has ever been the case.

From a subpopulation viability perspective, we have found reproductive success of AHR nests initiated late in the breeding season (mid-July) is often lower due to fewer eggs typically being laid in a clutch and can further be reduced if not initiated in time to successfully fledge chicks (DMB, pers. obs.). Our sandbar habitat model did not assess differences in productivity throughout the nesting season as there is little information on the success of late renesting on sandbar habitat. Additional systematic monitoring of late renesting on sandbars would allow for a more thorough assessment of this issue.

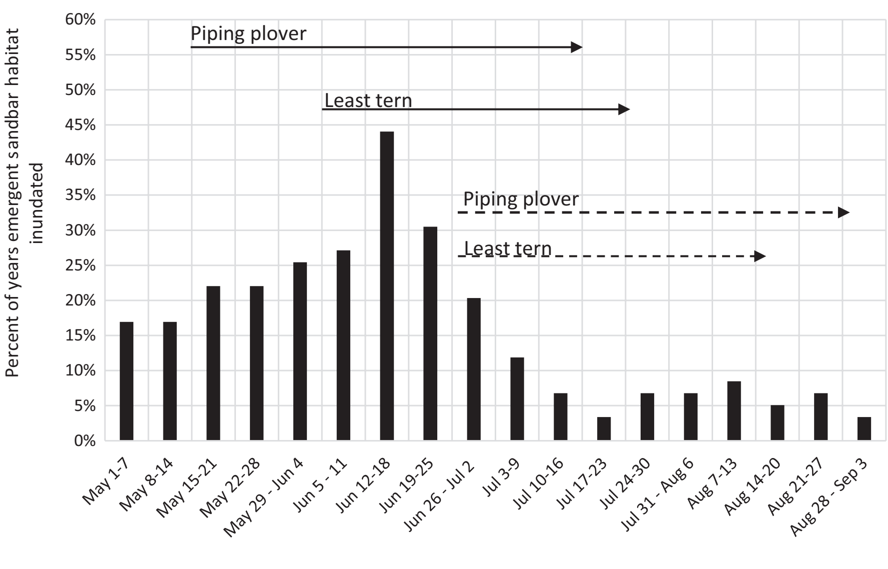

FIGURE 1 Weekly sandbar model results indicating the percent of years when sandbar habitat in the contemporary LPR was inundated along with the period necessary for successful nesting and brood rearing for each species. Bars indicate the percent of years when sandbar habitat was inundated for one or more days during that week. Solid lines represent periods necessary for successful nesting beginning at peak nest initiation dates. Dashed lines represent periods necessary for successful nesting following mid-June inundation events

TABLE 1 Emergent sandbar habitat model results for the LPR Segment including the number of annual habitat inundation events during the nesting period (1 May to 30 August) and total habitat inundation duration in days

	5th	25th	Median	75th	95th
Number of inundation events	0	1	1	2	3
Inundation duration (days)	0	1	6	14	34

4 | DISTRIBUTIONS OF NEST INITIATION DATES AND ASSOCIATED NESTING PERIODS

AJB correctly note that our analysis of nest initiation dates only includes data from the AHR (2001–2013) and nearly all the nest initiation dates come from off-channel habitats. As indicated in our manuscript, development of on-channel nesting periods was not possible as there are very few on-channel nest records in the AHR and there is no systematic season-long monitoring of on-channel habitat in the LPR. AJB state that use of nest initiation data from static, human-created, off-channel habitat is an incomplete representation of species breeding phenology which could easily result in incorrect or misleading conclusions when applied to species' behavior in dynamic river systems. We too shared this concern.

In our study, we assessed the appropriateness of our nesting periods by comparing them to the range of nest initiation dates reported in the LPR (Brown & Jorgensen, 2008, 2009, 2010; Brown, Jorgensen, & Dinan, 2011, 2012, 2013) to identify any disparities. Ninety percent of reported LPR nest initiation dates fell within the 90% nesting periods we developed using AHR data (Brown & Jorgensen, 2008, 2009, 2010; Brown et al., 2011, 2012, 2013; Farnsworth, Baasch, Smith, & Werbylo, 2017; PRRIP 2015). AJB did not dispute this finding.

The only additional information for the LPR segment is found in Kirsch (1996). Kirsch compared least tern nesting dates (1987–1990) and found no difference in nesting periods for on-channel and off-channel habitats. Kirsch did, however, note that there was more late nesting and renesting on river habitat than on sandpits due to nest inundation. This is also consistent with the findings of our study.

5 | FORMATIVE RIVER STAGE, EMERGENT SANDBAR HEIGHT, AND NESTING HEIGHT

AJBs' critique of our emergent sandbar habitat model focuses on four main issues: (1) the use of primarily off-channel nest initiation dates to develop the least tern and piping plover nesting periods; (2) the lack of a detailed description of sandbar height data collection and analysis methods; (3) the model assumption of a constant maximum sandbar height in relation to peak stage of habitat-forming flow events (AJB refer to this as the stage gap); and (4) the model assumption that species nests occur at mean sandbar height. The use of off-channel nest initiation dates has been discussed in the previous section titled "Distributions of Nest Initiation Dates and Associated Nesting Periods." Each of the remaining critiques will be addressed in turn followed by a discussion of model performance.

5.1 | Sandbar height data collection and analysis methods description

Given the range of disciplines addressed in our manuscript (i.e., hydrology, hydraulics, sandbar dynamics, and species nesting ecology), our focus on the emergent sandbar model, and the target audience of this journal, we chose to simplify the methods section of the manuscript. An expanded description of the method used to evaluate sandbar heights in the AHR can be found in PRRIP (2015). We refer readers to that document.

5.2 | Sandbar height model parameter values

AJB's critique in this area focuses on our assumption of a constant sandbar height (stage gap) for all habitat-forming peak flow events, which we defined as the maximum mean daily peak discharge occurring during a 1.5-year period ending on 1 July of the current model year. AJB state that our use of a single value ignores evidence suggesting a pattern of increasing stage gap with increasing discharge. AJB provide two lines of evidence. The first is in the form of several studies (Brice, 1964; Cant & Walker, 1978; Mohrig & Smith, 1996; Smith, 1971) that, as AJB state, "indicate that sandbars submerged during low-magnitude discharges often have shallow gaps at their crests." AJB link this general observation to the stage gap for habitat-forming peak flow events by hypothesizing that there is a Froude limit to vertical sandbar growth that results in an increasing stage gap with increasing discharge. This hypothesis is logical but untested. Accordingly, we have no way to address the veracity of this component of the critique or assess the potential magnitude of a Froude effect in relation to the many other factors that influence sandbar height, including bed material grain size (Ikeda, 1984), sediment supply (Germanoski & Schumm, 1993), and event duration (Crowley, 1981).

AJBs' second line of evidence is related to the findings of Alexander, Schultze, and Zelt (2013). AJB indicate that LPR sandbars surveyed in the spring of 2011 were created during a large 2010 high flow event and sandbars surveyed in the summer and fall of 2011 were created during a smaller 2011 peak flow event that occurred after the spring bar survey. AJB then cite a smaller stage gap for summer/fall 2011 surveys as evidence that the stage gap is smaller for lower-magnitude events. We refer readers to figure 8 of Alexander et al. (2013), which includes peak flow stages and sandbar frequency distributions. Depending on the gage that is referenced, between 10% and 40% of the summer and fall 2011 bar height frequency distributions exceed 2011 peak stage.

Summer and fall 2011 bar area exceeding 2011 peak stage could not have been created during the 2011 peak flow event instead

TABLE 2 Results of AHR sandbar height analyses during the period of 2010–2015

	2010	2011	2014	2015
Event duration (days)	54	98	33	77
Even volume (millions of cm)	566	1,541	261	1,594
Peak date at Kearney Gage	6/17/2010	6/25/2011	6/14/2014	6/18/2015
Mean peak discharge for AHR (m^3/s)	233	251	190	434
Median sandbar height below peak (m)	0.45	0.38	0.5	0.44
Standard deviation of sandbar height below peak (m)	0.14	0.18	0.18	0.18

figure 8 demonstrates they likely represent portions of 2010 bars that persisted through the 2011 event. For these surveys to be used as evidence for a smaller stage gap at lower discharges, the data would need to be parsed to remove bar area that that persisted from 2010. For this reason, we solely used Alexander et al.'s (2013) spring bar height distribution to develop our LPR sandbar height model parameter estimate, with the caveat that we related the median (not mean as stated by AJB) height from the distribution to the stage associated with the mean daily peak flow (as opposed to instantaneous peak) to be consistent with other model input parameters.

We have also analyzed AHR sandbar heights following four peak flow events ranging from 190 to 434 m^3/s in magnitude (2-year to 13-year return interval) with event durations ranging from 33 to 98 days (Table 2). We did not observe an increase in stage gap with increasing discharge. Instead, median sandbar height appears to increase slightly with increasing event duration, although median heights are not statistically different from one another.

5.3 | Model assumption of nesting at median sandbar height

In this portion of their critique, AJB cite tables from Ziewitz, Sidle, and Dinan (1992) and tables/figures from three other publications (Alexander et al., 2013; Brown & Jorgensen, 2008; Smith & Renken, 1991) as empirical evidence to support statements that (1) sandbars with nests tend to have mean elevations that are higher than unoccupied bars and (2) nest heights tend to be located on higher regions of a sandbar's topography. AJB then conclude that since least terns and piping plovers select higher sandbars and nest in higher locations on those sandbars, our model certainly underestimates the potential for successful nesting. We note that Ziewitz et al. (1992) reported mean and maximum sandbar heights at used and systematic sites in the AHR and LPR were not significantly different. Likewise, Brown and Jorgensen (2008) reported mean and maximum sandbar height for used and unused LPR bars in their analysis were not statistically different. Despite the lack of a statistical difference in bar height at used and unused sites, these species may indeed tend to nest on higher bars and/or higher regions of a sandbar's topography. Comparisons of observed inundation events with emergent sandbar model results provide a straightforward way to assess AJB's conclusion that our model, therefore, underestimates the potential for successful nesting.

5.4 | Emergent sandbar model performance

In our original manuscript (Section 3.3), we assessed model performance through the comparison of observed instances of on-channel nest inundation in the historical and contemporary AHR and contemporary LPR to model predictions for those events. For the purposes of our response, we have expanded these comparisons to encompass LPR inundation events during 1989–1990 (Kirsch, 1996; Sidle, Carlson, Kirsch, & Dinan, 1992) as well as nesting and inundation events during the period of 2008–2017 (Brown & Jorgensen, 2008, 2009, 2010; Brown, Jorgensen, & Dinan, 2014, 2015, 2016, 2017; Brown et al., 2011, 2012, 2013). Comparison results are presented in Table 3.

Our model is consistently conservative in that it slightly underpredicts the potential for and length of inundation when compared to observed inundation events (Table 3). This is largely due to our decision to use mean daily discharge values in sandbar inundation calculations. During high flow events, daily instantaneous peak discharge is often substantially higher than mean daily discharge. A comparison of annual instantaneous peak and mean daily peak discharges for the period of 1954–2016 provides an indication of the magnitude of differences (Table 4). During this period, 50% of instantaneous peak discharges were more than 238 m^3/s greater than the mean daily peak discharge, which equates to a 0.13 m difference in peak stage. Put another way, our model underestimates the maximum stage associated with instantaneous peak discharges by more than 0.13 m in 50% of years. As a result, our model necessarily under-predicts the potential for nest inundation on any given day.

6 | LEAST TERN AND PIPING PLOVER POPULATION ECOLOGY

This portion of AJBs' critique asserts that the fledge ratio-based assessment of the potential for long-term maintenance of stable, on-channel species subpopulations (no off-channel habitat) described in

TABLE 3 Comparisons of observed on-channel habitat conditions and nesting in the lower Platte River in relation to Farnsworth et al. (2017) emergent sandbar habitat model predictions

Year	Reported habitat inundation	Model inundation	Piping plover nesting observations	Piping Plover model success window	Least tern nesting observations	Least tern model success window
1989	High flows on 28 June inundated many sandbars	Bars inundated on 28 June to 2 July	18 nests, 7 flooded, no hatch or fledge info	No potential	85 nests, 21 inundated, 0.57 fledglings per pair	10 days
1990	Sandbars inundated 14 June to 19 June	Bars inundated 16 June to 20 June and on 26 July	28 nests flooded, 13 renests, 6 flooded, no hatch or fledge info.	No potential	94 nests inundated, 93 renests, 0.25 fledglings per pair	No potential
2008	High flows mid-May through mid-June. Bar habitat available after mid-June	Bars inundated 28 May through 13 June	3 nests, 1 hatched (July 24). No fledging info.	10 days	150 nests, 63 confirmed/likely hatched, no fledging info.	29 days
2009	Peak flow 21 June completely inundated many sandbars	No inundation	47 nests, 14 inundated, 12 confirmed/likely hatched. No fledging info.	Season-long	264 nests, 50 inundated, 110 confirmed/likely hatched. No fledging info.	Season-long
2010	Large mid-June peak flow inundated sandbars	Bars inundated 11-June to 24-June	8 nests prior to flooding, none after	No potential	5 nests prior to flooding, Four colonies after. No fledging info.	18 days
2011	Bars inundated in late May and again in late June	No inundation	10 nests, 7 inundated in May, 3 confirmed/likely hatched. No fledging info.	Season-long	98 nests, 56 inundated, 38 confirmed/likely successful. No fledging info.	Season-long
2012	No inundation observed	Bars inundated on 30 May	4 nests, no hatch info.	24 Days	74 nests, no hatch info.	43 days
2013	Many bars at least partially inundated in late May	Bars inundated 27 May to 12 June.	11 nests, 4 likely hatched. No fledging info.	No potential	53 nests, 9 likely hatched. No fledging info.	15 days
2014	Bars inundated until mid-July	Bars inundated intermittently 12 May to 4 July	No nests	No potential	26 nests, no hatch or fledge info.	4 days
2015	Bars inundated May to mid-July	Bars inundated intermittently 7 May to 3 July	No nests	No potential	8 nests, no hatch or fledge info.	9 days
2016	Majority bars inundated to mid-June	Bars inundated intermittently 20 April to 22 June	No nests	No potential	33 nests, no hatch or fledge info.	5 days
2017	Most sandbars inundated until early to mid-June	Bars inundated intermittently 1 May to 27 May	3 nests. No hatching info.	18 days	70 nests, 16 chicks, 13 fledglings	32 days

TABLE 4 Difference in instantaneous and mean daily discharge and stage in the lower Platte River

	Difference in discharge (m^3/s)	Difference in stage (m)	Difference in stage (in)
5th percentile	58	0.04	1.69
25th percentile	120	0.08	3.00
Median	238	0.13	5.16
75th percentile	388	0.17	6.66
95th percentile	924	0.37	14.58

our Discussion Section was too simple to address complex questions about metapopulation dynamics. We respond to this criticism by demonstrating that our simple assessment leads to the same inference as the recent Catlin et al. (2016) piping plover metapopulation study that included the LPR segment.

Our model predicted that there was no potential for piping plover reproductive success in 42% of years in the contemporary LPR. The long-term average fledge ratio target proposed to be necessary in the Platte basin to maintain a stable piping plover population is 1.13 fledglings per breeding pair (Lutey, 2002). Therefore, average piping plover productivity in years with some potential for reproductive success would need to exceed 1.95 fledglings per breeding pair (1.13/0.58) to achieve the fledge ratio target of 1.13 over the long term. We noted that we are not aware of any habitat that supports this level of average reproductive success leading us to the conclusion that it is unlikely that LPR on-channel habitat alone can support a stable piping plover subpopulation.

Catlin et al. (2016) examined three piping plover subpopulations on the lower Platte and Missouri Rivers during the period of 2008–2013, including the evaluation of habitat loss and renewal due to natural peak flow events. Model results indicated a low probability of metapopulation extinction over 100 years. However, the persistence of the lower Platte River subpopulation as well as the metapopulation were reported to be dependent on static off-channel habitat that provided a stable source of nesting habitat through time. This conclusion is consistent with our assessment that in-channel habitat in the contemporary LPR is not capable of sustaining a stable subpopulation of piping plovers and that off-channel habitats provide the stable source of habitat necessary to do so.

We are not aware of the existence of a similar metapopulation study for least terns, but would note that there appears to be greater potential for the maintenance of a stable, on-channel subpopulation in the LPR segment as the average fledge ratio estimate (0.84 fledglings per pair) to achieve the Lutey (2002) objective over the long term has at least been periodically reported on LPR on-channel habitats (Brown & Jorgensen, 2008, 2009).

7 | MANAGEMENT AND POLICY IMPLICATIONS

In this section of their critique, AJB argue that the creation and maintenance of off-channel nesting habitat in the contemporary AHR is an inferior alternative to on-channel habitat that could be created through some form of river restoration that would eliminate the need for human intervention. This is a direct appeal to nature (Moore & Baldwin, 1993) which assumes, without supporting evidence, that restoration of historical AHR channel morphology and hydrology would produce sandbar habitat with a high potential for reproductive success. Our emergent sandbar habitat model for the historical AHR, which utilizes historical hydrology and channel morphology, indicates very limited potential for least tern or piping plover reproductive success.

AJB also cite the contemporary LPR as an example of a resilient and dynamic river system that benefits these species, inferring that it is a restoration example for the AHR. This ignores the reality of the similarities in the magnitude of off-channel nesting in both the AHR and LPR. In the AHR, approximately 96% of nests initiated since 2001 have occurred on off-channel habitats. Likewise, in the contemporary LPR, a plurality of nests are initiated on off-channel habitats. Since 2008, approximately 90% of reported LPR piping plover nests and 70% of reported LPR tern nests have been initiated on off-channel habitat (Brown & Jorgensen, 2008, 2009, 2010; Brown et al., 2011, 2012, 2013, 2014, 2015, 2016, 2017).

From an implementation perspective, AJB also ignore the reality of socioeconomic and resources constraints. The Platte River is one of the most highly developed river systems in the world with 9 billion m^3 of reservoir storage distributed across multiple large irrigation and flood control reservoirs (Murphy et al., 2004, Simons and Associates Inc. & URS Greiner Woodward Clyde 2000). The PRRIP is a collaborative endangered species recovery program (PRRIP 2006a) tasked with providing defined benefits to these species while still providing for necessary agricultural and municipal water uses in the Platte River basin including the domestic water supply for millions of people in the Denver metropolitan area (PRRIP 2006a).

The PRRIP utilizes adaptive management to reduce uncertainty regarding key scientific and technical uncertainties and aid decision-making (Compass Resource Management, Inc. 2016; PRRIP 2006b). In relation to least terns and piping plovers, the PRRIP invested nearly a decade in implementation of large-scale adaptive management experiments to test the effectiveness of on- and off-channel habitat creation and management strategies. Once those experiments were completed, the PRRIP conducted a formal structured decision-making process and fully evaluated trade-offs and consequences of various on- and off-channel habitat management strategies. This process resulted in a decision to adjust actions for least terns and piping plovers in a manner that incorporates a combination of off-channel habitat, on-channel habitat, and flow management guidance (Compass Resource Management, Inc. 2016).

ACKNOWLEDGMENT

We would like to thank all members of the Platte River Recovery Implementation Program's Independent Science Advisory Committee and Technical Advisory Committee as well as editorial staff for Ecology and Evolution for their helpful and insightful comments. The Platte River Recovery Implementation Program provided support for this project. The authors are unaware of any real or perceived conflict of interests.

CONFLICT OF INTEREST

None declared.

AUTHORS' CONTRIBUTION

All authors contributed in all phases of the development of our response to the letter to the editor as well as all analyses of data contained therein.

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DOI: 10.1002/ece3.4109

LETTER TO THE EDITOR

WILEY Ecology and Evolution Open Access

Reproductive ecology of interior least tern and piping plover in relation to Platte River hydrology and sandbar dynamics

1 | INTRODUCTION

Historical and contemporary use of large, economically important rivers by threatened and/or endangered species in the United States is a subject of great interest to a wide range of stakeholders. In a recent study of the Platte River in Nebraska, Farnsworth et al. (2017) (hereinafter referred to as "the authors" or "Farnsworth et al.") used distributions of nest initiation dates taken mostly from human-created, off-channel habitats and a model of emergent sandbar habitat to evaluate the hypothesis that least terns (*Sternula antillarum)* and piping plovers (*Charadrius melodus*) are physiologically adapted to initiate nests concurrent with the cessation of spring river flow rises. The authors conclude that (1) these species are not now, nor were they in the past, physiologically adapted to the hydrology of the Platte River, (2) habitats in the Platte River did not, and cannot support reproductive levels sufficient to maintain species subpopulations, (3) the gap in local elevation between peak river stage and typical sandbar height, in combination with the timing of the average spring flood, creates a physical environment which limits opportunities for successful nesting and precludes persistence by either species, and (4) the presence of off-channel habitats, including human-created sand and gravel mines, natural lakes, and a playa wetland, allowed the species to expand into the Platte River basin.

We suggest the authors (1) overlooked published data on the relationship between formative river stage, sandbar height, and nest heights, (2) used nest initiation dates taken from static off-channel habitats and overemphasized the importance of mean daily hydrographs to imply that the hydrology of the Platte River system is not suitable for terns and plovers, (3) incorrectly characterized tern and plover biology, population ecology, and metapopulation dynamics, and (4) overlooked portions of the historical record which demonstrate terns and plovers were regularly present and successfully nested along the central Platte River (CPR) and lower Platte River (LPR).

2 | FORMATIVE RIVER STAGE, EMERGENT SANDBAR HEIGHT, AND NESTING HEIGHT

Elevation of sandbars relative to river stage is a foundational component of the authors' analysis as it determines whether habitat will be available or unavailable (i.e., emergent sandbars exposed above river flow level or sandbars that are fully inundated) for nesting. The sensitivity analysis presented by Farnsworth et al. (2017) showed that assumptions of sandbar heights (depth below peak river flow stage, hereafter referred to as a "stage gap"; see Figure 1 herein) accounted for the clear majority (>90%) of the variance in their emergent sandbar habitat nesting success window estimates. The authors' stage gap assumptions and applications are problematic because of (1) the decision to not describe sandbar height data collection and analysis methods for unpublished values, (2) the assumption of a constant stage gap for each study reach despite empirical evidence to the contrary, and (3) the assumption that most nests are placed at the mean sandbar height.

The authors used mean values for the stage gap, one published (Alexander, Schultze, & Zelt, 2013) and one unpublished (the authors' unpublished data are illustrated in their figure 7). Alexander et al. (2013) focused their height measurements on the so-called "high platform" of emergent sandbars (see figure 3 of Alexander et al., 2013; and Figure 1 herein) rather than the entire topography of sandbars and demonstrated that their measurements overlapped with the height ranges of tern and plover nests (see figure 15 of Alexander et al., 2013). The range of sandbar heights published by Alexander et al. (2013) were shown to represent the 50th to 99th percentiles of the full sandbar topographic distribution. If the curves shown in figure 7 of Farnsworth et al. represent the full topographic distribution of sandbars in the CPR above a common reference plane, then the distributions should exclude values below approximately the median elevation value to be comparable with the Alexander et al. (2013) values. The effect of this shift would cause the mean stage gap reported in Farnsworth et al. (2017) for the CPR to decrease by about 7 to 10 cm, thereby increasing the number of years with successful nesting windows.

The authors' assumption of a constant mean value for the magnitude of the stage gap in each reach of the Platte River ignores evidence, suggesting a pattern of increasing stage gap with increasing discharge. Previous studies (Brice, 1964; Cant & Walker, 1978; Mohrig and Smith 1996; Smith 1971) indicate that sandbars submerged during low-magnitude discharges often have shallow gaps at their crests (0.10 m or less; Figure 2). Observations of sandbars during (Ashworth et al. 2000; Crowley 1983) and following (Alexander et al., 2013) moderate- to high-magnitude flow events demonstrate that the stage gap can be as much as 1 to 2 m. This concept is illustrated in figure 8 of Alexander et al. (2013), which shows

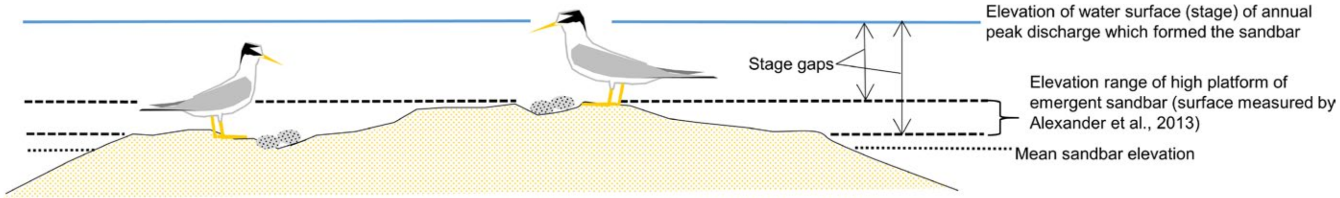

FIGURE 1 Illustration of the concept of a "stage gap" between the elevation of the top surface of an emergent sandbar and the elevation of the water surface (stage) during the annual peak discharge when the bar formed. Note that both nesting sites are on the high platform of the bar surface, but the slight topographic variation in the high platform results in different stage gaps and therefore different potential for flooding at each nesting site. Note also that the mean sandbar elevation may or may not be representative of the nesting elevation

that the stage gap for sandbars in the LPR formed by the 2010 flood (3,850 m^3/s, median stage gap ~0.8 m) was much larger than the stage gap for sandbars formed by the 2011 flood (1,285 m^3/s, median stage gap range of 0.15–0.45 m, depending on reference gage). Although Farnsworth et al. do not make clear where their value of median stage gap for the LPR was taken from, we believe the value was taken from a "group-median" value of 2 feet (~0.61 m) reported in the summary of Alexander et al. (2013). That value was a specific statistical value (median of median sandbar heights) reported in the summary of Alexander et al. (2013) and is different than the median of the complete distribution of bar heights for the 2010 flood shown in figure 8 of that publication. Regardless, the stage gap used by Farnsworth et al. (2017) is likely associated with the much larger 2010 flood, and is between approximately 0.15 and 0.45 m larger than the stage gap reported by Alexander et al. (2013) for the more moderate 2011 flood (shown in figure 8 of that publication), and further demonstrates the need to account for variability of the stage gap with variability in discharge.

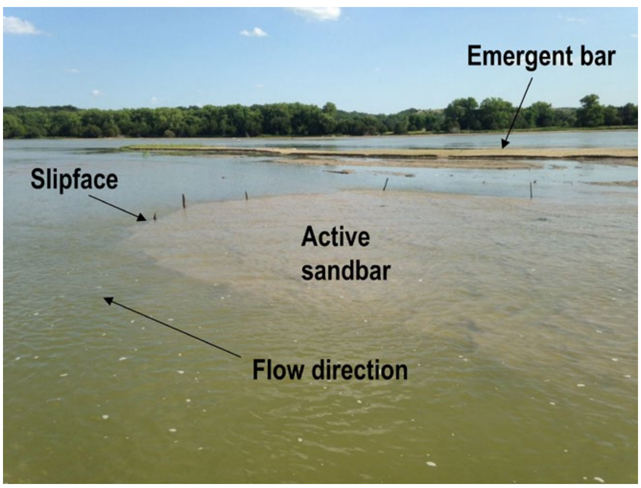

FIGURE 2 River-level photograph of emergent and submerged (active) sandbars in the wide, braided, Niobrara River of northern Nebraska. The photograph was taken during baseflow conditions in August of 2014. The water depth over the top of the submerged sandbar in the foreground ranged from approximately 3–10 cm. The slipface of the submerged sandbar is marked by the vertical sticks. Note the flat surface of the emergent sandbar in the background; the high platform is the area above the top of the scalloped margin of the sandbar. The emergent sandbar is approximately 40–50 m long

The stage gap data presented by Farnsworth et al. illustrated in figure 7 of their paper show variation in the stage gap with variable discharge, although their data generally show a decrease in median stage gap with increasing discharge (their lowest discharge created the largest median stage gap, see figure 7 in Farnsworth et al.). This odd stage gap pattern reinforces the need for an explicit description of their sandbar height data collection and analysis methods. Because of the strong control of the assumption of sandbar height on determination of successful nest windows, we suggest that Farnsworth et al. should have accounted for variation in stage gap with discharge rather than using a single value for each reach under all discharges. The larger stage gap for less frequent floods and smaller gap for more frequent floods would have the effect of increasing the number of years with successful nest windows because most years would have a smaller gap than suggested by the constant values used in each reach by Farnsworth et al.

Finally, the authors assume parity between median sandbar height and the height of nests on river sandbars, despite the fact that empirical evidence indicates (1) sandbars selected by the species for nesting tend to have mean elevations that are higher than unoccupied sandbars in the same reach and (2) nest sites selected by individual birds tend to occupy the higher regions of a sandbar's topography (see figure 1 and table 1 of Smith & Renken, 1991; tables 3 and 4 of Ziewitz, Sidle, & Dinan, 1992; table 7 of Brown and Jorgensen (2008), and figure 15b and 15c of Alexander et al., 2013). The consequence of selection of nest sites at higher elevations by the species is reduced risk of nest inundation. This concept is demonstrated in table 5 of Ziewitz et al. (1992), which shows that median and maximum nest elevations were safe from inundation in 40% and 90% of years, respectively (measurements were made in CPR and LPR, 1958–1988). As terns and plovers select higher sandbars and nest in higher locations on those sandbars, the number of years with successful nesting windows is certainly higher than those reported by Farnsworth et al. (2017).

3 | COMPARISON OF AVERAGE PLATTE RIVER HYDROGRAPH WITH NEST INITIATION DATE DISTRIBUTIONS

In section 3.1 of Farnsworth et al., the authors use an overlay of the long-term mean daily hydrograph (long-term mean daily discharge values for each day of the year) for segments of the Platte River with distributions of nest initiation dates for both species (figure 8 in Farnsworth et al.) to assert that the annual spring rise typically occurs after the nest initiation date for both species. The authors use this simple overlay to suggest (see abstract, section 3.1. and discussion of that paper) that the hydrology of the Platte River creates adverse physical conditions for nesting because the typical spring rise would occur after nest establishment and, due to the large stage gaps assumed by the authors, typically inundate established nests.

Although the mean daily hydrograph can be useful for understanding basic hydrologic patterns at a location in a river, such hydrographs mask variability, particularly in the timing of the annual instantaneous peak flow, which is the typical emergent sandbar habitat formative event. For example, the mean daily hydrograph illustrated in figure 8 of Farnsworth et al. shows the late spring rise in the historical and contemporary CPR occurs in mid- to late June, but the peak flow record at the long-term stream gage at the downstream end of the CPR (USGS gage no. 06774000, period of record 1896 to 2016, 13 years of missing records) indicates that 60% of annual instantaneous peaks occurred before June 1 (February through May), while 30% occurred sometime in June, and the rest at other times of the year. Although the long-term gage is not within the Farnsworth et al. study reach (termed AHR by Farnsworth et al.), for the overlapping periods of record, more than 80% of peak flows at USGS gages within the AHR (06770000, 06770200, 06770500) are either earlier, or within 10 days of the peak flows at the long-term gage (06774000). The peak flow records at these USGS gages on the CPR all indicate that at least 50% of peak flows occurred sometime between February 1 and May 31, and between 36% and 48% of peaks occurred before May 1. On the LPR, the peak flow record (USGS gage no. 06805500, period of record 1953–2016) indicates that 26% of instantaneous peak flows occurred before May 1 (February through April), 50% before June 1, and 30% occurred sometime in June. Farnsworth et al. account for variability in flood timing within their sandbar availability model using the daily records, but in Section 3.1 use their figure 8 to suggest a general dissonance between the timing of nest initiation and the timing of annual high flows. A more informative way to visualize and compare the general timing of nest initiation with annual peaks would have been to plot the timing and magnitude of instantaneous peaks for each reach over the nest initiation distributions. Such an overlay would inform the reader of the year-to-year variability in flood timing relative to the nest initiation distribution and would be a more accurate portrayal of hydrologic conditions relevant to nesting.

The authors' distributions of nest initiation dates only include data from "all on-channel and off-channel" (Farnsworth et al., page 2) from the CPR for the years 2001–2013. Although not stated in their paper, nearly all (more than 96%, n = 1,089) of the nests reported in the CPR during this 13-year period were found on human-created off-channel habitats (mostly sand and gravel mines; Baasch, 2014; Howlin, Strickland, & Derby, 2008), where suitable nesting habitat is always available when terns and plovers arrive in spring. Using nest initiation data from static, human-created, off-channel habitat is an incomplete representation of the species' breeding phenology and range of nest initiation dates. This can easily result in incorrect or misleading conclusions when applied to species' behavior in dynamic river systems where nesting habitat is not always available for nesting upon the birds' arrival in spring. Nest initiation in many avian species (e.g., Gilbert & Servello, 2005), including terns and plovers (Elliott-Smith & Haig, 2004; Thompson et al., 1997), is variable and occurs in response to environmental conditions. For example, least tern nest initiation on the LPR from 2008 to 2013 occurred later at river habitats (median = 16 June) compared to off-channel habitats (median = 10 June, $t_{1,193} = 4.97$, $p < .001$; JGJ, MBB, pers. obs.). Least tern mean nest initiation dates on the Yellowstone River, Montana, where off-channel habitats are not available, occurred 16 June, 30 June, and 1 July in 1994, 1995, and 1996, respectively, following cessation of spring rises that occurred as late as mid- to late June (Bacon & Rotella, 1998).

On the lower Mississippi River, which Farnsworth et al. suggest has hydrology more compatible with the species life history, least tern nest initiation (and inundation) is influenced by high flows that often extend into June or July (Dugger, Ryan, Galat, Renken, & Smith, 2002; Smith & Renken, 1993; Szell & Woodrey, 2003). Even though there may not be an extensive historical record showing nest initiation dates substantially different than what has been recently observed, as the authors state, more contemporary studies (e.g., Bacon & Rotella, 1998) do show least tern and piping plover nest initiation can be temporally variable and occur in response to variable hydrological conditions.

4 | TERN AND PLOVER POPULATION ECOLOGY

Farnsworth et al. suggest that meeting or exceeding reproductive rates (fledge ratios) found in a report (Lutey, 2002) are necessary to maintain "stable to growing populations" of piping plovers and least terns along the Platte River. They provide calculations that purport to show the biologically improbable reproductive rates (e.g., 7.06 fledglings/pair for piping plovers) regularly needed during the years when their hydrological analysis suggests nesting was possible on the Platte River. These calculations led the authors to their principal conclusion that the historical CPR was, and contemporary LPR is, incapable of supporting least tern and piping plover populations.

The analytical approach used by the authors is too simple to address complex questions about metapopulation dynamics. Metapopulations persist as component populations that appear and disappear over space and time (Catlin et al., 2016; McGowan, Catlin, Shaffer, Gratto-Trevor, & Aron, 2014; Zeigler et al., 2017). The authors' calculations incorrectly assume closed populations (or that immigration and emigration are equal) within the CPR and within the LPR, which is not valid because (1) it is inconsistent with the ecology or behavior of either species and (2) does not recognize individual birds are capable of dispersing to and breeding in other locations when conditions along the Platte River are not conducive for nesting or that birds from other areas are capable of colonizing the Platte River when habitat is available. Observations of increasing local populations of least terns in areas where reproductive rates (<0.51 fledglings per pair) were well below the rates used by the authors (0.70 fledglings per pair) underscore the limitations of not considering all aspects of the species ecology when addressing questions of local population persistence (Kirsch & Sidle, 1999).

Piping plovers and least terns are capable of dispersing widely and occupying nesting habitats over broad spatial scales (Catlin et al., 2016; Elliott-Smith & Haig, 2004; Hunt et al., 2015; Roche, Gratto-Trevor, Goossen, & White, 2012; Roche et al., 2016; Thompson et al., 1997; Ziegler et al. 2017). Both species are relatively long-lived and can experience high reproductive success and high reproductive failure (Elliott-Smith & Haig, 2004; Thompson et al., 1997). These are significant aspects of both species' life history strategies that allow them to occupy and persist in dynamic environments. Both species will renest if their nests fail during early stages of incubation (Elliott-Smith & Haig, 2004; Thompson et al., 1997), and both species can maintain viable populations without annual breeding, breeding successfully, or achieving a certain reproductive rate at all sites or in arbitrarily defined river segments (Catlin et al., 2016; Lott, Wiley, Fischer, Hartfield, & Scott, 2013; McGowan et al., 2014). Piping plovers are known to successfully breed in one area, disperse long distances, and breed again within the same nesting season (Hunt et al., 2015). Birds occupying new or replenished habitats may experience reproductive success followed by declines in local populations and reproduction as habitat quality declines (Catlin et al., 2016; Cohen, Houghton, & Fraser, 2010). A more germane question about the terns and plovers that nested on the historical, and which continue to nest on the contemporary Platte River, is how those birds interacted, and interact, with other regional populations of their species' metapopulation. Successful nesting occurred, and until recently (late 20th century) still occurred, on in-channel habitats in the historical CPR and still occurs on in-channel habitats in the contemporary LPR. These habitats contributed to, and still do contribute, to the overall metapopulation of both species in the midcontinent of North America.

5 | HISTORICAL RECORD

The authors expressed doubts about the historical occurrence of least terns and piping plovers nesting on in-channel (sandbars) habitat of the Platte River and suggest human-created off-channel habitats were both species' primary nesting habitat which allowed them to "expand into and persist in a basin where hydrology is not ideally suited to their reproductive ecology (Farnsworth et al., pages 9–10)." To support their contentions, the authors refer only to 20th-century nesting on sandbars and human-created habitats along the CPR and off-channel nesting by least terns during 2 years at a single playa wetland in the Rainwater Basin of south-central Nebraska and along lake shorelines.

A more rigorous review of the historical record shows that least terns and piping plovers were found along the Platte and other regional rivers since the earliest recorded ornithological observations. Lewis and Clark observed least terns and piping plovers along the Missouri River in 1803–1804, as did numerous others during the late 1800s and early 1900s (Catlin et al., 2010). Least terns were observed at the Platte–Missouri River confluence in 1823 (Ducey, 2000). The earliest observation of piping plovers on the Platte River occurred on 8 July 1857 when members of the Warren Expedition collected five piping plover specimens and observed least terns at the confluence of the Loup and Platte rivers, a location 160 km upstream from the Platte–Missouri river confluence and between the two river sections considered by the authors (Ducey, 2000). Least terns were observed upstream of the historical CPR on the Platte River near the Colorado border in 1859 (Ducey, 2000).

In the first major review of Nebraska avifauna, Bruner, Wolcott, and Swenk (1904) concluded piping plovers were fairly common migrants that bred along the Platte, Loup, and Niobrara rivers and at lakes in the Sandhills of north-central Nebraska. Bruner et al. (1904) described the least tern as a common migrant and "not a rare breeder" in Nebraska, citing nesting records along the Missouri and Niobrara rivers and at a Rainwater Basin playa wetland in 1896 and 1897 (Tout, 1902). Both species have been widely observed breeding on the Platte and other Great Plains rivers, as well as other habitats, and historically, both species were widespread and numerous. Various authors (Currier, Lingle, & VanDerwalker, 1985; National Research Council, 2005; USFWS, 2006) have concluded the Platte and other Great Plains rivers were areas of regular breeding prior to major anthropogenic modifications of the rivers. Contemporary nesting by piping plovers and/or least tern populations on other Great Plains rivers, such as the Niobrara (Adolf, Higgins, Kruse, & Pavelka, 2001), which possess similar hydrographs, and which lack off-channel habitats, provides additional evidence contradicting the notion that adjacent off-channel habitats are a prerequisite for these species to colonize and breed within a river segment.

6 | MANAGEMENT AND POLICY IMPLICATIONS

The authors state that a shift in the Platte River Recovery Implementation Program's (PRRIP) activities directed toward least tern and piping plover recovery away from in-channel habitat restoration to off-channel habitat maintenance represents a success of adaptive management that is "unique among riverine restoration programs" (Farnsworth et al., page 10). We believe conclusions about threatened and endangered species management and recovery, as well as stewardship of natural resources, must be made considering the full spectrum of tradeoffs and consequences. Loss of habitat due to human alterations of natural systems is the principal reason regional populations of least terns and piping plovers declined, remain small compared to historical levels, and why they were listed under the Endangered Species Act and remain on the federal Endangered Species List (USFWS, 1988, 1990). It should be noted the least tern has been proposed for federal delisting based on a number of factors, including, but not limited to, conservation efforts and increasing populations in some areas (see USFWS, 2013). Industry (i.e., sand and gravel mining) in the Platte River basin has created sequences of short-lived patches of off-channel nesting habitat incidental to their business activities which have played a role in the population dynamics of these two species for many decades. Off-channel tracts of habitat along, but disconnected from, the Platte River require perpetual investments of capital and maintenance to provide adequate nesting areas for terns and plovers when they are no longer being used by industry; intensive management, including native predator exclusion and control (Keldsen & Baasch, 2016), are required to achieve and maintain reproduction by the two species in these areas.

On-channel habitats, such as those used by the birds on the historical CPR and contemporary LPR, existed or presently exist (LPR) only in resilient, dynamic river systems and are maintained by hydrological and geomorphic processes and benefit a diversity of species (Alexander et al., 2013; Currier et al., 1985). A decision to formally withdraw from river restoration and shift focus to maintaining relatively small and intensively managed tracts of off-channel habitat in the CPR disregards consequences beyond the scope of these two species and relegates the status of least terns and piping plovers in this region to species that are conservation reliant—imperiled species whose threats can only be managed rather than eliminated (Goble, Wiens, Scott, Male, & Hall, 2012; Scott, Goble, Haines, Wiens, & Neel, 2010). Decisions to render a species conservation reliant have been questioned (Goble et al., 2012; Scott et al., 2010) because, even though species recovery goals may be achieved, populations are only maintained through perpetual human intervention. Dynamic, albeit altered, river systems such as the Platte River and others in the Great Plains, which presently maintain nesting habitat used by least terns and piping plovers, play an important role in the ongoing recovery of both species.

7 | CONCLUSIONS

We appreciate the authors' efforts toward modeling sandbar availability in relation to river hydrology; however, their analysis has shortcomings which limit the study's usefulness. These shortcomings, as well as incomplete characterizations of the species' ecology and the historical record, negate the author's assertions that least tern and piping plovers are not adapted to occupying and nesting on river sandbars on the Platte River system. Decisions relegating imperiled species to conservation reliant status need to be made only after considering the full range of tradeoffs and consequences.

ACKNOWLEDGMENTS

We appreciate comments from Dan Catlin, Richard Holland, Robb Jacobson, EJ Raynor, Jeff Runge, and one anonymous reviewer that improved earlier versions of this manuscript. All authors contributed equally to the text. Jason Alexander drafted the figures.

CONFLICT OF INTEREST

None declared.

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