

Comment on Stenglein & van Deelen 2022 correcting Stenglein & van Deelen 2016

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We commend Stenglein & van Deelen for taking a step towards reproducibility of their findings about the Wisconsin wolf population's growth characteristics [1, 2]. That step involved sharing some of the data and analyses on fecundity and pups per pack among Wisconsin wolves. However, the correction [1] still triggers concerns about reproducibility of the original work [2], about the new analyses presented in the correction [1], and related work described below. The crux of the concerns is the authors' insistence they have detected a biologically meaningful change in growth dynamics at 1995, and therefore some Allee effect must explain the accelerated growth,

“We did not find reduced fecundity in pups per pack or in the proportion of breeding females in the population pre-1995 compared to 1995–2007 (S3 Appendix). However, the proportion of lone wolves prior to 1995 (roughly 10% of the population) was higher compared to 1995–2007 when only 4% were lone wolves [22]. The difference in proportion of lone wolves could be due to sampling and detection issues; however a real difference provides support for a mate-finding component Allee effect in early recovery...” p. e0269290, [1], emphases added).

Our concern remains that, first and foremost, the methodological artifact of a change in census methods in 1995 must be ruled out before biological differences can be considered and claimed. The correction [1], neither adequately considers nor rules out a methodological artifact and does not share all the data, as we explain below in detail:

- (A) The time period and analysis area in the correction [1] do not match those in the original work where they write “We derived parameters for the model from empirical research specific to the Great Lakes wolf population” [2].
- (B) The primary field data are neither precise enough nor sufficiently free of artifacts to support both analyses in [1, 2].
- (C) Inspection of primary field data suggests the authors did not account for uncertainty in their primary response variables.
- (D) Novel assertions were presented without supporting data in the correction [1] and without citing or summarizing contrary findings.

- A. The correction [1] presented data on percent of lone wolves, pups per pack, and proportion of breeding females (Appendix Tables S3.1 and S3.2 [1] hereafter loners, pups, breeders for simplicity), citing [3] for the period 1980-2007 in Wisconsin. However, the original work [2] spanned 1980-2011. Therefore, the data presented in the correction [1] are inadequate to support the time span of the original analyses. Also, the original analysis [2] concerned the entire wolf populations of Wisconsin and Michigan (combined into a region they referred to as the Southern Lake Superior region or SLS). Yet, the

correction [1] presented data only for Wisconsin (Appendix Table S3.2). Although [4] estimated loners across Michigan 1999–2006, it did not report breeding females or pups. The correction does not cite [4] although the original did so [2] see ref 26. We are puzzled that the data on lone wolves in [4] played no role in the correction [1], and we remain in the dark about those two demographic classes for Michigan wolves. This seems an important set of data to evaluate the mate-finding hypothesis for either state. Therefore, the correction [1] do not fit the claim “We derived parameters for the model from empirical research specific to the Great Lakes wolf population” and the correction is inadequate to support the conclusions about the SLS in the original work [2].

- B. Even if additional data were presented in another correction for Wisconsin 2008-2011 and Michigan 1980-2011 to match the original work [2], we urge more caution in considering the possible effects of the documented changes in census methods. Census methods changed several times including notably in the winter of 1994-1995, which plays a critical role in the inferences of the original and the correction [1, 2]. The changes included hundreds of private volunteers and eventually quality control checks [5-7]. For example, changes in census methods affected estimates for hazards and incidence of disappearance of radio-collared wolves [8, 9]. Because rates of disappearance of radio-collared wolves also varied seasonally and increased in snowy periods, the predominant census method of snow track surveys would be particularly vulnerable to under- or over-counting pack sizes. Citing a book and one of its chapters on Wisconsin’s wolves [3, 10], the correction [1] gives an impression that loners, breeding females, and pups were measured accurately and precisely. However, readers should have been informed of the uncertainty and precision associated with those estimates. To wit, an annual average of 13% of Wisconsin wolf packs had a radio-collared individual and such collaring did not selectively target breeding females, loners, or pups [11, 12]. Therefore, the ostensible temporal changes in representation of those three demographic classes reported in the correction [1] were estimated from a combination of winter snow-track surveys or summer howling surveys of Wisconsin wolf packs, most of which lacked radio-collared members. Moreover, the inference in the correction [1] that the percentage of loners had increased would require some evidence to differentiate a loner from a pack member on a lengthy, distant extraterritorial movement, which was defined for Wisconsin wolves with radio collars [13]. If one cannot distinguish those two classes of wolves, one cannot infer loners represent wolves seeking mates. Likewise, the inference in the correction [1] that the number of pups stayed stable over time would usually require marked pups or yearlings, e.g., [14]. Although we are willing to believe that summer howling surveys to distinguish packs that bred from packs that did not breed might be quite accurate, the methods used in Wisconsin have not been described scientifically for area covered, interobserver reliability, years of sampling, etc. Also, the authors should address an experimental study in Europe that found even experts were not perfect in such binary discrimination between packs with pups and packs without, and moreover, experts were inaccurate in counting the number of pups even when the pups replied to howling surveys [15]. Another basis for estimating pups statewide came from the annual comparison of the same pack’s size in the previous year to its size in the current year. That comparison carries with it attendant uncertainties about migration, mortality, pack fission, etc.

However, the description of which packs in which years were subjected to one or more surveys and aerial sightings remains undescribed [3, 10]. Finally, if only a sample of loners, pups, and breeding females was presented in the correction [1], that is not clear from the text and the criteria for inclusion and exclusion have not been described. Loners, breeding females, and pups are notoriously difficult to count [16]. Indeed, those who collated the source field data expressed great uncertainty and reasonably left estimates imprecise. Readers can review the data in reports for the periods in question, which are available online at

http://faculty.nelson.wisc.edu/treves/data_archives/WDNR%20ER%20Bureau%20reports.zip. Notably, the authors of the correction [1] were employed by the state agency that created these reports. One author (TvD) played a role in the initiation of the quality control in 2003 or 2004 [17], so the lack of detail about methods for counting wolves is puzzling. Imprecise estimates might be sufficient for broad-brush management decisions, but perhaps not for the demographic model in the original and correction [1, 2]. Arguing for a biological explanation for acceleration or deceleration in population dynamics must account transparently for the several changes in census methods in both Wisconsin and Michigan [6, 7, 12, 18]. The three-fold increase in the number of volunteers counting wolves in 1994-1995 and the use of similar numbers or even more volunteers every year thereafter [6, 7, 12, 18] might have resulted in observation of fewer loners, to which the correction and original article assign biological importance [1, 2]. Census-takers working in pairs or teams or canvassing the same area multiple times might locate a pack member missed by a single census, changing a record of a loner to a record of a pack. Therefore, we question the new analyses presented in Appendix Table S3.1 [1] on not only statistical but also biological grounds.

- C. Finally, the correction [1] makes two assertions of fact without evidence, “**There are no changes or improvements of any consequence to the Wisconsin wolf counting methodology over time** *that would have resulted in artificial increases in wolf numbers.*” p. e0269290, [1], emphases added). The boldface portion contradicts several published articles above and as follows. Their own source wrote, “The 1994- 1995 wolf population was 66% above the wolf population present in 1993-1994 (50-57 wolves). This increase probably represents more than just natural reproduction. Some wolves were probably missed in 1993-1994 surveys.” p. 10, [19]. Furthermore, the correction seems to dismiss findings without citing them. One finding was of particular significance to both original and correction [1, 2]. Namely, inter-annual growth of the Wisconsin wolf population changed after census methods changed and non-linear growth patterns were confounded with those changes in census methods [6, 7]. Also, the italicized phrase is a novel claim whose relevance is unclear. If relevant, the data to support the statement are missing from [1].

In conclusion, the correction [1] only partially improves the reproducibility of the original work [2]. The same issue applies to related models of Wisconsin wolf population dynamics [20-22]. Moreover, the correction [1] does not account scientifically for uncertainty and imprecision in its primary response variables used in novel analyses.

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