State of California
Natural Resources Agency
Department of Fish and Wildlife
Wildlife Branch

Appendix D (Peer Review) for the Status Review for Mojave Desert Tortoise (*Gopherus agassizii*)

By

California Department of Fish and Wildlife

Wildlife Diversity Program, 2024-03

Status Review for Mojave Desert Tortoise (*Gopherus agassizii*)

Report to the Fish and Game Commission

February 2024

APPENDIX D. COMMENTS FROM PEER REVIEWERS ON THE MOJAVE DESERT TORTOISE STATUS REVIEW

Pursuant to Fish and Game Code section 2074.6, the review process included independent and competent peer review of the draft status review by persons in the scientific/academic community acknowledged to be experts on Mojave Desert Tortoise and related topics, and possessing the knowledge and expertise to critique the scientific validity of the status review contents. Appendix D contains the specific comments provided to the Department by the individual peer reviewers, the Department’s written response to the comments, and any amendments made to the status review (Fish & G. Code, § 2074.6; Cal. Code Regs., tit. 14, § 670.1, subd. (f)(2)). Independent experts that reviewed the status review are listed in Table D1, below.

Table D1. Status Review Peer Reviewers

Name	Affiliation
Jeffery Lovich	USGS
Kristina Drake, Kerry Holcomb, Corey Mitchell	USFWS Desert Tortoise Recovery Office
Kenneth Nussear	University of Nevada, Reno

Comments by external reviewers and response from the Department. Line numbers refer to lines in the version of the status review sent to external reviewers (available at end of this appendix)

GENERAL COMMENT (Lovich): This is a very thorough and well-written review but there is a lot more literature available and I will point some out. The desert tortoise is one of the most-studied turtle in the United States (Lovich, J.E., and J.R. Ennen. 2013. A quantitative analysis of the state of knowledge of turtles of the United States and Canada. Amphibia-Reptilia 34:11-23.). Particularly surprising was finding no citation for Ernst and Lovich. 2009. Turtles of the United States and Canada. Johns Hopkins University Press. 827 pp. That book summarizes more data and publications on desert tortoises that are not included in this report. Based on the available scientific information presented, the CDFW makes a compelling case for listing the tortoise as endangered in California. The weight of scientific evidence presented supports the contention that populations continue to decline since their listing as threatened decades ago. However, extinction would probably take a long time to occur given the number of tortoises that still exist, their longevity, and the availability of topographic refugia to respond to global warming as pointed out by Cam Barrows' publications.
RESPONSE: Have added citations for Ernst and Lovich 1994 version of the book, especially in section 2 on Biology. Note: As stated in section 1.2, the status review "is not intended to be an

exhaustive review of all published scientific literature on Mojave Desert Tortoise; rather it is intended to summarize key points relevant to the status of the species and address regulatory report requirements. "

GENERAL COMMENT (DTRT): Throughout the report, the referenced findings related to translocation/augmentation outcomes and associated literature for *G. agassizii* do not reflect the full body of available literature. Please review the document and include appropriate references and findings translocation outcomes. For example, publications such as Brand et al. 2016, Dickson et al. 2019, Drake et al. 2012, Esque et al. 2010, Farnsworth et al. 2015, Field et al. 2007, Harju et al. 2019, Hinderle et al. 2015, Nafus et al. 2017, Nussear et al. 2012, Mack and Berry 2023 should all be considered cumulatively. Additionally, all most no information is available on the long-term effects of translocation. Only one published paper reports outcomes for translocated tortoises for 10 years (Mack and Berry 2023), and this study did not include resident and control tortoise comparisons, excluding the ability to evaluate the efficiacy of translocation. We need long-term studies (i.e., 15-25 yrs) with balanced designs (translocated, resident, and control tortoises) to evaluate translocation outcomes and its effectiveness as a conservation tool.
RESPONSE: Due to this and other feedback, the section on translocation was extensively altered. References were added (Brand et al. 2016, Dickson et al. 2019, Drake et al. 2012, Esque et al. 2010, Farnsworth et al. 2015, Field et al. 2007, Harju et al. 2019, Hinderle et al. 2015, Nafus et al. 2017, Nussear et al. 2012, Mack and Berry 2023), and specific statements about the efficacy of translocation were reworked.

GENERAL COMMENT (Nussear): Overall I agree with the assessment. Given that after more than 30 years of protection under both state and federal ESAs. While recovery planning efforts have been found to provide sound recommendations, difficulties in implementation and enforcement of implementations (e.g. maintaining closed roads and routes) have contributed toward continued habitat loss and degradation. With continued growth of urban areas and infrastructure, expansion of military training areas, expansive recreation, challenges of invasive species with respect to wildfire and nutrition, subsidization of key predators, and a changing climate the tortoise faces a challenging road to recovery, and indeed continues to decline in much of its range.
While the right decision for the species, this decision will no doubt draw scrutiny and contestation. Toward improving the factual evidence brought to bear, there are several areas were the literature cited could be improved as the attribution is either incorrect, or incomplete.

LINE 140 (DTRT)

Suggested edit: "his Status Review of the Mojave desert tortoise (*Gopherus agassizii*, tortoise; also known as Agassiz's desert tortoise)." Edit throughout document.
RESPONSE: The USFWS doesn't capitalize the full name, however the Department made the decision to fully capitalize Mojave Desert Tortoise.

LINE 144-158 (DTRT)

Suggested edit: The tortoise was designated a threatened species under CESA in 1989. On March 23, 2020, the Commission received a petition from Defenders of Wildlife, Desert Tortoise Council, and Desert Tortoise Preserve Committee to change the status of the tortoise from threatened to endangered. On April 13, 2020, the Commission referred the Petition to the Department for evaluation pursuant to Fish and Game Code section 2073 and published a formal notice of receipt of the petition (Cal. Reg. Notice Register 2020, No. 18-Z, p. 693). At its meeting on August 20, 2020, the Commission received the Department's petition evaluation report. which was based on available information and recommended to the Commission that the petition be accepted. At its October 14, 2020, meeting, the Commission accepted the petition to change the status of the tortoise from threatened to endangered (Cal. Reg. Notice Register 2020, No. 44-Z, p. 1445). As a result, the Department was directed to complete this Status Review, which is a detailed evaluation of the current status of the tortoise and includes its recommendation regarding whether the tortoise's status should be changed from threatened to endangered.

RESPONSE: This section has been extensively reworked to get closer to statutory requirements

LINE 169-177 (DTRT)

Suggested edit: In 2011, studies of tortoise genetics, morphometrics, and ecology led experts to conclude that the species complex formerly known as the "desert tortoise" in fact consists of two separate species—Mojave desert tortoise ~~,~~ and Sonoran desert tortoise (*G. morafkai*), (Murphy et al. 2011). Five years later, in 2016, the Sonoran desert tortoise was further split into two species – Sonoran desert tortoise and thornscrub tortoise (*G. evgoodei*) (Edwards et al. 2016). The Mojave Desert Tortoise~~,~~ retains the binomial *G. agassizii*, and ranges contemporarily across the Mojave and Sonoran deserts of southeastern California, southern Nevada, and small areas of Arizona north of the Colorado River as well as southwestern Utah.

LINE 172 (DTRT)

Citation for recommendation above: Murphy, R.W., Berry, K.H., Edwards, T., Leviton, A.E., Lathrop, A. and Riedle, J.D., 2011. The dazed and confused identity of Agassiz's land tortoise, Gopherus agassizii (Testudines, Testudinidae) with the description of a new species, and its consequences for conservation. *ZooKeys*, (113), p.39.

RESPONSE: The executive summary acts as an abstract without references. The Murphy et al. 2011 reference is cited in section 2.1 on Taxonomy

LINE 172 (DTRT)

Citation for recommendation above: Edwards, T., Karl, A.E., Vaughn, M., Rosen, P.C., Torres, C.M. and Murphy, R.W., 2016. The desert tortoise trichotomy: Mexico hosts a third, new sister-species of tortoise in the Gopherus morafkai–G. agassizii group. *ZooKeys*, (562), p.131.

RESPONSE: The executive summary acts as an abstract without references. The Edwards et al. 2016 reference is cited in section 2.1 on Taxonomy.

RESPONSE: This paragraph has been deleted but in the taxonomy section (2.1) the text now reads "In 2011, studies of tortoise genetics, morphometrics, and ecology led experts to conclude that the species complex formerly known as "Desert Tortoise" in fact consists of two separate species—Mojave Desert Tortoise and Sonoran Desert Tortoise (G. morafkai). The Mojave Desert Tortoise, also known as Agassiz's Desert Tortoise, retains the binomial G. agassizii, and ranges currently across the Mojave and Sonoran deserts of southeastern California, southern Nevada, and small areas of Arizona and Utah north of the Colorado River as well as southwestern Utah....... More recent work by Edwards et al. (2016) separates Desert tortoises living in the thorn scrub and tropical deciduous forests of southern Mexico into another species Gopherus evgoodei."

LINE 180 (Lovich)

I was surprised that no papers by David Germano were cited. This line should cite GERMANO, D. J. 1994. Growth and age at maturity of North American tortoises in relation to regional climates. Can. J. Zool. 72:918-931. AND GERMANO, D. J. 1994. Comparative life histories of North American tortoises. National Biological Survey, Fish and Wildlife Research 13.

RESPONSE: The executive summary acts as an abstract without references.

LINE 180 (DTRT)

Recommended citation for line 180: Peterson, C.C., 1996. Anhomeostasis: seasonal water and solute relations in two populations of the desert tortoise (Gopherus agassizii) during chronic drought. Physiological Zoology, 69(6), pp.1324-1358.

RESPONSE: The executive summary acts as an abstract without references. Pederson et al. 1996 is cited in section 2.2 on Life History

LINE 180 (DTRT)

Recommended citation for line 180: Medica, P.A., Nussear, K.E., Esque, T.C. and Saethre, M.B., 2012. Long-term growth of desert tortoises (Gopherus agassizii) in a southern Nevada population. *Journal of Herpetology*, pp.213-220.

RESPONSE: The executive summary acts as an abstract without references. Medica et al. 2012 has been added to the relevant text in section 2.2 on Life History

LINE 180 (Lovich)

30 eggs per year is impossible. This claim is later associated with a citation by Berry and Murphy but they say that nowhere in the publication. Instead, someone assumed that if tortoises can have up to 10 eggs in a clutch and up to three clutches/year they can produce 30. The literature says annual egg production can be 16-18 eggs, about half the number given.

RESPONSE: Altered text to read "typically lay one or two clutches of eggs (about 6 eggs per clutch)"

LINE 181 (DTRT)

Recommended citation for line 181: Mitchell, C.I., Friend, D.A., Phillips, L.T., Hunter, E.A., Lovich, J.E., Agha, M., Puffer, S.R., Cummings, K.L., Medica, P.A., Esque, T.C. and Nussear, K.E., 2021. ‘Unscrambling’ the drivers of egg production in Agassiz’s desert tortoise: climate and individual attributes predict reproductive output. Endangered Species Research, 44, pp.217-230.

RESPONSE: The executive summary acts as an abstract without references. Mitchell et al. 2021 is cited IN relevant text in section 2.2 on Life History.

LINE 182 (DTRT)

Recommended citation for line 182: Spotila, J.R., Zimmerman, L.C., Binckley, C.A., Grumbles, J.S., Rostal, D.C., List Jr, A., Beyer, E.C., Phillips, K.M. and Kemp, S.J., 1994. Effects of incubation conditions on sex determination, hatching success, and growth of hatchling desert tortoises, Gopherus agassizii. *Herpetological Monographs*, pp.103-116.

RESPONSE: The executive summary acts as an abstract without references. Rostal et al. 2002 is a reference for incubation temperatures in section 2.2

LINE 182 (DTRT)

Recommended citation for line 182: Bjurlin, C.D. and Bissonette, J.A., 2004. Survival during early life stages of the desert tortoise (Gopherus agassizii) in the south-central Mojave Desert. Journal of Herpetology, pp.527-535.

RESPONSE: The executive summary acts as an abstract without references. Bjurlin and Bissonette 2004 is cited on relevant text in section 2.2 on Life History

LINE 175 - 179 (DTRT)

Suggested edit: The Mojave Desert Tortoise is a long-lived, desert-dwelling reptile. Consequently, tortoises must use behavioral and physiological adaptations to avoid extreme body temperatures <15 to >35°C (<59 to >95°F Zimmermann et al. 1994) and dehydration (Peterson 1996), as well as budget stored energy (Henen 1997, Peterson 1996) They primarily regulate their temperature by using underground burrows where the air is cooler and higher in humidity than ~~the~~ outside air in summer and warmer in winter, which results in tortoises spending more than 90% of their lives underground (Zimmermann et al. 1994).

RESPONSE: Text has been altered to “The Mojave Desert Tortoise is a long-lived, desert-dwelling reptile that uses behavioral and physiological adaptations to avoid extreme temperatures and dehydration, and to budget stored energy. Mojave Desert Tortoises primarily regulate their temperature by using underground burrows where the air is cooler and higher in humidity in summer, and warmer in winter. They can spend more than 90% of their lives underground." The executive summary does not contain references.

LINE 180-184 (DTRT)

Suggested edit: Females become sexually mature at 12–20 (mean 18.8, Medica et al. 2012) years old and typically lay one or two clutches of eggs (~ 6 eggs per clutch) per year; however, some females have been document to oviposit more than two clutches (Mitchell et al. 2021). Tortoise nests are typically placed near the mouth or entrance to the burrow or within suitable soil (Ennen et al 2012). Nest predation is common, with 12-26% of nests generally destroyed by predators (Ennen et al. 2012, Bjurlin & Bissonette 2004). Reported incubation time in the wild varies from 67–104 days (Berry and Murphy 2019) and incubation temperatures determine the sex of the hatchlings, with hotter temperatures (>32.8°C) producing female-skewed clutches (Spotila et al. 1994).

RESPONSE: The executive summary acts as an abstract without references. Text has been altered to read "Females become sexually mature at 12–20 years old, typically lay one or two clutches of eggs (about 6 eggs per clutch) per year. Nest predation is common, with 12–47% of nests lost to predators annually. Reported incubation time in the wild varies from 67–104 days and incubation temperatures determine the sex of the hatchlings, with hotter temperatures producing female-skewed clutches." 47% is the depredation rate on nests in 1998 in Bjurlin & Bissonette 2004. Suggested references (Medica et al 2012, Mitchell et al. 2021, Ennen et al. 2012, Bjurlin & Bissonette 2004) have been added to the relevant text in section 2.2 on life history.

Line 185-190 (Nussear)

Your summation of dietary preferences given in lines 185 to 190 is inaccurate - we have published information indicating that they neither avoid plants with high potassium, nor exotics - although these can be detrimental to health. With respect to annual forage they are really more of a generalist"

RESPONSE: The information referred to has been deleted.

LINE 185-186 (DTRT)

Suggested edit: Tortoises selectively feed on annual forbs, annual and perennial grasses, and herbaceous perennial plants and will consume some cacti.

RESPONSE: Done

LINE 191-198 (DTRT)

Suggested edit: Tortoise habitat typically occurs on alluvial fans and plains and colluvial/bedrock slopes that facilitate the digging of burrows. Tortoises need sufficient forage as well as large shrubs and bushes for shade and protection of burrows. They are associated with saltbush, creosote bush, white bur-sage, and cheesebush. At higher elevations, tortoises are more likely to be found near Joshua tree, Mojave yucca, and blackbrush. Tortoises occur in very low densities or are absent where shrub cover is sparse, and annual food plants are available only intermittently (e.g., the lower elevations in Death Valley). They also occur at low densities in moderately to severely disturbed areas, regardless of desert or region.

RESPONSE: The executive summary has been shortened and much of this paragraph has been cut.

LINE 191 (Lovich)

G. agassizii can also occupy boulder piles as they often do in Joshua Tree National Park. See Cummings, K.C., J.E. Lovich, S.R. Puffer, T.R. Arundel, and K.D. Brundige. 2020. Micro-geographic variation in burrow use of Agassiz's desert tortoises in the Sonoran Desert of California. Herpetological Journal 30:177-188.

RESPONSE: The executive summary is not that detailed but have added "by using underground burrows or rock shelters (Cummings et al., 2020)" in the relevant place in section 2.2.

LINE 197-198 (DTRT)

A terrestrial development index of approximately 7 (or 7% developed) resulted in mean maximum encounter rates of live tortoise that approached zero -- see Carter et al. 2020. Recommended citation - Carter, S.K., Nussear, K.E., Esque, T.C., Leinwand, I.I., Masters, E., Inman, R.D., Carr, N.B. and Allison, L.J., 2020. Quantifying development to inform management of Mojave and Sonoran desert tortoise habitat in the American southwest. Endangered Species Research, 42, pp.167-184.

RESPONSE: The results from Carter et al 2020 are discussed in section 4.1 on habitat modification and destruction.

LINE 199-201 (DTRT)

Suggested edit: Ravens are a major predator of juvenile tortoises while coyotes target both juvenile and adult tortoises. Raven populations have expanded dramatically in the desert due to resource subsidies from humans (Holcomb et al. 2021).

RESPONSE: The executive summary acts as an abstract without references. Holcomb et al. 2021 is cited in section 4.4 on Predation.

LINE 201 (DTRT)

Recommended citation for Line 201: Holcomb, K.L., Coates, P.S., Prochazka, B.G., Shields, T. and Boarman, W.I., 2021. A desert tortoise–common raven viable conflict threshold. *Human–Wildlife Interactions*, *15*(3), p.14.

RESPONSE: The executive summary acts as an abstract without references. Holcomb et al. 2021 is cited in section 4.4 on Predation.

LINE 203-207 (DTRT)

Suggested edit: In California, the range of the tortoise includes the Mojave Desert and Colorado Subunit of the Sonoran Desert and even a sliver of the Great Basin desert~~s~~, from the southern end of the Owens Valley south of the town of Lone Pine in Inyo County to the Mexican border

near the southeastern corner of the state, and from the Colorado River in the east to the lower slopes of the Peninsular , Sierra Nevada, and Transverse mountains in the west.
RESPONSE: The executive summary has been shortened and much of this text has been cut. Text now reads "In California, the range of the Mojave Desert Tortoise includes the Mojave Desert and portions of the Sonoran and Great Basin deserts. "

LINE 208 (DTRT)

Surveys began in 2001. Edit accordingly.
RESPONSE: Done

LINE 210-221 (DTRT)

Suggest updating tortoise trends based on Zylstra et al. 2023:
Zylstra, E.R., Allison, L.J., Averill-Murray, R.C., Landau, V., Pope, N.S. and Steidl, R.J., 2023. A spatially explicit model for density that accounts for availability: a case study with Mojave desert tortoises. Ecosphere, 14(3), p.e4448.
RESPONSE: Have updated this using the results from Zylstra et al. 2023.

LINE 233 (DTRT)

Comment to line 233 "critical habitat units" - Critical habitat was designated based on the best available data available prior to 1994. The Service considers Critical habitat to be areas considered essential for the conservation of a listed species.
RESPONSE: The relevant sentence has been removed in the editing of the executive summary

LINE 255 (DTRT)

This statement is incorrect. "large scale translocations do not tend to have high survival rates". Most unpublished and published data related to small scale and large scale translocations indicate that survival is similar between resident, control, and translocated tortoises. Mortality rates do vary by rate based on climate (drought), habitat condition, and predator-prey dynamics in the area.
RESPONSE: Have deleted this sentence following a re write of the translocation section.

LINE 255 (Nussear)

Your statement on translocations on line 255 is potentially misleading: *"Large scale tortoise translocations do not tend to have high survival rates."* What have you defined as a high survival rate? Is this relative to 100%? Relative to resident and control populations inhabiting the same areas and conditions? The potential losses if tortoises are otherwise removed, or worse yet left in place where development or increased military training will occur? Without explicit decisions about what your criteria are this sounds arbitrary
RESPONSE: Have deleted this sentence following a rewrite of the translocation section.

LINE 223-225 (DTRT)

Suggested edit: The population data available indicate that there were sharp drops in density before listing as threatened, and those losses have continued to the point where most tortoise habitats no longer supports viable tortoise densities and adult densities are rapidly declining.
This sentence has been deleted following a rewrite of the population status due to using Zylstra et al. 2023.

LINE 226-236 (DTRT)

Suggested edit: The slow maturation and low reproductive rates of tortoises mean~~s~~ that if past and current management is successful at addressing threats and stemming the decline of tortoise populations, it would still take at more than 25 years of positive population growth to

reach the USFWS Recovery Criteria (U.S. Fish and Wildlife Service 2022*a*). For example, the USFWS 1994 Recovery Plan estimates that when adult survivorship is 98%, population growth would be less than 0.5% per year, and would take 140 years to double in size. Contemporary annual survival rates for both adults and juveniles are much lower than 98% in all areas, making population stability, let alone growth, unlikely. Collectively, the available data show that in the critical habitat units, tortoise densities are low to very low, and despite 30 years of state and federal protection as a threatened species, tortoise populations continue to decline and do not show consistent signs of recovery.
RESPONSE: This paragraph has been reworked to shorten the executive summary. It now reads in part "For example, the USFWS 1994 Recovery Plan estimates that when adult survivorship is 98%, population growth would be less than 0.5% per year, and would take 140 years to double in size. Annual survival rates for both adults and juveniles are much lower than 98% in most areas, and since the late 1970s, the number of juveniles detected on surveys has also fallen sharply, to the point that in some recent surveys in the western Mojave Desert almost no juveniles were found. "

LINE 238-241 (DTRT)

Suggested edit: The dramatic declines of tortoise populations are likely due to the extensive number and interconnected nature of the threats they face. The important threats fall into two categories, those that directly kill adults and juveniles, and those that cause longer-term changes to habitat availability and quality.
RESPONSE: Done

LINE 242-249. (DTRT)

Suggested edit: In long-lived species that are slow to reproduce, decreased survival has long lasting impacts on the population viability and can alter demographic rates for decades. Increased numbers of predators including ravens and coyotes reduce the survival of juvenile and adult tortoises, respectively. Development within the tortoise range often creates roads that can lead to road-killed tortoises, and extensive networks of trails for off highway vehicles on public land increase the chance that tortoises will be run over in areas without paved roads. Moreover, road infrastructure provides subsidies in the form of roadkill and garbage to ravens and coyotes. Well-designed fences and culverts can help prevent tortoises and other wildlife from being killed by vehicles along major roads, but little fencing has been built since 2011.
RESPONSE: Done

LINE 250-255 (DTRT)

Suggested edit: Habitat modification, fragmentation, and destruction reduces the amount of habitat that can support tortoises in the long-term and reduce the size of remaining habitat patches. Although a large proportion of the tortoise's range is under federal control, renewable energy, housing, illegal cannabis, and other types of development reduce the amount of habitat available. Most concerningly, subsidized predators like the raven and coyote leverage habitat fragmentation and disturbances to expand their densities throughout "undisturbed" habitats. The Department of Defense is a large landowner in the tortoise's range and frequently expands the areas that it uses for training, requiring the translocation of hundreds of tortoises. Large scale tortoise translocations do not tend to have high survival rates.
RESPONSE: Done

LINE 256 (Nussear)

Line 256: the effects of climate change are likely under stated you state "Additional factors have direct and indirect impacts on tortoises and their habitat. Climate change, which is likely to cause hotter and periodically drier conditions in the desert tortoise range, will increase their physiological stress and change activity patterns." it will likely make areas of habitat unsuitable, potentially alter reproduction, hibernation, and many other facets of tortoise ecology. I think this is well beyond the changing of activity patterns and increased physiological stress. I think that Barrows did a paper on this with tortoises in Joshua tree, and there is certainly more that could be referenced here.
RESPONSE: Have added "In combination, the impacts of climate change will likely result in less available suitable habitat." But this is a brief summary, and section 4.6 on Climate change and drought goes into more detail.

LINE 259 (DTRT)

Suggested edit: The nutritious native vegetation tortoises feed on is being outcompeted
RESPONSE: Done

LINE 270-274 (DTRT)

Consider updating with Zylstra et al. 2023 density information. "However, there is still a large amount of available habitat and even at low densities, in 2014 there were estimated to be more than 61,000 adult tortoises within the TCAs. This is a decrease from an estimated 310,000 adults in 2004, and as densities have continued to fall since 2014, current abundance is likely lower than 60,000 adult tortoises".
RESPONSE: Have updated with information from Zylstra et al. 2023

LINE 356 (Lovich)

What about G. evgoodi? See EDWARDS, T., A. KARL, M. VAUGHN, P. ROSEN, C. MELÉNDEZ TORRES, AND R. W. MURPHY. 2016. The desert tortoise trichotomy: Mexico hosts a third, new sister-species of tortoise in the Gopherus morafkai–G. agassizii group. ZooKeys. 562:131-158.
RESPONSE: Have added "More recent work by Edwards et al. (2016) separates Desert tortoises living in the thorn scrub and tropical deciduous forests of southern Mexico into another species Gopherus evgoodei. "

LINE 366 (Lovich)

There are G. agassizii and hybrids "east of the Colorado River in the Kingman area of AZ. See EDWARDS, T., K. H. BERRY, R. D. INMAN, T. C. ESQUE, K. E. NUSSEAR, C. A. JONES, AND M. CULVER. 2015. Testing taxon tenacity of tortoises: evidence for a geographical selection gradient at a secondary contact zone. Ecology and Evolution. 5:2095-2114.
RESPONSE: Have added "However, there is “anomalous" population of G. agassizii east of the Colorado River in the Black Mountains of Arizona (Edwards et al. 2015)."

LINE 357-362 (DTRT)

Suggested edit: Desert tortoises are members of the order Testudines, family Testudinidae, genus *Gopherus*. When the Commission listed Desert Tortoise as threatened in 1989, *Gopherus agassizii* was understood to range from southeastern California, across southern Nevada, through western Arizona, and south into Sonora and Sinaloa, Mexico. In 2011, studies of tortoise genetics, morphometrics, and ecology led experts to conclude that the complex formerly known as “desert tortoise” in fact consists of two separate species, Mojave desert tortoise and Sonoran desert tortoise (Murphy et al. 2011, Iverson et al. 2017). Five years later,

in 2016, the Sonoran desert tortoise was further split into two species – Sonoran desert tortoise and thornscrub tortoise (G. evgoodei) (Edwards et al. 2016).
RESPONSE: Text now reads "More recent work by Edwards et al. (2016) separates Desert tortoises living in the thorn scrub and tropical deciduous forests of southern Mexico into another species Gopherus evgoodei."

LINE 363-365 (DTRT)

Suggested edit: "Desert tortoises east of the Colorado River in Arizona and northern Mexico are now classified as Sonoran desert tortoise, also known as Morafka's desert tortoise (*Gopherus morafkai*)." See the 2022 USFWS 5-year review for more details regarding tortoise populations found east of the Colorado River that are genetically G. agassizii.
RESPONSE: See above comments for additions to text regarding this population of tortoises. This document is California specific and doesn't focus on this population.

LINE 379 (Lovich)

what about the largest female they reported? It was bigger
RESPONSE: Have amended sentence to "Generally males are larger than females (Ernst and Lovich 1994) but the largest measured wild individual was a female in 1986 whose carapace length was 374 mm (Berry and Murphy 2019)"

LINE 396 (Lovich)

See comment in line 4 of the spreadsheet
RESPONSE: This references the comment about line 191 and the text in section 2.2 now reads "by using underground burrows or rock shelters (Cummings et al., 2020)"

LINE 397 (DTRT)

Medica et al. 2012 reported a mean of 18.8, please include.
RESPONSE: Done

LINE 402 (DTRT)

Citation referenced above. Include in literature. Mitchell, C.I., Friend, D.A., Phillips, L.T., Hunter, E.A., Lovich, J.E., Agha, M., Puffer, S.R., Cummings, K.L., Medica, P.A., Esque, T.C. and Nussear, K.E., 2021. 'Unscrambling' the drivers of egg production in Agassiz's desert tortoise: climate and individual attributes predict reproductive output. *Endangered Species Research*, *44*, pp.217-230.
RESPONSE: Done

LINE 403 (Nussear)

Line 403: "There are anecdotal reports of females nest guarding against humans and Gila Monsters, but there is no parental care once eggs have hatched (Berry and Murphy 2019)"
This is the wrong reference to cite here - you should probably cite Gienger and Tracy 2008
In general throughout this assessment it appears that you put entirely too much emphasis on Berry and Murphy 2019 - rather than more direct references.
RESPONSE: Changed to "Tortoise nests are typically placed near the mouth or entrance to the burrow or within suitable soil (Ennen et al. 2012), and there is no parental care once eggs have hatched (Berry and Murphy 2019)." Made the changes since Gila Monsters not being widespread in California and human attacks on nests not necessarily being a major issue.

LINE 404 (DTRT)

"Gila Monsters": Gila monsters occur at low densities in only a few locations in California and likely do not pose a threat to tortoise nest success for this reason.

RESPONSE: Changed to "Tortoise nests are typically placed near the mouth or entrance to the burrow or within suitable soil (Ennen et al. 2012), and there is no parental care once eggs have hatched (Berry and Murphy 2019). "due to Gila Monsters not being widespread in California and human attacks on nests not necessarily being a major issue

LINE 392-394 (DTRT)

Suggested edit: They also found that the overlap in the area in an individual's home range from one year to the next was ~35% and did not vary significantly by sex. Individuals tend to have fidelity to home ranges and activity centers, even after a fire (Drake et al. 2015, Lovich et al. 2018).

RESPONSE: Done

LINE 401-402 (DTRT)

Suggested edit: Females lay 0–3 clutches in the spring and the number of eggs laid per clutch ranges from 1–10. Females typically lay one or two clutches of eggs (~ 6 eggs per clutch) per year; however, some females have been document to oviposit more than two clutches (Mitchell et al. 2021). Tortoise nests are typically placed near the mouth or entrance to the burrow or within suitable soil (Ennen et al 2012).

RESPONSE: Done

LINE 403-404 (Lovich)

Not true. See Agha, M., J.E. Lovich, J.R. Ennen, and E. Wilcox. 2013. Nest-guarding by female Agassiz's desert tortoise (Gopherus agassizii) at a wind-energy facility near Palm Springs, California. The Southwestern Naturalist 58:254-257.

RESPONSE: Changed to "Tortoise nests are typically placed near the mouth or entrance to the burrow or within suitable soil (Ennen et al. 2012), and there is no parental care once eggs have hatched (Berry and Murphy 2019). " due to Gila Monsters not being widespread in California and human attacks on nests not necessarily being a major issue

LINE 409 (DTRT)

Replace 52% with 26%. Nest predation is common, with 12–26% . Comment - I cant seem to find 55% nest predation stat in Berry and Murry 2019. Please revise accordingly.

RESPONSE: Percentages changed to 26-47% based on yearly numbers in Bjurlin and Bissonette 2004

LINE 410 (Nussear)

Line 410: "When nests are not predated, hatchling success is about 80% " - The verb here should be depredated, predated is to come before something - e.g. [pree-deyt] verb (used with object), pre·dat·ed, pre·dat·ing. to date before the actual time; antedate: He predated the check by three days. to precede in date: a house that predates the Civil War.

RESPONSE: Done

LINE 412 (DTRT)

Delete "At that age they become less vulnerable to predators.

RESPONSE: Done

LINE 418 (DTRT)

Add scientific names to "red brome, cheat grass, red stem filaree, and African mustard".

RESPONSE: Done

LINE 419 (Nussear)

Line 419–420: "but tortoises avoid eating exotic grasses when possible as they are low in nitrogen and require relatively large amounts of water to process."
no, they don't. See Esque 1984, and Tracy et al. 2006
RESPONSE: Deleted. Text now reads "Much of the range of the desert tortoise is highly invaded by nonnative plants including grasses like red brome (Bromus rubens) and cheatgrass (Bromus tectorum). Experimental studies found that grass diets that included no forbs were detrimental to tortoises, leading to weight loss, poor body condition, or even death (Hazard et al. 2009, Drake et al. 2016). This was the case even when the diet included native grasses (Drake et al. 2016). "

LINE 433 (Nussear)

Line 433: Berry and Murphy (2019) report that desert tortoises spend >90% of their lives underground. - this has been reported by numerous other studies, and entirely too much accredited to this reference - see also lines 438 - 441. kines 444 - 445, and I can't even list how many places. Repeatedly gives the appearance of a really shallow review of the primary literature.
RESPONSE: Noted, and the thoroughness of the citations provide throughout is appreciated. However, as stated in section 1.2, the status review " is not intended to be an exhaustive review of all published scientific literature on Mojave Desert Tortoise; rather it is intended to summarize key points relevant to the status of the species and address regulatory report requirements."

LINE 435 (Lovich)

You may want to cite HUTCHISON, V. H., A. VINEGAR, AND R. J. KOSH. 1966. Critical thermal maxima in turtles. Herpetologica. 22:32-41. and ZIMMERMAN, L. C., M. P. O'CONNOR, S. J. BULOVA, J. R. SPOTILA, S. J. KEMP, AND C. J. SALICE. 1994. Thermal ecology of desert tortoises in the eastern Mojave Desert: seasonal patterns of operative and body temperatures, and microhabitat selection. Herpetological Monographs. 8:45-59.
RESPONSE: Have expanded the range of temperatures when tortoises go to shade based on info in Zimmerman et al 1994

LINE 447 (Lovich)

See Ennen, J.R., K.P. Meyer, and J.E. Lovich. 2012. Female Agassiz's desert tortoise activity at a wind energy facility in southern California: the influence of an El Niño event. Natural Science 4:30-37. doi:10.4236/ns.2012.41006.
RESPONSE: Changed/ added so text now reads "Tortoises moved less, used fewer burrows, and had smaller home ranges during drought years as compared to wet years in the mid-1990s (Duda et al. 1999). However, at a different site in the late 1990s, the relationships between precipitation and activity area, rate of movement, and burrows used were less clear (Ennen et al. 2012), suggesting that there are many interacting forces that determine tortoise activity and movement levels**."**

LINE 409-412 (DTRT)

Suggested edit: Nest predation is common, with 12–26% of nests generally destroyed by predators (Berry and Murphy 2019, Ennen et al. 2012, Bjurlin & Bissonette 2004). When nests are not predated, hatchling success is about 80% (Bjurlin and Bissonette 2004). Newly hatched tortoises are about 4–5 cm in length (Bjurlin and Bissonette 2004) and their shells do not fully ossify until they are 5–7 years old. For more information about predation, see section 4.4.

RESPONSE: Percentages changed to 26-47% based on yearly numbers in Bjurlin and Bissonette 2004

LINE 434-436 (DTRT)

"Tortoises are active when their body temperatures are between 19.0°C and 37.8°C (66.2–100°F), they retreat to shade when body temperatures are 37–38°C (98.6–100.4°F), and body temperatures of 43°C (109.4°F) are deadly (Brattstrom 1965)". Review and add Zimmerman, L.C., O'Connor, M.P., Bulova, S.J., Spotila, J.R., Kemp, S.J. and Salice, C.J., 1994. Thermal ecology of desert tortoises in the eastern Mojave Desert: seasonal patterns of operative and body temperatures, and microhabitat utilization. Herpetological Monographs, pp.45-59.
RESPONSE: Have expanded the range of temperatures when tortoises go to shade based on info in Zimmerman et al 1994

LINE 460-461 (Nussear)

Lines 460–461: "Therefore, desert tortoise habitat typically consists of alluvial fans and plains and colluvial/bedrock slopes (Nussear et al.
2012)". This isn't the best reference for this, how about Germano 1994, or Nussear and Tuberville 2014? See also 465 and 466
RESPONSE: Have changed citation to Germano et al. 1994

LINE 515-417 (DTRT)

Delete these sentences "Tortoises favor native plants and plant parts that are high in water and low in potassium (Oftedal et al. 2002). Potassium is potentially toxic and requires a large amount of water and nitrogen to excrete.".
RESPONSE: Deleted

LINE 451 (Lovich)

Citation?
RESPONSE: Have added Ernst and Lovich 1994 as a reference to this cluster of sentences

LINE 461 (Lovich)

How about burrows under caliche layers?
RESPONSE: Although not mentioned specifically, this sentence is sufficiently broad enough to cover caliche layers. “Due to their dependence on burrows, they require soils, topography, geological features, and vegetation that facilitate the creation of burrows or dens (Andersen et al. 2000).”

LINE 482 (Lovich)

Berry 1984 not in lit cit
RESPONSE: Citations within a quote are not included in the bibliography

LINE 485 (Lovich)

Lower elevation areas free of tortoises include the Salton Trough. See Lovich, J.E., T. Edwards, K.H. Berry, S. Puffer, K. Cummings, J. Ennen, M. Agha, R. Woodard, K. Brundige, and R.W. Murphy. 2020. Refining genetic boundaries in the western Sonoran Desert for Agassiz’s desert tortoise (Gopherus agassizii): the influence of the Coachella Valley on gene flow among populations in southern California. Frontiers of Biogeography 12:1-14. https://escholarship.org/uc/item/54r0m1cq.
RESPONSE: Have added some text to the section on range and distribution "While caution should be used in using these types of data, there appear to be fewer occurrences in the

northern part of the range and in the Death Valley/Mojave Central Trough (see grey area on Figure 3), and few occur in low areas near the Salton Sea (Lovich et al. 2020)**."**

LINE 494 (DTRT)

Suggested edit: In California, the range of the Mojave Desert Tortoise includes the Mojave Desert and portions of the Colorado subunit of the Sonoran and Great Basin Deserts
RESPONSE: Done

LINE 507 (DTRT)

Suggested edit: In 2016, park staff began surveying for tortoises and formally collecting incidental observation data, and subsequent genetic analysis of tortoise blood and scat suggested "evidence of a naturally reproducing Mojave desert tortoise population in Anza Borrego Desert State Park" (Manning 2018).
RESPONSE: Done

LINE 516-520 (DTRT)

Suggested edit: The distribution of desert tortoises within California is uneven, and portions of the range no longer provide suitable tortoise habitat due to agriculture, development, and military activity. Data on tortoise occurrences from the California Natural Diversity Database (CNDDB) and the Global Biodiversity Information Facility (GBIF) were used to plot the distribution
RESPONSE: Done

LINE 548 (DTRT)

"Outbreeding depression has not been studied in G. agassizii." Also see Averill-Murray and Hagerty 2014 for discussion/calculations related to outbreeding depression. Translocation Relative to Spatial Genetic Structure of the Mojave Desert Tortoise,
Gopherus agassizii. Chelonian Conservation and Biology 13:35-41.
RESPONSE: Altered text to read "Outbreeding depression has not been well studied in G. agassizii; however, the potential negative impacts of outbreeding are expected to occur at long time scales (~600 years; Averill-Murray and Hagerty 2014). This suggests that habitat quality and predator numbers are more important than outbreeding depression when evaluating suitable recipient sites for translocation. Despite this, Sánchez-Ramírez et al. (2018) advise caution when moving tortoises long distances for translocation or population augmentation. For more details about translocations see section 5.2"

LINE 538-551 (DTRT)

Please also consider Scott, P.A., Allison, L.J., Field, K.J., Averill-Murray, R.C. and Shaffer, H.B., 2020. Individual heterozygosity predicts translocation success in threatened desert tortoises. Science, 370(6520), pp.1086-1089. and the Translocation of Mojave Desert Tortoises from Project Sites: Plan Development Guidance:
https://www.fws.gov/sites/default/files/documents/Revised%20USFWS%20DT%20Translocation%20Guidance.20200603final.pdf
RESPONSE: This paper is focused on tortoises from captive origins, and is not a great fit for this section of the status review.

LINE 638 (DTRT)

The use of square transects with 3 km sides was initiated in 2004, prior to this different transect lengths/shapes were used for line distance surveys

RESPONSE: Added text "In 2001–2003, two person teams surveyed TCAs using line transect surveys. Transects were searched out to 8–10 m from the centerline. The shape and length of the transect changed year to year (USFWS 2006). Starting in 2004, square transects with 3 km sides were set up to provide good coverage of each TCA, and a random selection of these transects are surveyed each year."

LINE 649 (DTRT)

As currently presented, the estimates in Table 2 for 2014 do not represent a survey in IV, CK, CM, FE, PT, or JT, but rather an extrapolated estimate based on trends outlined in USFWS 2022a. Recommend updating the table to reflect either only years surveyed or adding notation to differentiate.

RESPONSE: Following the inclusion of Zylstra et al. 2023, this table has been moved to the Appendix. Have listed the density estimates from line sampling from Allison and McLuckie, and bolded the densities estimated from trends as presented in USFWS 2022a. Added following text to legend "In 2014, the density estimates for the Western Mojave TCAs and Chocolate Mountain are estimated from line distance sampling and are found in Allison and Mcluckie (2018). The bolded estimates from Ivanpah and the Colorado Desert TCAs (excluding Chocolate Mountain) come not from that years' line distance sampling but are mean densities calculated from trends using data from previous years (USFWS 2022a)"

LINE 639-640 (DTRT)

Suggested edit: Two surveyors walk line transects along the boundary of the square or as close to it as is feasible, where the lead surveyor walks in a straight line on a specified compass bearing, trailing 25m of cord, and the second crew member follows at the end of the line.

RESPONSE: Done

LINE 640-642 (DTRT)

Suggested edit: They record the distance and bearing from the survey line to all tortoises seen and live tortoises are measured and sexed. In addition, data from tortoises carrying radio transmitters are used to estimate what portion of tortoises are above ground. These data are then used to calculate the proportion of tortoises that are detectable during the entire period transects are walked in an area.

RESPONSE: Text modified to "In addition, data from tortoises carrying radio transmitters are used to estimate what portion of tortoises are above ground and detectable during the transects."

LINE 684 (DTRT)

Spatially explicit estimates based on line distance data presented in Zylstra et al. 2023 demonstrate that in 2020 all TCA’s are below the 3.9 threshold.

Have updated this section to use results from Zylstra et al 2023

LINE 682-685 (DTRT)

"The most recent surveys (2019–2021) show that in the Eastern and Western Mojave Recovery Units, all of the TCAs surveyed were below the 3.9 adult tortoises/km2 threshold. In the Colorado Desert Recovery Unit, two were at the threshold, two were below it, and only one TCA (Fenner) was above (U.S. Fish and Wildlife Service 2022a)". Comment - Spatially explicit estimates based on line distance data presented in Zylstra et al. 2023 demonstrate that in 2020 all TCA’s are below the 3.9 threshold.

RESPONSE: Have updated this section to use results from Zylstra et al 2023

LINE 688 (DTRT)

Recommend updating figures 8 and 9 based on updated values in Table 2
RESPONSE: Done

LINE 698 (DTRT)

Table 2. 2014, density estimate values listed for this year come from two different sources, estimates calculated from annual line distance sampling in TCAs (Chocolate Mtn and SC; Allison and McLuckie 2018) and extrapolated estimates based on trends (all other TCAs) from USFWS 2022a. However, FK and OR were also surveyed in 2014. Recommend consistency in citing estimates, either 1) list density estimates for all areas surveyed in 2014 (AG, SC, FK, OR) from Allison and McLuckie 2018, include extrapolated estimates for other TCAs not surveyed and **add notation to differentiate** OR 2) list extrapolated estimates for all **including notation to differentiate extrapolated estimates** from actual years surveyed.
RESPONSE: Following the inclusion of Zylstra et al. 2023, this table has been moved to the Appendix. Have listed the density estimates from line sampling from Allison and McLuckie, and bolded the densities estimated from trends as presented in USFWS 2022a. Added following text to legend "In 2014, the density estimates for the Western Mojave TCAs and Chocolate Mountain are estimated from line distance sampling and are found in Allison and McLuckie (2018). The bolded estimates from Ivanpah and the Colorado Desert TCAs (excluding Chocolate Mountain) come not from that years' line distance sampling but are mean densities calculated from trends using data from previous years (USFWS 2022a)"

LINE 698 (DTRT)

Table 2. 2015, missing values for Ivanpah and Chocolate Mountain (USFWS 2016)
RESPONSE: Done

LINE 698 (DTRT)

Table 2. 2016, missing values for Chocolate Mountain, please update to include (USFWS 2016)
RESPONSE: Done

LINE 698 (DTRT)

Table 2, 2017, no value should be listed for Ivanpah, this TCA was not surveyed in 2017, please delete (USFWS 2018)
RESPONSE: Done

LINE 698 (DTRT)

Table 2, 2018, please correct the coefficient of variation for the Ord-Rodman estimate from 20.79 to 30.79 (USFWS 2019b)
RESPONSE: Done

LINE 698 (DTRT)

Table 2, 2019, missing values for Chocolate Mountain, please update (USFWS 2020a)
RESPONSE: Done

LINE 700 (DTRT)

Table 2, need to add USFWS 2022a citation
RESPONSE: Done

LINE 718 (Lovich)

Estimating live tortoises from sign is not a reliable method.
RESPONSE: Added text "These early monitoring programs sometimes relied on tortoise sign (tracks, scats, burrows, or carcasses) as well as observations of live tortoises, or employed

mark-recapture methods to obtain estimates of abundance or density. It should be noted that survey methods that rely on sign to estimate numbers of live tortoises are not reliable. In addition, mark recapture methods contain several assumptions that are violated in surveys of tortoises (Corn 1994), and the lack of spatial information in conventional mark recapture analysis leads to inflated estimates of density (Mitchell et al. 2021b). Therefore, estimates of density before 2001 must be approached with caution and direct comparisons between density estimates from mark recapture and line transect density methods are not advised. However, we can use these studies to give a rough picture of the state of tortoise populations in the late 20th century." Deleted "From 1979–1980 to 2020–2021, densities of adults in the corresponding TCAs fell 93% in Fenner, 96% in Chuckwalla, 89% in Chemehuevi, and 93% in Ivanpah" as this is a flawed direct comparison.

LINE 738 (DTRT)

"In addition, the BLM density estimates are only for the single plot per TCA". Comment - In addition, these results are likely biased high due to violations of statistical assumptions (Mitchell et al. 2021). Mitchell, C. I., K. T. Shoemaker, T. C. Esque, A. G. Vandergast, S. J. Hromada, K. E. Dutcher, J. S. Heaton, and K. E. Nussear. 2021. “Integrating Telemetry Data at Several Scales with Spatial Capture-Recapture to Improve Density Estimates.” Ecosphere 12: e03689.

RESPONSE: Added text "In addition, mark recapture methods contain several assumptions that are violated in surveys of tortoises (Corn 1994), and the lack of spatial information in conventional mark recapture analysis leads to inflated estimates of density (Mitchell et al. 2021b)." Added text "Comparing the density estimates in Berry and Medica (1995) to the USFWS estimates in 2001–2021 is not appropriate due to the differences in methodology described above. However, comparing the mark recapture density estimates between 1979 and 1992 can give us a sense of the general scale of decline even if the estimates themselves are biased high (Berry and Medica 1995, Mitchell et al. 2021b). "

LINE 711 and forward (Lovich)

These plot-based surveys cannot reliably be compared to data from line distance sampling data as that is like comparing apples to oranges. In the omitted Ernst and Lovich 2009 citation (page 564) mentioned above we compared and contrasted the techniques, their strengths and weaknesses. Plot-based surveys cannot be reliably extrapolated to surrounding areas and have been heavily criticized in the literature for their limitations. See CORN, P. S. 1994. Recent trends of desert tortoise populations in the Mojave Desert, p. 85-93. In: Biology of North American Tortoises. R. B. Bury and D. J. Germano (eds.). United States Department of the Interior, National Biological Survey. Fish and Wildlife Research 13. AND BURY, R. B., AND P. S. CORN. 1995. Have desert tortoises undergone a long-term decline in abundance? Wildlife Society Bulletin. 23:41-47. While I believe the plot-based data are valuable when those limitations are considered, you need to clarify that they are very different techniques and may not be useful for integration of data on declines.

RESPONSE: Bury and Corn 1995 question the assertions in Berry 1984 that there has been large scale declines in the desert tortoise densities up until that point and to claims of a 60-90% decline from 1900-1970s. The status review does not touch on population status or density prior to Berry 1984's strip transects which have rough density classes. Corn 1994 has a similar data set to Berry and Medina 1995, however because the violations of assumption in mark recapture in 60 days surveys, they present the data as relative abundance. The overall trends are similar over 1979-1990 as reported in Berry and Medina. Have reworded the section on Berry and Medica 1995's results to make it more clear about their limitations. See above

LINE 768 (Lovich)

Freilich worked on a one square mile plot (the Barrow Plot) in JTREE. That's "well-defined"
RESPONSE: Removed "and since they did not have a well-defined effective trapping area, their density estimates are rough. "

LINE 816 (Lovich)

Desert tortoises have the following life history traits: long-lived, late maturing, variable nest success due to predation, high adult survival, bet-hedging reproductive strategy (see ENNEN, J. R., J. E. LOVICH, R. C. AVERILL-MURRAY, C. B. YACKULIC, M. AGHA, C. LOUGHRAN, L. TENNANT, AND B. SINERVO. 2017. The evolution of different maternal investment strategies in two closely related desert vertebrates. Ecology and Evolution:1-13.), and relatively high juvenile survival to compensate for variable nest success. Classic studies of turtles with similar traits are: CONGDON, J. D., A. E. DUNHAM, AND R. C. LOBEN SELS. 1993. Delayed sexual maturity and demographics of Blanding's turtles (Emydoidea blandingii): Implications for conservation management of long-lived organisms. Conserv Biol. 7. AND CONGDON, J. D., A. E. DUNHAM, AND R. C. VAN LOBEN SELS. 1994. Demographics of common snapping turtles (Chelydra serpentina): implications for conservation and management of long-lived organisms. Amer. Zool. 34:397-408. You even show fairly high rates of juvenile survivorship on page 37. Without compensation for high nest mortality if hatchlings (you say this is high on page 37 line 903 and with the Daly et al. citation on page 37) populations could not survive.
RESPONSE: Have added text "In long-lived species like the tortoise, if adult survivorship drops, reproductive rates or juvenile survival would have to increase dramatically to keep populations stable. Analysis by the USFWS (1994) estimated that “a 10% increase in adult mortality can require a 300% increase in juvenile survivorship” to maintain a stable population. Many of the threats to adult survival also affect juveniles, making it unlikely that juvenile survivorship can naturally increase to the levels needed to compensate for the decreasing adult survival documented above"

Page 34 Figure (Lovich)

All of the presumed confidence intervals overlap each other so they aren't really different
RESPONSE: Assume this refers to figure 12. Have added/altered relevant text to read "In the yearly transect surveys done in the TCAs, the median midline carapace length did not change significantly between 2001 and 2015 (Figure 10). However, fewer juveniles small enough to be classified as outliers (the small circles below the lower ‘whisker’ in the box and whisker plot of Figure 10) were found in 2007–2015 compared to 2001–2005. In 2011, only one juvenile (midline carapace length <180 mm) was found, and in 2012 none were found. In some areas, the youngest tortoises found in recent years were at least 30 years old (Holcomb 2022a). Despite a steady median carapace length across 2001–2015, the range of carapace lengths decreased, with most of that change due to fewer smaller individuals found. Even with thousands of adults in a population, if sufficient juvenile tortoises are not surviving to breeding age, the population will decline without interventions like head-starting, although that decline may take decades to manifest (Lovich et al. 2018)."

LINE 856-857 (Lovich)

Prey switching was the mechanism proposed

RESPONSE: Text amended to read "It should be noted that other factors that impact survival, such as predation, roadkill, and disease were not tested independently" prey switching is discussed more in section 4.5 on predation.

LINE 870-881 (DTRT)

Comment - Esque et al. 2010 highlighted that we have too many subsidized predators (e.g., coyotes) throughout the Mojave Desert and that prolonged drought conditions likely created a shift in predator-prey dynamics. Increased mortality for G. agassizii was observed range-wide in 2008-2009. Please rephrase to include the importance of this finding.

RESPONSE: Prey switching and Esque et al 2010 is talked about at the end of the section 4.4 on predation. The addition of Cypher et al. 2018 adds some counterpoints to the discussion. Text read "During periods of suppressed rodent and prey populations following dry years, it has been suggested that coyotes will switch to preying on tortoises (Esque et al. 2010). This may help explain the widespread high mortality rates due to predation in 2008 (Esque et al. 2010). However, work by Cypher et al. (2018) did not necessarily support that hypothesis. In a study following the 2008 translocation of tortoises to an area south of Fort Irwin, they collected data on the relative abundance of rodents and rabbits, as well as the contents of coyote scats in 2009–2014. The years 2011–2014 were very dry compared to the wetter years of 2009–2010. While the frequency of occurrence of rodents in scat was lower in dry years (24.3%–46.3%) than in the wet years (53%–65%), the frequency of tortoises in scat was also lower in dry years (2.4%–2.6%) compared to wet years (5.6%–5.8%). These results suggest that it is unlikely coyotes switched to tortoise prey because of lack of rodents. Instead, as coyotes ate fewer rodents in the dry years, their amount of anthropogenic food sources increased (Cypher et al. 2018). While 2008 may have been an anomalous widespread pulse in predation pressure (Esque et al. 2010), there is a lack of rigorous evidence that coyotes regularly prey switch to tortoises when rodent or lagomorph populations are low because of drought. "

LINE 897 (Lovich)

is 300% the right number?

RESPONSE: Full quote is "Indeed, somewhere in the order of only 1% of all eggs need survive to reproductive age. On the other hand, a 10% increase in adult mortality can require a 300% increase in juvenile survivorship. Furthermore, any reduction in the fecundity of adults exacerbates this further."

LINE 901 (DTRT)

"Several factors limit the number of hatchlings that are produced in the wild each year."

Comment See Mitchell et al. 2021 for more information related to the drivers of egg production. The authors modeled reproductive output as a factor of climate and individual attributes and detected a declining trend in egg production across all recovery units over time.

RESPONSE: Citation was previously added. Altered text to read "Several factors limit the number of hatchlings that are produced in the wild each year. Temperature, precipitation and body size influence the number eggs females lay (Mitchell et al. 2021a), with the maximum being 12-18 eggs a year (J. Lovich Pers comm 2023). "

LINE 902 (Lovich)

See earlier comment about 30 eggs/year being wrong

RESPONSE: Altered text to read "Several factors limit the number of hatchlings that are produced in the wild each year. Temperature, precipitation and body size influence the number eggs females lay (Mitchell et al. 2021a), with the maximum being 12-18 eggs a year (J. Lovich Pers comm 2023). "

LINE 918 (Lovich)

This addresses a proximate (not enough turtles) not an ultimate (impacts continue to kill turtles in the wild) cause. See FRAZER, N. B. 1992. Sea turtle conservation and halfway technology. Conservation Biology. 6:179-184. for a critique of headstarting.

RESPONSE: True, but this distinction may not be necessary here.

LINE 901-917 (Lovich)

juvenile survival rates aren't that low. See comments line 23 of spreadsheet

RESPONSE: Have deleted that sentence.

LINE 953 (DTRT)

Again, you say survival rates of juveniles are low but you say 100% on page 37 line 928

RESPONSE: That is a modelled survival rate that hasn't been ground truthed and focused mostly on predation risk from ravens. Other factors make it unlikely annual survival would be 100%

LINE 986-987 (Lovich)

The west Mojave is highly built up and growing. See HUNTER, L. M., M. D. J. GONZALEZ G, M. STEVENSON, K. S. KARISH, R. TOTH, T. C. EDWARDS, R. J. LILIEHOLM, AND M. CABLK. 2003. Population and land use change in the California Mojave: Natural habitat implications of alternative futures. Population Research and Policy Review. 22:373-397.

RESPONSE: Added some text at the end of the paragraph to add context about how the results of the Carter et al. 2020 paper may not hold into the future "However, these categories of development used above do not take into account unpaved roads and tracks for off-highway vehicles (OHVs) which are allowed on BLM land (see section 4.2), and given the pace of a variety of development in the desert, the conclusions may be less applicable in the future."

LINE 997 (Lovich)

Cite Hunter et al. above?

RESPONSE: This paper is interesting, but it is from 2003 and offers 2 potential development possibilities by 2020 with amounts of DT tortoise habitat in conflict with development. With the information easily available it would be hard to judge which scenario most closely matches reality and it is unclear it would add much to what information is already presented.

LINE 1034 (Lovich)

Cite Lovich and Bainbridge for recovery

RESPONSE: Done "Recovery from disturbance can take a long time in desert ecosystems (Lovich and Bainbridge 1999). "

LINE 1043 (Lovich)

How about fire as an impact esp. on bases like China Lake where lots of ordinance is fired

RESPONSE: Unable to find specific information about fires on DoD land.

LINE 1055 (Lovich)

Citation is Lovich and Ennen, not et al.

RESPONSE: Changed. "

LINE 1057 (Lovich)

after "infrastructure" add "for wind"

RESPONSE: The relevant sentence has been removed due to further editing

LINE 1112 (Nussear)

line 1112 Cannabis operations - this seems like a trivial inclusion. 12 km^2? This seems to be about the equivalent of party balloon effects, surprised to see this here.

RESPONSE: As noted, the visited acres of illegal cannabis grows are likely an underestimate of the true number of acres and it is probable that active and abandoned acres will continue to grow. The Department felt it is worthy to mention as something to keep an eye on in the future.

LINE 1117 (Lovich)

Guard dogs or any dogs?

RESPONSE: In the context of cannabis operations the dogs are mostly guard dogs. Pet/ feral dogs can be an issue generally near homes.

LINE 1208 (Lovich)

West where? Mojave?

RESPONSE: Have modified to clarify "According to the BLM, in 2008 there were four times the number of off-highway vehicles in western states than in 1998 (Bisson 2008)."

LINE 1258 (DTRT)

Suggested edit: Grasses are high in fiber, contain less digestible energy, and little protein (Hazard et al. 2009; Drake et al. 2016),

RESPONSE: That text is within a quote, alterations would not be appropriate

LINE 1242-1243 (DTRT)

"Fueled in part by nitrogen pollution carried by wind from the Los Angeles Basin which enriches desert soils (Fenn et al. 2010), invasive Mediterranean grasses have spread through much of the Mojave Desert." Comment- nitrogen pollution is not a significant contributor to the spread and establishment of invasive Mediterranean grasses. Habitat disturbance, recreation activities, and loss of native plants plays the biggest roles.

RESPONSE: Have deleted the relevant part of the sentence.

LINE 1297 (DTRT)

Suggested edit: The best studied predators of tortoises are ravens , coyotes, and badgers. " Include scientific name the first time predators are referenced in document.

RESPONSE: Have added scientific names to the document.

LINE 1341-1343 (DTRT)

Suggested edit: Ten years later, 104 were dead, an estimated 60% of which were killed by coyotes (Esque et al. 2010; Mack and Berry 2023). Increased tortoise mortality due to coyote depredation was observed throughout the tortoise's range (Esque et al. 2010).

RESPONSE: Sentence has been altered to read "Coyotes are thought to be a major predator of adult tortoises. In a study of translocated tortoises in the Superior-Cronese CHU, between 2008 and 2018 an estimated 60% were killed by predators, likely coyotes based on nearby tracks and scat (Esque et al. 2010, Mack and Berry 2023). " Esque et al. 2010 range wide results are discussed in the paragraph that follows this text.

LINE 1357 (DTRT)

Add Emblidge et al. 2014 citation after badger. Suggest adding this citation from Endangered Species Research 28:109-116 and maybe a statement that evidence is mounting that badgers may play an important role in heavy localized mortality event.

RESPONSE: Have added the text "Badgers are thought to be partially responsible for high levels of mortality of tortoises in 2012-2013 on and near Ft. Irwin and may be important predators in certain locales (Emblidge et al. 2015). "

LINE 1360 (Lovich)

The following two citations also discuss prey switching: Lovich, J.E., S.R. Puffer, K. Cummings, T.R. Arundel, M.S. Vamstad, and K.D. Brundige. 2023. High female desert tortoise mortality in the western Sonoran Desert during California's epic 2012–2016 drought. Endangered Species Research 50:1-16. https://doi.org/10.3354/esr01215 and Lovich et al. 2014 already in lit cit.
RESPONSE: The coyote predation/scavenging discussion in Lovich et al. 2014 is included the section on predation. The 2023 reference was useful for the section on impacts of drought.

LINE 1505 (Nussear)

line 1505 - 1506 " foraging for annuals in the burned areas, while using the cover of perennial shrubs only found in unburned areas (Drake et al. 2015). "
This really isn't true, and not what Drake et al says if you read beyond just the abstract. Tortoises also used cover in burned areas, and that consisted of both burned and unburned perennials in the scar of the burn. - see also Snyder et al. 2019
RESPONSE: Altered text to "Tortoises tend to remain in same areas after fire (Lovich et al. 2018), and one study found that tortoises used burned and unburned areas nearly equally, starting the first year after the fire (Drake et al. 2015). Tortoises moved into the burned areas seasonally to forage for preferred annuals and herbaceous perennials (Drake et al. 2015). The use of burned habitats did not appear to affect their health or reproduction in the short term. However, the expansion of red brome grass in burned areas and the injuries that fire can cause tortoises remained concerns (Drake et al. 2015)."

LINE 1531 (Lovich)

You might cite SCHUMACHER, I. M., D. C. ROSTAL, R. A. YATES, D. R. BROWN, E. R. JACOBSON, AND P. KLEIN, A. 1999. Persistence of maternal antibodies against Mycoplasma agassizii in desert tortoise hatchlings. American Journal of Veterinary Research. 60:826-831. as there is no evidence of transmission of URTD from females to their embryos
RESPONSE: Was unable get a copy of this paper and mother to offspring transmission is not mentioned in the document.

LINE 1534 (Lovich)

add "potentially" I'm not aware of evidence that tortoises have to smell to find food
RESPONSE: Have added the word potentially "The disease both directly kills tortoises and can potentially interfere with their sense of smell and therefore their ability to forage for food and can potentially negatively affect their reproductive fitness (Germano et al. 2014, Jacobson et al. 2014)"

LINE 1527-1528 (DTRT)

Suggested edit: The disease presents as lesions in the nasal cavity and inflammation of mucosa of the upper respiratory tract, muchoid discharge from the nares, damaged nasal scales due to chronic muchoid discharge
RESPONSE: Done

LINE 1569 (DTRT)

Delete this sentence. There is no evidence of this. Being captured by humans for research and/or translocation can stress tortoises and make them more susceptible to URTD.

RESPONSE: Unclear what this comment refers to as the original sentence says "Being captured by humans for research and/or translocation can stress tortoises and make them more susceptible to URTD. " However, that sentence has been deleted in the general editing process.

LINE 1580 (Lovich)

Change associated to correlated
RESPONSE: Done. "Shell lesions were correlated with high mortality rates of desert tortoises in Chuckwalla Bench in 1982–1988 "

LINE 1569-1570 (DTRT)

Edit this sentence to the following: Official handling protocols have strict guidelines in place to minimize human-mediated transfer of pathogens stress as much as possible (U.S. Fish and Wildlife Service 2020b, a).
RESPONSE: text altered to "Official handling protocols include strict guidelines to minimize human mediated transfer of pathogens and stress (USFWS 2020b). "

LINE 1636 (Lovich)

morafkai misspelled
RESPONSE: Fixed

LINE 1643 (Lovich)

15.4 tortoises/km squared at my Palm Springs tortoise site as cited in Lovich et al. 2011 already in lit cit
RESPONSE: This whole section has been deleted.

LINE 1647 (DTRT)

"the most recent estimates of abundance…" Predicted abundances at the recovery unit level are available for 2020 from Zylstra et al 2023
RESPONSE: Have deleted this section and deleted the table with abundances from 2014

LINE 1648 (DTRT)

Predicted abundances at the recovery unit level are available for 2020 from Zylstra et al 2023
RESPONSE: Have deleted this section and deleted the table with abundances from 2014

1658 (DTRT)

Recommend incorporating trends and predicted densities from Zylstra et al. 2023 into this section
RESPONSE: Have deleted this section

LINE 1678 (Lovich)

While adult sex ratios in desert tortoises tend to be equal the issue is much more complicated. See these citations: LOVICH, J. E., AND J. W. GIBBONS. 1990. Age at maturity influences adult sex ratio in the turtle Malaclemys terrapin. Oikos. 59:126-134. AND Lovich, J. E. 1996. Possible demographic and ecologic consequences of sex ratio manipulation in turtles. Chelonian Conservation and Biology 2:114-117. AND Lovich, J.E., J.W. Gibbons, and M. Agha. 2014. Does the timing of attainment of maturity influence sexual size dimorphism and adult sex ratio in turtles? Biological Journal of the Linnean Society 112:142-149. AND Lovich, J.E., S.R. Puffer, K. Cummings, T.R. Arundel, M.S. Vamstad, and K.D. Brundige. 2023. High female desert tortoise mortality in the western Sonoran Desert during California's epic 2012–2016 drought. Endangered Species Research 50:1-16. https://doi.org/10.3354/esr01215
RESPONSE: Have added Lovich 2023 as a citation, see below.

LINE 1680 (Lovich)

Not true. See Lovich, J.E., S.R. Puffer, K. Cummings, T.R. Arundel, M.S. Vamstad, and K.D. Brundige. 2023. High female desert tortoise mortality in the western Sonoran Desert during California's epic 2012–2016 drought. Endangered Species Research 50:1-16. https://doi.org/10.3354/esr01215

RESPONSE: This comment refers to sex ratios. The sex ratio text has been moved to section 4.6 Climate Change and Drought and now reads "There is some evidence that drought is affecting sex ratios of adult tortoises. Unequal sex ratios are thought to lower effective population size, which in small populations with limited connectivity could exacerbate inbreeding (Frankham 1995). In 2015–2016, Lovich et al. (2023) surveyed two sites in Shaver's Valley about 70 km southeast of Palm Springs along the boundary of the Joshua Tree and Chuckwalla TCAs. At both sites there was a male bias in live tortoises. At the cooler, wetter site there was an even sex ratio in tortoises found dead, but in the hotter and drier Chuckwalla site, more females were found dead. It is possible that the energetic requirements required for reproduction make females less likely to survive long-term drought conditions (Lovich et al. 2023)."

LINE 1680 (Nussear)

Line 1680 you state "Unfortunately, there are no published data on sex ratios in the 17 TCAs (Berry and Murphy 2019)," - this isn't really the case, Allison and Mcluckie, Esque et al, and many other studies and datasets exist.

RESPONSE: Deleted

LINE 1658-1659 (Lovich)

Are these "small populations"?

RESPONSE: Have deleted section on small populations.

LINE 1671-1676 (Lovich)

This is discussed in more detail in Lovich, J.E., J.R. Ennen, M. Agha, and J.W. Gibbons. 2018. Where have all the turtles gone, and why does it matter? BioScience 68:771–781. The long lives of tortoises can give the perception of population persistence even with no juvenile recruitment.

RESPONSE: Moved text to section 3.2 Trends in Density and Abundance has been added "Even with thousands of adults in a population, if sufficient juvenile tortoises are not surviving to breeding age, the population will decline without interventions like head-starting, although that decline may take decades to manifest (Lovich et al. 2018)."

LINE 1694 (Lovich)

cite Lovich, J.E., S.R. Puffer, K. Cummings, T.R. Arundel, M.S. Vamstad, and K.D. Brundige. 2023. High female desert tortoise mortality in the western Sonoran Desert during California's epic 2012–2016 drought. Endangered Species Research 50:1-16. https://doi.org/10.3354/esr01215

RESPONSE: Resolved, see above

LINE 1815 (Lovich)

"The" Mojave Desert Tortoise

RESPONSE: Fixed

LINE 1847 (Lovich)

How about Utah?

RESPONSE: Added Utah. "The Desert Tortoise Management Oversight Group (MOG), formed in 1994, is comprised of senior managers from USFWS, BLM, state transportation agencies, state wildlife agencies, county governments, and non-governmental organizations (NGOs) that work in the tortoise range in Arizona, Nevada, Utah, and California. "

LINE 1871 (DTRT)

"In 2008 and 2011….". 2008 was a draft for review. Please only use 2011.
RESPONSE: Deleted 2008

LINE 1871 (DTRT)

Suggested edit: "the USFWS published revisions to the a Revised Recovery Plan…"
RESPONSE: Done

LINE 1880 (DTRT)

delete 2008
RESPONSE: Done

LINE 1886 (DTRT)

Edit to "As part of the revised 2011 Revised Recovery Plan".
RESPONSE: Done

LINE 1957 (Lovich)

You included the Yermo logistics base earlier but not here (and they have tortoises)
RESPONSE: Amended "DoD facilities within the Mojave Desert Tortoise range include Naval Air Weapons Station China Lake, Edwards Air Force Base, Fort Irwin, Marine Air Ground Task Force Training Command and Marine Corps Air Ground Combat Center Twenty-Nine Palms, Marine Corps Logistics Base Barstow, and the Chocolate Mountain Aerial Gunnery Range. "

LINE 2079 (Nussear)

Line 2079 - competition, you should probably address that there is active grazing of sheep and cattle in California, and whether that overlaps with desert tortoises (it does), and where and to what extent that occurs.
RESPONSE: This section has been reworked and a new section 4.4 Competition has been added to better align the document with statutory requirements. The text now reads "Grazing by livestock is a major part of the recent history of the desert. While grazing on BLM lands was historically permitted in tortoise range (Berry et al. 2014) after federal listing in 1990 it was halted in the CHUs. However, grazing is allowed on private inholdings within the CHUs, which are often unfenced. The documented impacts of livestock on tortoises include competition for food, trampling to death, and causing the collapse of burrows (see Berry and Murphy (2019)). Livestock also degrade habitat by creating or expanding trails which reduces annual plant cover and can (but does not always) promote wind erosion and compaction (Webb and Stielstra 1979, Lovich and Bainbridge 1999). "

LINE 2097 (Nussear)

Line 2097: Climate change - there are local and regional modeling efforts that demonstrate a predicted loss of habitat. The potential for this to impact tortoise populations lies far beyond the potential for the military to train more.
RESPONSE: True, have added this sentence "Modelling by Barrows (2011) predicts that under 2°C (3.6°F) of warming with 50 mm decrease in precipitation, habitat area will decrease by about 88% in the Sonoran Desert portion and by about 66% in the Mojave Desert portion."

LINE 2172 (Lovich)

You should cite Lovich, J.E., J.R. Ennen, S.V. Madrak, and B. Grover. 2011. Turtles, culverts and alternative energy development: an unreported but potentially significant mortality threat to

the desert tortoise (Gopherus agassizii). Chelonian Conservation and Biology 10:124-129. Culverts can be death traps for tortoises.
RESPONSE: This section has been deleted, but have added this sentence section 4.2 on road fencing "However, proper design is key, culverts can become death traps for tortoises if not properly designed and implemented (Lovich et al. 2011)."

LINE 2176 (Lovich)

Cite Hunter et al. above?
RESPONSE: This section has been deleted to bring the document in line with regulatory requirements

LINE 2230-2237 (DTRT)

General Comment. Given the declining status Mojave desert tortoises in California and continued habitat loss and degradation due to increased human activity and infrastructure, we agree that the Department's recommendation to change the status of Mojave desert tortoises from threatened to endangered is warranted in California.

LINE 2330 (Lovich)

There is no discussion of the negative effects of fencing on tortoises and other wildlife and there is a huge literature on that needs to be mentioned
RESPONSE: Have emphasized that the fencing has to be well designed "Erecting well designed tortoise exclusion fencing along major roadways and funneling them into appropriate crossings is a key recovery action. "

LINE 2374 (Lovich)

Has anyone ever quantified the effectiveness of these efforts? It may use funds that could be more meaningful in other recovery efforts
RESPONSE: There may not be specific quantification of the impact of outreach in this particular case, but there is a large body of research about effective ways to communicate with the public and how it can impact behavior change.

LINE 2397-2401 (DTRT)

Suggested edit: Population augmentation is currently accomplished through two types of projects, mitigation-driven translocation and release of head-started juveniles. Mitigation-driven translocation involves moving tortoises from a site where they would be harmed and into an appropriate recipient site. Head-starting is a strategy to reduce predation mortality on juvenile tortoises by hatching and rearing juveniles in captivity until they are large enough to avoid most predators. In the future, conservation-based translocations of adults may also be possible.
RESPONSE: Much of this section has been moved to section 5.2 Management Efforts. The first suggested text changes were made but the Department will leave any discussion of conservation-based translocation to a future Recovery Plan

LINE 2406-2411 (DTRT)

Suggested edit. There are a number of considerations that need to be taken into account when tortoises are translocated as laid out in the USFWS's guidance on translocating tortoises from project sites Plan Development Guidelines (U.S. Fish and Wildlife Service 2020b).
Considerations Major concerns include the habitat suitability of potential translocation sites

and the disease prevalence of both tortoises being moved and at the recipient site possibility of disease transfer from transplants to resident tortoises.
RESPONSE: Much of this section has been moved to section 5.2 Management Efforts, but the suggested text edits were made.

LINE 2408 (DTRT)

Suggested edit: Considerations recipient site of potential translocation sites and the disease prevalence of both tortoises being moved into and at the recipient site.
RESPONSE: The section on translocation was heavily modified and moved. This sentence has been deleted.

LINE 2409 (DTRT)

In reference to resident tortoises - This is only part of it. The residents can also transfer pathogens to the translocated and increased contacts rates could change the background disease dynamics at the site.
RESPONSE: Have clarified with the suggested edits above.

LINE 2410 (DTRT)

In reference to "ITP holders monitor" - Please consider the monitoring guidance in USFWS 2020b vs requiring the monitoring of small numbers of translocated tortoises.
RESPONSE: Have re arranged the paragraphs and add the text "The Department" to clarify that these are monitoring actions via CDFW ITPs and not guidance issued by USFWS

LINE 2412 (DTRT)

In reference to "sufficient burrows of appropriate size...": Existing burrows should not be a requirement. The focus should be on shelter sites in general. They must be able to seek shade and protection immediately, but that doesn't need to be within a burrow. The abundance of other types of shelter is likely more important, as tortoises released into a new environment would need to find the existing burrow vs taking immediate shelter under shrubs, boulders, etc.
RESPONSE: This paragraph discusses actions related to ITPs issued by CDFW which can differ from the USFWS guidance on burrows vs shelter sites. Have rearranged the paragraphs and added some text to make that more clear "The Department requires that ITP holders monitor any tortoises translocated, and has teams carefully examine recipient sites for soil and vegetation communities that are suitable for all life stages of the tortoise, evaluate the presence and abundance of predators, and make sure there are sufficient burrows of appropriate size so that translocated tortoises can quickly find shelter"

LINE 2419 (DTRT)

Start this paragraph as... "There is evidence from more than a dozen sites that translocation, including large-scale translocation, can be an important conservation tool (Brand et al. 2016, Dickson et al. 2019, Drake et al. 2012, Esque et al. 2010, Farnsworth et al. 2015, Field et al. 2007, Harju et al. 2019, Hinderle et al. 2015, Nafus et al. 2017, Nussear et al. 2012). Finding recipient sites for for large numbers of tortoises is challenging. If donor sites are chosen because resident populations are depleted ..."
RESPONSE: Have included these references in this paragraph "Beyond the survival of tortoises involved in large scale translocations, there have been many studies looking at how body conditions and temperature (Brand et al. 2016), environmental feature and conditions (Nafus et al. 2017, Dickson et al. 2019), physiological stress (Drake et al. 2012), proximity of anthropogenic resources (Esque et al. 2010), movement and space use (Nussear et al. 2012,

Farnsworth et al. 2015, Hinderle et al. 2015), and water availability (Field et al. 2007) affect the outcomes of translocations. These results should be used to keep improving and refining decision making around translocations." This text is now in section 5.2 Management Efforts

LINE 2429 (Nussear)

you misrepresent the findings in Esque 2010 - animals that were in control groups also suffered similar mortality rates, as did animals throughout the range of the tortoise. Another oversight is that you don't factor in the number of animals lost from habitat if they are removed and not translocated. This is an important consideration - The better option is to find alternative siting for things like solar facilities etc that result in the loss and degradation of tortoise habitat, but the continued lack of the ability to say no to these large scale disturbances leaves you with little choice.

RESPONSE: The translocation section was extensively rewritten to incorporate this and other feedback

LINE 2402 onward (Lovich)

This section doesn't do much to change my perception of the lack of effectiveness of translocation based on the literature. You should cite: SULLIVAN, B. K., E. M. NOWAK, AND M. A. KWIATKOWSKI. 2015. Problems with mitigation translocation of herpetofauna. Conservation Biology. 29:12-18. AND GERMANO, J. M., K. J. FIELD, R. A. GRIFFITHS, S. CLULOW, J. FOSTER, G. HARDING, AND R. R. SWAISGOOD. 2015. Mitigation-driven translocations: are we moving wildlife in the right direction? Frontiers in Ecology and the Environment. 13:100-105. AND GERMANO, J. M., AND P. J. BISHOP. 2008. Suitability of amphibians and reptiles for translocation. Conservation Biology. 23:7-15.

RESPONSE: The translocation section was extensively rewritten to incorporate this and other feedback

LINE 2413-2414 (DTRT)

In reference to "most of the tortoises translocated under IPTs…." - Does the Department try to keep them within 4 miles or is this a result of moving from harm's way into adjacent habitat? Putting such restraints on the distance tortoises can be moved will limit the ability to get tortoises into good quality, high priority augmentation sites that are consistent with greater conservation objectives.

RESPONSE: Have added the text "(although distance is only one of many considerations when choosing a recipient site)" This sentence is now in section 5.2 Management Efforts

LINE 2456- (DTRT)

Edit translation to translocation

RESPONSE: Done

LINE 2489 (DTRT)

In reference to "high death rates". Unlikely. Studies showed former captives did very well when in good health upon release. More likely factors were the lack of stringent translocation suitability evaluations and rigorous health assessments as are now requirements.

RESPONSE: The translocation section was extensively rewritten to incorporate this and other feedback

LINE 2486-2499 (DTRT)

Suggest editing this paragraph to the following. "The failure of these large and long-term translocations to either keep translocated tortoises alive or the resident population stable

suggests translocation may often not be an effective management strategy without figuring out and addressing the drivers of declines within the subject populations. Augmentation of populations through translocations may buy time and keep tortoises present on the landscape while the threats causing declines are addressed. The majority of the tortoises translocated into LSTS came from captivity and were likely not well adapted to surviving in the wild, which is likely a factor in their high death rates. Most official translocations in California involve moving wild tortoises from a project site to a nearby area, and so may not face the same difficulties in survival that releasing captive tortoises appear to create. However, the evidence from Ord-Rodman suggests that even an addition of large numbers of new adults to a nearby area can slow but does not prevent population declines. The low survival rates of translocated adults and the lack of genetic integration of males suggest that large scale translocation may not provide much recorded benefit to recipient populations and does not necessarily remove the translocated tortoises from harm's way. Thus, identification of the reasons for the depleted population in the recipient site is important to ensure translocation is conducted in a manner appropriate to facilitate survival, and to prevent its failure as a minimization measure."
RESPONSE: The translocation section has been modified extensively, but this particular text is now "However, given the continuing decline of tortoise populations in general, translocations may often not be an effective conservation strategy without addressing the drivers of declines within the subject populations. At best, augmentation of populations through translocations can buy time and keep tortoises present on the landscape while the threats causing declines are addressed. "

LINE 2487-2488 (Lovich)

If it isn't an effective strategy, why pursue it?
RESPONSE: The translocation section was extensively rewritten to incorporate this and other feedback

LINE 2520 (Lovich)

The Frazer citation above should be incorporated in this section
RESPONSE: Have added text " Daly et al. (2019) points out that by itself, head-starting is unlikely to lead to population recovery if larger issues that depress survival such as raven density and habitat degradation are not addressed. Another consideration is that unless factors that depress adult survival are also reduced, focusing on putting more juveniles in a "degraded environment in which their parents have already demonstrated that they cannot flourish" is not an effective long-term solution (Frazer 1992). "

LINE 2541 (DTRT)

Delete "yearly"
RESPONSE: Done

LINE 2545 (Lovich)

How would making sex ratio data public help stakeholders given the complexities of interpreting sex ratios listed above in this spreadsheet?
RESPONSE: Have deleted this paragraph

LINE 2545 (Nussear)

Line 2545 - Regarding sex ratio data - these are easily obtained. Just ask the FWS for it, I have done so repeatedly and they have always been happy to provide it. This seems like a straw man argument that is a result of poor communication.

RESPONSE: Have deleted this paragraph

LINE 2568 (Lovich)

Adaptive management is thrown around by people that don't fully understand what it means. In its simplest form it is using policy as a testable hypothesis, monitoring its effectiveness, adjusting the policy to increase effectiveness and repeating the cycle. Is that what you mean? It requires a substantial investment of time and people as shown in the Glen Canyon Dam Adaptive Management Program https://www.usbr.gov/uc/progact/amp/index.html.

RESPONSE: Have altered to "Implement a formal Recovery Plan"

LINE 2615 (Lovich)

Why only 5 years for a species with a cohort generation time of about 25 years that lives to be 50 or so? Isn't recruitment an important component of success?

RESPONSE: Ideally the monitoring period would be longer for such a long lived animal, but until the Department effectively organizes and analyzes the data they have, asking permit holders to do more monitoring seems like an unnecessary burden.

LINE See section 2.2. (DTRT)

Comment. Too much of 2.2 Species Description and Life History is extrapolated from Berry and Murphy 2019. Please review broader literature for appropriate citations and information.

RESPONSE: Some primary references have been added to this section thanks to the suggestions of multiple reviewers, but as stated in section 1.2, the status review is not intended to be an exhaustive review of all published scientific literature on Mojave Desert Tortoise; rather it is intended to summarize key points relevant to the status of the species and address regulatory report requirements.

State of California
Natural Resources Agency
Department of Fish and Wildlife

DRAFT REPORT TO THE FISH AND GAME COMMISSION
STATUS REVIEW OF MOJAVE DESERT TORTOISE
(*Gopherus agassizii*)

[DATE]

Mojave Desert Tortoise, BLM photo by Dana Wilson

Charlton H. Bonham, Director
Department of Fish and Wildlife

Suggested citation:

California Department of Fish and Wildlife (CDFW). [DATE]. Status Review of Mojave Desert Tortoise (*Gopherus agassizii*). Report to the California Fish and Game Commission. California Department of Fish and Wildlife, 715 P Street, Sacramento, CA 95814. 188 pp., with appendices.

CONTENTS

LIST OF FIGURES

LIST OF TABLES

LIST OF APPENDICES

LIST OF ABBREVIATIONS, ACRONYMS, AND TERMS

CEQA – California Environmental Quality Act
NEPA – National Environmental Policy Act
CESA – California Endangered Species Act
CNDDB – California Natural Diversity Database
Commission – California Fish and Game Commission
Department – California Department of Fish and Wildlife
CHU – Critical Habitat Unit
RU – Recovery Unit
TCA –Tortoise Conservation Area

DoD – Department of Defense
ESA – Endangered Species Act
NPS – National Park Service
USFWS – United States Fish and Wildlife Service
BLM – Bureau of Land Management
ITP – Incidental Take Permit
NEPA – The National Environmental Policy Act
et al. – “and others”

EXECUTIVE SUMMARY

This Status Review of Mojave Desert Tortoise (*Gopherus agassizii*; also known as Agassiz's Desert Tortoise) has been prepared by the California Department of Fish and Wildlife (Department) for the California Fish and Game Commission (Commission) pursuant to the requirements of the California Endangered Species Act (CESA; Fish & G. Code, § 2050 et seq.).

The Mojave Desert Tortoise was designated a threatened species under CESA in 1989. On March 23, 2020, the Commission received a petition from the Defenders of Wildlife, the Desert Tortoise Council, and the Desert Tortoise Preserve Committee to change the status of the Mojave Desert Tortoise from threatened to endangered. On April 13, 2020, the Commission referred the Petition to the Department for evaluation pursuant to Fish and Game Code section 2073 and published a formal notice of receipt of the petition (Cal. Reg. Notice Register 2020, No. 18-Z, p. 693). At its meeting on August 20, 2020, the Commission received the Department's petition evaluation report. The Department based its evaluation on available information and recommended to the Commission that the petition be accepted. At its October 14, 2020 meeting, the Commission accepted the petition to change the status of the Mojave Desert Tortoise from threatened to endangered (Cal. Reg. Notice Register 2020, No. 44-Z, p. 1445). As a result, the Department was directed to complete this Status Review, which is a detailed evaluation of the current status of the tortoise and includes its recommendation regarding whether the tortoise's status should be changed from threatened to endangered.

This Status Review is based on the best scientific information currently available to the Department regarding each of the components listed under section 2072.3 of the Fish and Game Code, and section 670.1 of Title 14 of the California Code of Regulations. In addition, this Status Review includes a preliminary identification of habitat that may be essential to the continued existence of the species, and the Department's recommendations for management activities and other recommendations for recovery of the species. (Fish & G. Code, § 2074.6.). This Status Review has been independently reviewed by scientific peers pursuant to Fish and Game Code section 2074.6.

Species Description, Biology, and Ecology

In 2011, studies of tortoise genetics, morphometrics, and ecology led experts to conclude that the complex formerly known as "Desert Tortoise" in fact consists of two separate species—Mojave Desert Tortoise and Sonoran Desert Tortoise. Mojave Desert Tortoise, also known as Agassiz's Desert Tortoise, retains the binomial *G. agassizii*, and ranges across the deserts of southeastern California, southern Nevada, and small areas of Arizona and Utah north of the Colorado River.

The Mojave Desert Tortoise is a long-lived, desert-dwelling reptile. Tortoise body temperature is closely linked to the temperature in the environment, and Mojave Desert Tortoises live in places that can fluctuate up to 40°C (104°F) seasonally. They primarily regulate their temperature by using underground burrows where the air is cooler and moister than the outside air in summer and warmer in winter and can spend more than 90% of their lives underground.

Females become sexually mature at 12–20 years old and lay a maximum of 30 eggs per year and nest in a den or burrow or under trees. Nest predation is common, with 12–55% of nests generally destroyed by predators. Reported incubation time in the wild varies from 67–104 days and incubation temperatures determine the sex of the hatchlings, with hotter temperatures producing female-skewed clutches.

Tortoises selectively feed on forbs, grasses, and herbaceous perennial plants and will consume cacti during droughts. They favor native plants and plant parts that are high in water and low in potassium. Much of the range of the desert tortoise is highly invaded by nonnative plants like red brome, cheat grass, red stem filaree, and African mustard, but tortoises avoid eating exotic grasses when possible as they are low in nitrogen and require relatively large amounts of water to process.

Desert tortoise habitat typically consists of alluvial fans and plains and colluvial/bedrock slopes that facilitate the digging of burrows. Tortoises need sufficient food plants as well as larger shrubs and bushes for shade and protection of burrows. They are associated with saltbush, creosote bush, white bur-sage, and cheesebush. At higher elevations, tortoises are more likely to be found near Joshua tree, Mojave yucca, and blackbrush. Tortoises occur in very low densities or are absent where shrub cover is sparse, precipitation is low, and annual food plants are available only intermittently (e.g., the lower elevations in Death Valley). They also occur at low densities in moderately to severely disturbed areas, regardless of desert or region.

Ravens are a major predator of juvenile tortoises while coyotes target both juvenile and adult tortoises. Raven populations have expanded dramatically in the desert due to resource subsidies from humans.

Status and Trends

In California, the range of the Mojave Desert Tortoise includes the Mojave Desert and portions of the Sonoran and Great Basin deserts from the southern end of the Owens Valley south of the town of Lone Pine in Inyo County to the Mexican border near the southeastern corner of the state, and from the Colorado River in the east to the lower slopes of the Sierra Nevada, Transverse, and Peninsular mountains in the west.

The most robust estimates of densities come from annual systematic surveys done in the Tortoise Conservation Areas (TCAs). These surveys began in 2004 and cover large areas of the best habitat for tortoises, including federally designated critical habitat. Most of the surveys provide consistent evidence that populations are declining at rapid rates. In 2004–2014, densities in the TCAs declined between 3.3% and 10.8% per year. These rates are unsustainable for most species, but especially for a long-lived and slow-reproducing species such as the desert tortoise. Sixty percent of the TCAs currently have densities below that which is necessary for population viability (3.9 adult tortoises/km^2), while another 30% are at the threshold. Only one

TCA currently has a tortoise density above what is needed for population viability. While we do not have estimates of density in all the TCAs prior to the desert tortoise being listed as threatened in 1989, densities in select TCAs varied between 35 and 90 adults/km^2 in the early 1980s, and between 35 and 70 adults/km^2 when they were listed. It is estimated that densities of adults in certain TCAs fell between 89% and 97% from the early 1980s to 2020–2021. Since the late 1970s, the number of juveniles detected on surveys has also fallen sharply, to the point that in recent surveys in the western Mojave Desert almost no juveniles were found. The population data available indicate that there were sharp drops in density before listing as threatened, and those losses have continued to the point where much of the best tortoise habitat no longer supports viable tortoise densities.

The slow maturation and low reproductive rates of tortoises means that if past and current management is successful at addressing threats and stemming the decline of tortoise populations, it would still take at least 25 years of positive population growth to reach the USFWS Recovery Criteria (U.S. Fish and Wildlife Service 2022*a*). For example, the USFWS 1994 Recovery Plan estimates that when adult survivorship is 98%, population growth would be less than 0.5% per year, and would take 140 years to double in size. Annual survival rates for both adults and juveniles are much lower than 98% in most areas, making population stability, let alone growth, unlikely. Collectively, the available data show that in the critical habitat units (which are assumed to be the best tortoise habitat), tortoise densities are low to very low, and despite 30 years of state and federal protection, tortoise populations continue to decline and do not show consistent signs of recovery.

Threats

The dramatic declines in Mojave Desert Tortoise populations are likely due to the extensive number and interconnected nature of the threats they face. The important threats fall in two categories, those that directly kill adults and juveniles, and those that cause longer-term changes to habitat availability and quality.

In long-lived species that are slow to reproduce, decreased survival has long lasting impacts on the population and can alter demographic patterns for decades. Increased numbers of predators including ravens and coyotes reduce the survival of juvenile and adult tortoises, respectively. Development within the tortoise range often creates roads that can lead to road-killed tortoises, and extensive networks of trails for off highway vehicles on public land increase the chance that tortoises will be run over in areas without paved roads. Well-designed fences and culverts can help prevent tortoises and other wildlife being killed by vehicles along major roads, but little fencing has been built since 2011.

Habitat modification and destruction reduces the amount of habitat that can support tortoises in the long-term. Although a large proportion of desert tortoise range is under federal control, renewable energy, housing, illegal cannabis, and other types of development reduce the amount of habitat available. The Department of Defense is a large landowner in desert tortoise range and frequently expands the areas that it uses for training, requiring translocation of hundreds of tortoises. Large scale tortoise translocations do not tend to have high survival rates.

Additional factors have direct and indirect impacts on tortoises and their habitat. Climate change, which is likely to cause hotter and periodically drier conditions in the desert tortoise range, will increase their physiological stress and change activity patterns. The nutritious native vegetation tortoises feed on are being outcompeted by nutritionally poor invasive grasses, which can lower tortoise survival rates. Fires fueled by invasive grasses decrease the amount of native vegetation available for tortoises to feed on and remove other important vegetation components of tortoise habitat.

Some threats appear to be declining since the species was listed. Upper respiratory tract diseases were a major concern when tortoises were listed as threatened. Encouragingly, the prevalence of diseased tortoises is lower than in previous decades, and it does not appear to be an acute threat to wild populations. The prevalence of gunshot deaths has also decreased in the past several decades, but it is unclear if this is due to change in human behavior or simply reflects a lower tortoise encounter rate due to declining tortoise density.

Historical and current conservation efforts have not proven sufficient to halt the population declines of desert tortoise. However, there is still a large amount of available habitat and even at low densities, in 2014 there were estimated to be more than 61,000 adult tortoises within the TCAs. This is a decrease from an estimated 310,000 adults in 2004, and as densities have continued to fall since 2014, current abundance is likely lower than 60,000 adult tortoises. Given that there are multiple interacting threats that are reducing the amount and quality of viable habitat and lowering survival rates of adults and juveniles, the available information suggests that tortoises populations will continue to decline for the foreseeable future. However, several of the major threats like raven predation on juveniles and the lack of tortoise exclusion fencing on highways are issues that can be addressed with the appropriate resources and policy changes. Implementing these actions where appropriate to improve survival in the short term is critical to give desert tortoises populations the resilience to weather longer term habitat and climactic effects.

Several recommended management actions are described in this report. Improved coordination and communication between the Department and other state and federal agencies would help the implementation of these actions. We also point to several needs for increasing capacity at the Department to better track the impact of threats and conservation actions on tortoise populations.

Recommendation—The Department provides this status review report, including its recommendation, to the Commission in an advisory capacity based on the best scientific information available. In consideration of the scientific information contained herein, the Department has determined that listing the Mojave Desert Tortoise as endangered under CESA is warranted at this time.

1. REGULATORY SETTING

1.1 Petition Evaluation Process

On March 23, 2020, the Commission received a Petition from Defenders of Wildlife, The Desert Tortoise Council, and The Desert Tortoise Preserve Committee to change the status of Mojave Desert Tortoise from threatened to endangered. On April 13, 2020, the Commission referred the Petition to the Department for evaluation pursuant to Fish and Game Code section 2073 and published a formal notice of receipt of the petition (Cal. Reg. Notice Register 2020, No. 18-Z, p. 693). At its meeting on April 16, 2020, the Commission officially received the Petition.

A petition to list, delist, or change the status of a species under CESA must include “information regarding the population trend, range, distribution, abundance, and life history of a species, the factors affecting the ability of the population to survive and reproduce, the degree and immediacy of the threat, the impact of existing management efforts, suggestions for future management, and the availability and sources of information. The petition shall also include information regarding the kind of habitat necessary for species survival, a detailed distribution map, and any other factors that the petitioner deems relevant” (Fish & G. Code, § 2072.3).

The Department’s charge and focus in its advisory capacity to the Commission is scientific, and it evaluates petitions based on the best scientific information available regarding potential listing factors including those listed above. At its meeting on August 20, 2020, the Commission received the Department’s petition evaluation report, which is intended to assist the Commission in making a determination as to whether the petitioned action may be warranted based on the sufficiency of scientific information (Fish & G. Code, §§ 2073.5 & 2074.2; Cal. Code Regs., tit. 14, § 670.1, subds. (d) & I). Focusing on the information available to the Department relating to each of the required information categories listed above, the Department recommended to the Commission that the petition be accepted.

At its public meeting on October 14, 2020, the Commission considered the petition, the Department’s petition evaluation and recommendation, and comments received. The Commission found that sufficient information existed to indicate the petitioned action may be warranted and accepted the petition for consideration. Upon publication of the Commission’s notice of its findings, the Mojave Desert Tortoise was designated a candidate species on October 19, 2020 (Cal. Reg. Notice Register 2020, No. 44-Z, p. 1445).

1.2 Status Review Overview

The Commission’s decision to designate the Mojave Desert Tortoise as a candidate species triggered the Department’s process for conducting a 12-month status review to inform the Commission’s decision on whether the change in status is warranted (Fish & G. Code, § 2074.6 and Cal. Code of Regs., title 14, § 670.1). At its meeting on October 14, 2021, the Commission granted the Department a six-month extension to complete the status review and facilitate external peer review.

This status review report is not intended to be an exhaustive review of all published scientific literature relevant to the Mojave Desert Tortoise. Rather, it is intended to summarize the best scientific information available relevant to the status of the species, provide that information to the Commission, and to serve as the basis for the Department's recommendation to the Commission on whether the petitioned action is warranted. This final report is informed by independent peer review of an earlier draft by scientists with expertise relevant to the Mojave Desert Tortoise. Specifically, this status review represents the Department's evaluation of whether the status of the tortoise should be changed from threatened to endangered. Species that are "threatened" are not presently threatened with extinction but are likely to become endangered in the foreseeable future without special protection and management. An "endangered" species is one that is in serious danger of becoming extinct throughout all or a significant portion of its range due to one or more of the following factors: present or threatened modification or destruction of its habitat; overexploitation; predation; competition; disease; or other natural occurrences or human-related activities. (Fish & G. Code, § 2062; § 2067; Cal. Code Regs., tit. 14, § 670.1, subd. (i)(1)(A).)). The status review report also identifies habitat that may be essential to the continued existence of the species and provides management recommendations for recovery of the species (Fish & G. Code, § 2074.6).

Receipt of this report is to be placed on the agenda for the next available meeting of the Commission after delivery. At that time, the report will be made available to the public for a 30-day public comment period prior to the Commission taking any action on the petition.

2. BIOLOGY

2.1 Taxonomy

Desert tortoises are members of the order Testudines, family Testudinidae, genus *Gopherus*. When the Commission listed Desert Tortoise as threatened in 1989, *Gopherus agassizii* was understood to range from southeastern California, across southern Nevada, through western Arizona, and south into Sonora and Sinaloa, Mexico. In 2011, studies of tortoise genetics, morphometrics, and ecology led experts to conclude that the complex formerly known as "Desert Tortoise" in fact consists of two separate species, Mojave Desert Tortoise and Sonoran Desert Tortoise (Murphy et al. 2011, Iverson et al. 2017). Mojave Desert Tortoise, also known as Agassiz's Desert Tortoise or Mohave Desert Tortoise, retains the binomial *G. agassizii*, and ranges across the deserts of southeastern California, southern Nevada, and small areas of Arizona and Utah north of the Colorado River. Desert tortoises east of the Colorado River in Arizona and northern Mexico are now classified as Sonoran Desert Tortoise, also known as Morafka's Desert Tortoise (*Gopherus morafkai*). Only the Mojave Desert Tortoise occurs in California. This status review uses the common name Mojave Desert Tortoise when referring to *G. agassizii* as the species is currently understood. Any reference to Agassiz's or Mohave Desert Tortoise in this document should be considered synonymous with Mojave Desert Tortoise.

2.2 Species Description and Life History

Much of the information in this section is summarized from a Berry and Murphy (2019) monograph on *Gopherus agassizii*. The Mojave Desert Tortoise is a long-lived, desert-dwelling reptile. The upper shell or carapace of adults ranges in size from 178mm to over 370mm in length. Shell color varies from light yellow to dark charcoal in hatchling tortoises and from light to dark brown in adults (Berry and Murphy 2019). The largest measured wild individual was a female in 1986 whose carapace length was 374 mm. The largest male measured in the wild was 330 mm carapace length (Berry and Murphy 2019).

Figure 1. Mojave Desert Tortoise. Pictures by Dana Wilson BLM (left) and Roy Averill-Murray USFWS (right).

Desert tortoises make extensive use of underground burrows to regulate body temperature and as protection from predators. Temperatures in burrows can be up to 20°C (36°F) cooler than summer air temperatures, especially very deep in the burrows (Berry and Murphy 2019). Home range size depends on sex, age, and environmental conditions. Over a 2-year study in the western Mojave Desert, male home range size was 39–47 ha and female home range size was 14–17 ha (Harless et al. 2009). Home ranges of juveniles tend to be smaller, and home ranges are larger during wet years than in dry years. Home ranges of individuals can overlap (O'Connor et al. 1994) and in the western Mojave Desert Harless et al. (2009) found that males overlap more with other tortoises than do females. They also found that the overlap in area in an individual's home range from one year to the next was ~35% and did not vary significantly by sex. Individuals tend to have fidelity to home ranges and activity centers, even after fire (Drake et al. 2015, Lovich et al. 2018).

Tortoises are long-lived and females are thought to become sexually mature at 12–20 years old, depending on locality (Woodbury and Hardy 1948, Turner et al. 1986, Curtin et al. 2009). Generation time is estimated to be around 25 years (U.S. Fish and Wildlife Service 1994). Mating occurs in late summer and fall, and females can mate with multiple males (Davy et al. 2011). Female tortoises can store sperm/delay implantation so that nesting and egg laying occurs in April–July depending on the region (Berry and Murphy 2019). Females lay 0–3 clutches in the spring and the number of eggs laid per clutch ranges from 1–10. Females nest in a den or burrow under large shrubs. There are anecdotal reports of females nest guarding against humans and Gila Monsters, but there is no parental care once eggs have hatched (Berry and Murphy 2019). Reported incubation time in the wild varies from 67–104 days (McLuckie and Fridell 2002) and incubation temperatures determine the sex of the hatchlings. Sex ratios were 1:1 at an incubation temperature of 31.3°C (88.3°F), while eggs incubated at under 30°C (86°F) produced only male hatchlings and only females hatched from eggs incubated over 32.5° (90.5°F) (Rostal et al. 2002). Nest predation is common, with 12–55% of nests generally destroyed by predators (Berry and Murphy 2019). When nests are not predated, hatchling success is about 80% (Bjurlin and Bissonette 2004). Newly hatched tortoises are about 4–5 cm in length (Bjurlin and Bissonette 2004) and their shells do not fully ossify until they are 5–7 years old. At that age they become less vulnerable to predators. For more information about predation, see section 4.4.

Tortoises selectively feed on annual and perennial forbs, grasses, and will consume cacti during droughts (Berry and Murphy 2019). Tortoises favor native plants and plant parts that are high in water and low in potassium (Oftedal et al. 2002). Potassium is potentially toxic and requires a large amount of water and nitrogen to excrete. Much of the range of the desert tortoise is highly invaded by nonnative plants like red brome, cheat grass, red stem filaree, and African mustard, but tortoises avoid eating exotic grasses when possible as they are low in nitrogen and require relatively large amounts of water to process. Experimental studies found that grass diets that included no forbs were detrimental to tortoises, leading to weight loss, poor body condition, or even death (Hazard et al. 2009, Drake et al. 2016). This was the case even when the diet included native grasses (Drake et al. 2016). According to Berry & Murphy (2019), tortoises "favored species of forbs or herbaceous perennials from several plant families: Asteraceae, Boraginaceae, Cactaceae, Fabaceae, Malvaceae, Nyctaginaceae, Onagraceae, and Plantaginaceae (Burge and Bradley 1976; Avery and Neibergs 1997; Jennings and Berry 2015)."

Tortoises are ectotherms whose body temperature is closely linked to the temperature in the environment around them. Mojave Desert Tortoises live in places that can fluctuate up to 40°C (104°F) seasonally and they primarily regulate their temperature by using underground burrows where the air is cooler and moister than the outside air in summer and warmer in winter. Depending on the type, length, and depth of burrow, average temperatures inside vary from 33.7–36.6°C (92.6–97.8°F) in the summer and 8.9–13.5°C (48–56.3°F) in the winter (Mack et al. 2015). Berry and Murphy (2019) report that desert tortoises spend >90% of their lives underground. Tortoises are active when their body temperatures are between 19.0°C and 37.8°C (66.2–100°F), they retreat to shade when body temperatures are 37–38°C (98.6–100.4°F), and body temperatures of 43°C (109.4°F) are deadly (Brattstrom 1965). However, tortoises can be active above ground at any time of year, especially if it has rained and they can drink, or if they need to move between shelters. They generally are underground or in rock shelters in late fall and winter, and in late spring through the hot summer. In early spring and fall they are more active above ground, feeding, travelling, and interacting with other tortoises (Berry and Murphy 2019). On a given day, air temperature determines when the tortoises are active above ground. In the cooler late winter and spring, they are active late morning to mid-afternoon. In the hotter summer and fall, if activity occurs, it tends to be in the cool of the morning and late evening. Smaller juvenile tortoises can be active at cooler temperatures than larger tortoises so tend to be active more days per year (Berry and Murphy 2019). Available water and forage have a strong impact on activity and movement. Tortoises had lower metabolic rates, moved less, used fewer burrows, and had smaller home ranges during drought years.

Tortoises also have additional behavioral and physiological strategies to deal with extremes of temperature and resource availability. During droughts, tortoises can lose up to 40% of their body mass. They can resorb water from their bladders and store sodium, chloride, and urea in their blood and in the bladder. When it rains, they drink, void their bladders, and rapidly increase their body weight (Peterson 1996, Berry and Murphy 2019).

2.3 Habitat Associations

Figure 2. Mojave Desert Tortoise in the Mojave Desert. Photo by Rachel London via USFWS

Mojave Desert Tortoises in California can be found in part of the southern Great Basin, Mojave, and western Sonoran deserts in southeastern California (Berry and Murphy 2019). Due to their dependence on burrows, they require soils, topography, geological features, and vegetation that facilitate the creation of burrows or dens (Andersen et al. 2000). Therefore, desert tortoise habitat typically consists of alluvial fans and plains and colluvial/bedrock slopes (Nussear et al. 2012). Tortoises also need appropriate vegetation communities for forage and shelter. Most burrows are found beneath shrubs, though they can also be dug into the sides of ephemeral streams.

The vegetation types that tortoises use varies across their range and by altitude. As Berry and Murphy (2019) put it:

> "Within the Mojave Desert ecosystem, tortoises occur in several vegetation associations. At lower elevations or adjacent to dry lake beds, saltbush associations (*Atriplex* spp.) and other members of the Chenopodiaceae provide habitat. The most common associations contain creosote bush (*Larrea tridentata*), usually with white bur-sage (*Ambrosia dumosa*) or cheesebush (*A. salsola*) and several other species of shrubs, cacti, and perennial grasses. With increasing elevation, multiple species of woody shrubs and tree yuccas (Joshua tree, *Yucca brevifolia,* and Mojave yucca, *Y. schidigera*) become more common, with blackbrush (*Coleogyne ramosissima*) associations present in higher elevations.
>
> The western Sonoran Desert is a warmer, hotter desert with a higher proportion of precipitation occurring in summer. This desert is also characterized by creosote bushes, but a major difference is the presence of microphyll woodlands of blue palo verde (*Parkinsonia florida*), smoke tree (*Psorothamnus spinosus*), and ironwood (*Olneya tesota*) in ephemeral stream channels separated by desert pavements or open desert with ocotillo (*Fouqueria splendens*) mixed with creosote bush, other shrubs, and cacti (Berry 1984).
>
> Tortoises occur in very low densities or are absent where shrub cover is sparse, precipitation is low and timing erratic, and annual food plants are available only intermittently (e.g., the lower elevations in Death Valley). They are also in low densities in moderately to severely disturbed areas, regardless of desert or region (e.g., Bury and Luckenbach 2002; Keith et al. 2008; Berry et al. 2013)."

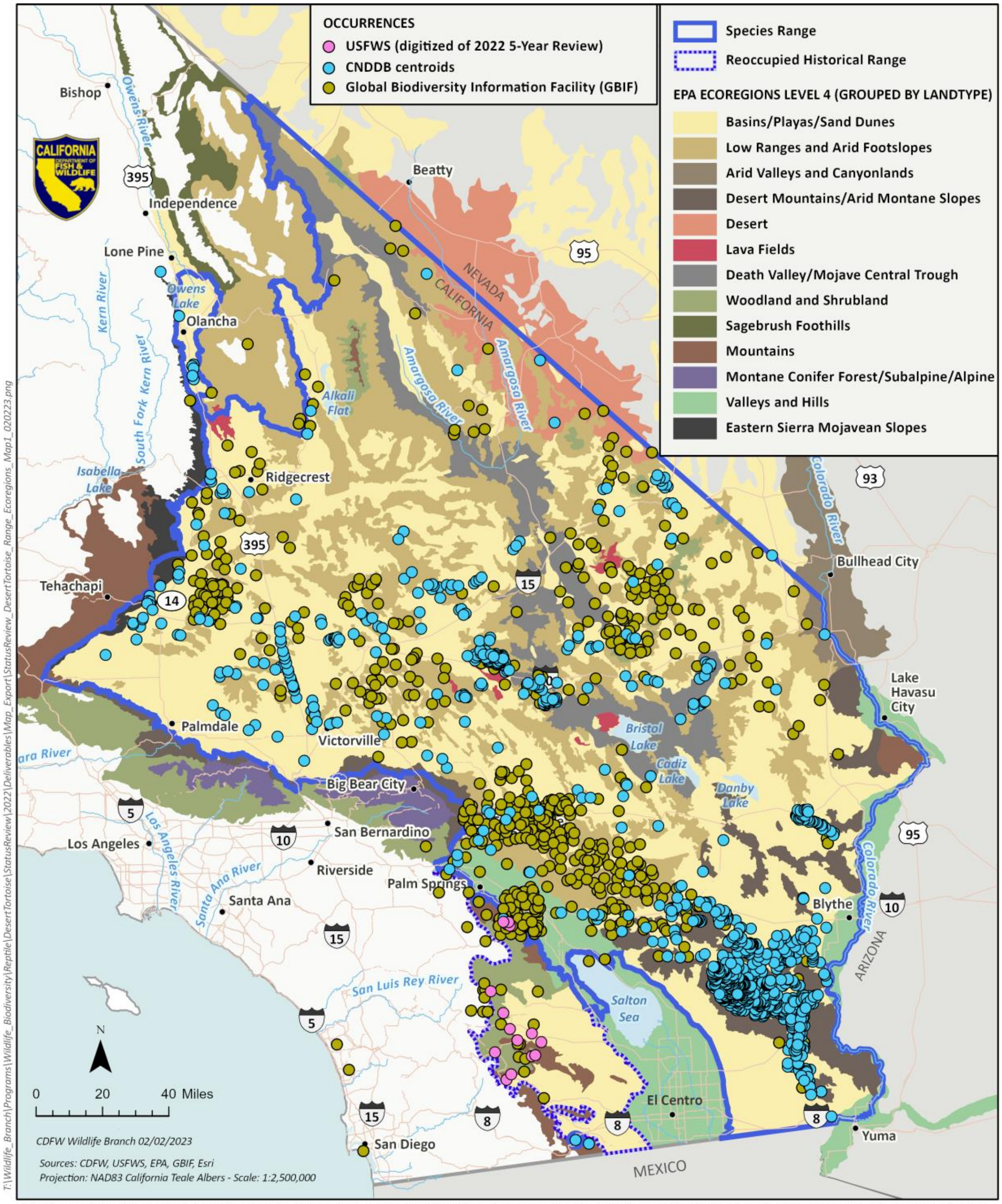
2.4 Range and Distribution

Range is the general geographical area in which a species occurs. For purposes of CESA and this status review, we are describing and evaluating the tortoise's range in California. Distribution describes the sites where individuals and populations of the species occur, and the spatial arrangement of individuals within the species' range.

In California, the range of the Mojave Desert Tortoise includes the Mojave Desert and portions of the Sonoran and Great Basin Deserts from the southern end of the Owens Valley south of the town of Lone Pine in Inyo County to the Mexican border near the southeastern corner of the state, and from the Colorado River in the east to the lower slopes of the Sierra Nevada, Transverse, and Peninsular mountains in the west (Berry and Murphy 2019).

The range of tortoises has also been dynamic due to the release of captive tortoises and potential immigration into areas from which they were previously extirpated. For example, tortoises were largely extirpated from the area of Anza Borrego Desert State Park by the 1940s (Manning 2018). In the early 1970s taking tortoises from the wild became illegal, and people began turning in their captive tortoises to the Department. Between 1970 and 1972 the Department released about 65 previously captive tortoises into the park. There were occasional sightings in the decades since, with more sightings since 2010. The tortoises there today could be descendants of released tortoises, however natural immigration to the park is possible as there is a tenuous corridor of suitable habitat that connects the park to habitat occupied by tortoises to the north. In 2016, park staff began surveying for tortoise and formally collecting incidental observation data, and subsequent genetic analysis of tortoise blood and scat suggested "evidence of a naturally reproducing Mojave Desert Tortoise population in Anza Borrego Desert State Park" (Manning 2018). These tortoises extend "the distribution of reproducing Mojave Desert Tortoises greater than 60 km south of Palm Springs and beyond the southern edge of the Colorado Desert Recovery Unit boundary depicted in the recovery plan (Service 2011a)" (U.S. Fish and Wildlife Service 2022*a*). We show this reoccupation of historical range in Figure 3, delineated using suitable ecoregion boundaries.

The distribution of desert tortoises within the California range is uneven, and portions of the range no longer provide suitable tortoise habitat due to agriculture, development, and military activity. Data on tortoise occurrences from the California Natural Diversity Database (CNDDB) and the Global Biodiversity Information Facility (GBIF) were used to plot distribution of observations in California (Figure 3). These datasets do not represent exhaustive and comprehensive inventories of desert tortoises in California and are largely presence-only datasets. While caution should be used in using these types of data, there appear to be fewer occurrences in the northern part of the range and in the Death Valley Mojave Central Trough (see grey area on Figure 3).



Disclaimer: Information presented on this map is for visual reference only. Consult primary data sources to ascertain the usability of this information for any use other than visual reference.

Figure 3. Map of the California range of the Mojave Desert Tortoise, occurrence locations, and Ecoregions. CNDDB data are sightings from 1935 to 2011. The GBIF occurrences are sightings that are confirmed by a picture from 1978 to 2022. The pink dots are the locations of tortoises in the reoccupied historical range as reported in U.S. Fish and Wildlife Service (2022a). Range boundary is from the California Wildlife Habitat Relationship System (California Department of Fish and Wildlife 2014).

2.5 Population Genetic Structure

For imperiled species, understanding the populations' genetic structuring is important for effective management. Head-starting and translocation are two actions used in desert tortoise conservation (see section 9.1 for more details), and the efficacy of both depends on knowledge of genetic boundaries to avoid the potentially negative impacts of artificially mixing individuals from different genetic populations (Sánchez-Ramírez et al. 2018).

The 1994 U.S. Fish and Wildlife Service (USFWS) Recovery Plan outlined recovery units consisting of "evolutionarily distinct" populations, with three recovery units occurring in California: Western Mojave, Eastern Mojave, and Colorado Desert Recovery Units (see section 3.1 for details). However, a recent study found that the best supported number of genetic clusters in California was five, with the Western Mojave Recovery Unit which encompasses much of the northern and western part of tortoise range in California, consisting of three genetic groups (Sánchez-Ramírez et al. 2018) (Figure 4). This differs from the earlier work of Hagerty and Tracy (2010) which found the Western Mojave Recovery Unit to be one genetic group. This means that populations within 200–300 km of each other which were previously considered genetically correlated and a single genetic unit for management purposes may actually be several genetically identifiable populations. Outbreeding depression has not been studied in *G. agassizii*, and the impacts of moving tortoises between genetic units are unknown, but Sánchez-Ramírez et al. (2018) advise caution when moving tortoises long distances for translocation or population augmentation. For more detail about translocations see section 9.1.

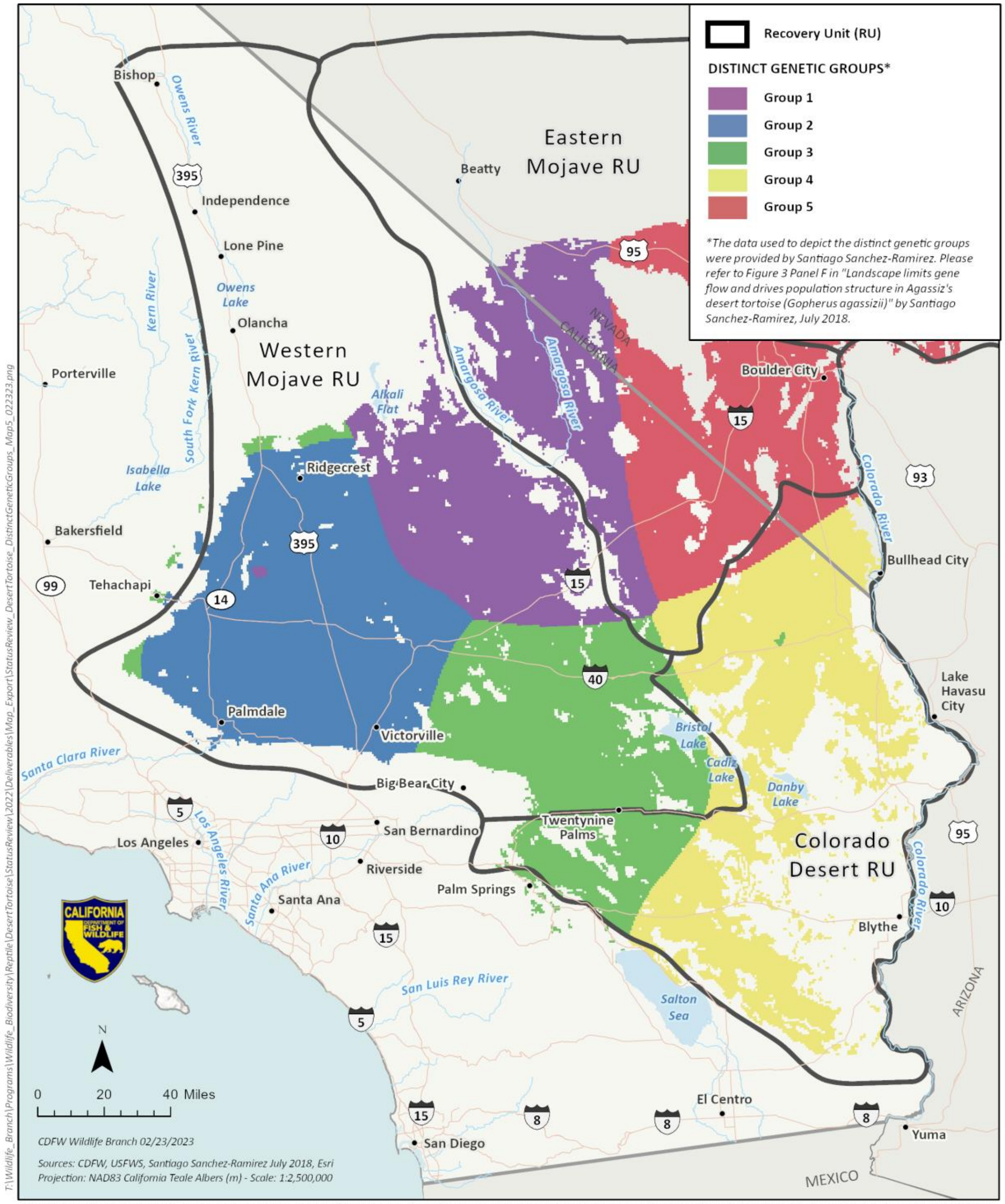
3. STATUS AND POPULATION TRENDS IN CALIFORNIA

3.1 Administrative Status

The Mojave Desert Tortoise has been protected as a threatened species under the California Endangered Species Act (CESA) (Title 14, §670.5) since 1989 and under the federal Endangered Species Act (ESA) since 1990. Unauthorized "take" of threatened and endangered species is prohibited. "Take" is defined under CESA as hunt, pursue, catch, capture, or kill, or attempt to hunt, pursue, catch, capture, or kill (*Id.*, § 86).

The 1994 USFWS Desert Tortoise Recovery Plan designated six federal recovery units that cover desert tortoise range in California, Arizona, Nevada, and Utah. The recovery units were based on genetics, morphology, behavior, ecology, and habitat use, and each was considered an "evolutionarily distinct" population. These recovery units were revised in the 2011 Recovery Plan with better information and mapping tools. Of the six, all the Western Mojave, the majority of the Colorado Desert, and the western portion of the Eastern Mojave (formerly the Northeastern Mojave) Recovery Units are within California (Figure 4).

The Western Mojave Recovery Unit is differentiated from the other recovery units by rainfall and vegetation (U.S. Fish and Wildlife Service 2011). Summers are warm and winters are cold, with most rainfall occurring in fall and winter. Tortoises in the Western Mojave Recovery Unit dig deep burrows (usually located under shrubs on bajadas) for winter hibernation and summer



Disclaimer: Information presented on this map is for visual reference only. Consult primary data sources to ascertain the usability of this information for any use other than visual reference.

Figure 4. Map of genetic groups of the Mojave Desert Tortoise. Superimposition of the boundaries of the Recovery Units over Figure 3 panel F in Sánchez-Ramírez et al. (2018). The base map is the "spatial interpolation of ancestry coefficients of Agassiz's desert tortoises using Krig modeling…combines areas of maximal ancestry proportion for each of the five genetic groups"

estivation. Above-ground activity occurs primarily in spring when winter annuals provide food (U.S. Fish and Wildlife Service 2011).

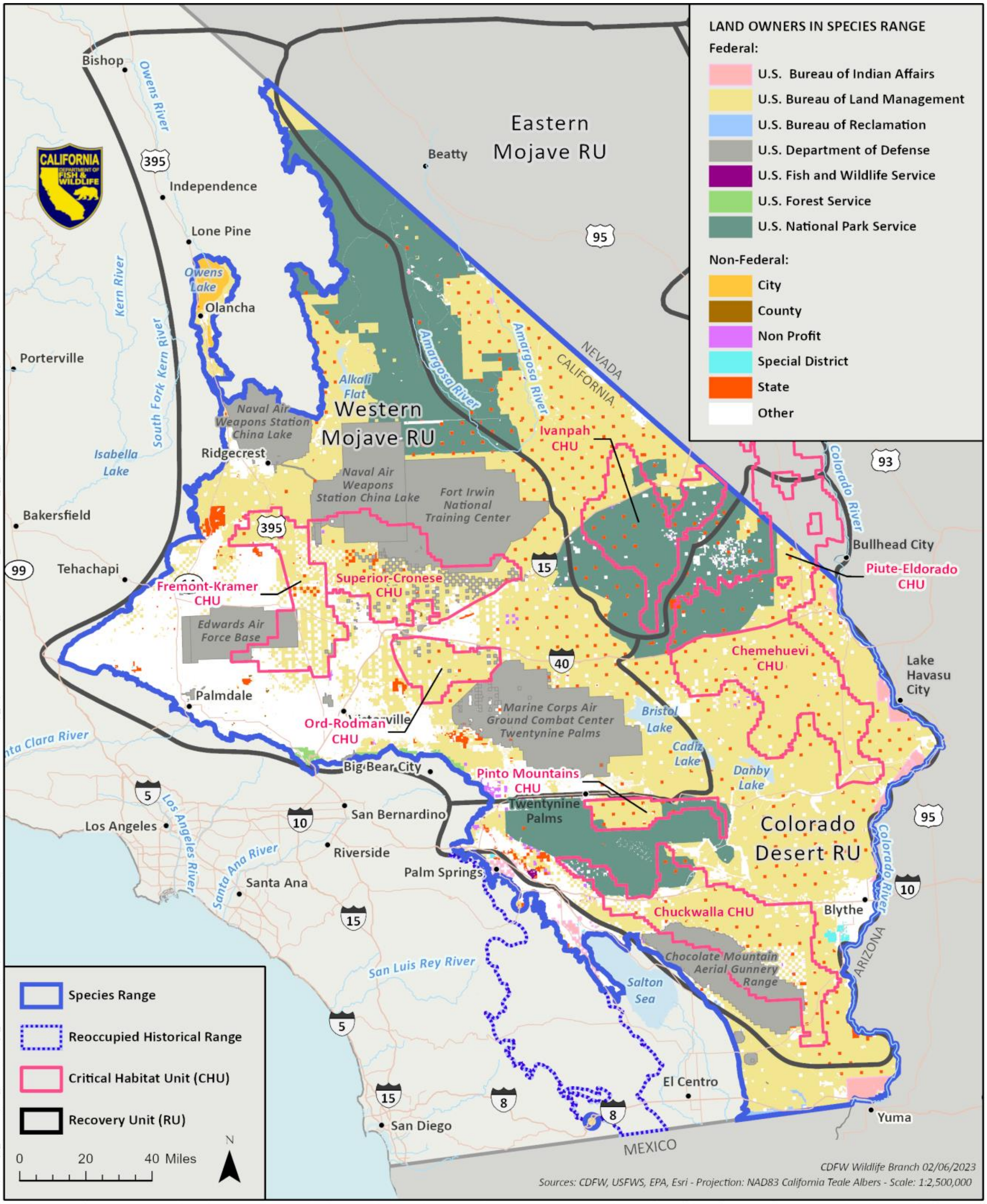
The Colorado Desert Recovery Unit receives about 1/3 of its annual rainfall in summer and supports distinct summer and winter annual plants that tortoises feed on. The climate is somewhat warmer than in other recovery units, with very few freezing days per year. Tortoises are found in the valleys, on bajadas, desert pavements, rocky slopes, and in the broad, well-developed washes (U.S. Fish and Wildlife Service 2011).

The Eastern Mojave Recovery Unit is separated from the Western Mojave Recovery Unit by an inhospitable barrier created by the Saline Valley, Death Valley, and Silurian Valley. Desert tortoises in the Eastern Mojave Recovery Unit are generally found in creosote bush scrub communities of flats, valley bottoms, alluvial fans, and bajadas. They are often active in spring, late summer, and early fall, as this region receives up to about 40% of its annual rainfall in summer and there are two distinct annual floras on which tortoises can feed (U.S. Fish and Wildlife Service 2011).

Each recovery unit contains one or more Critical Habitat Units (CHUs). Under section 3 of the ESA, the Department of the Interior is directed to designate the specific areas supporting those physical and biological features that are essential for the conservation of the species. The Department of Interior designated critical habitat areas for the Mojave Desert Tortoise in early 1994 (59 FR 5820) that encompass over 24,281 km^2 in the Mojave and Colorado deserts (U.S. Fish and Wildlife Service 2011). The critical habitat units are administrative areas managed to give reserve-level protection to desert tortoise populations while maintaining and protecting other sensitive species and ecosystem functions (U. S. Fish and Wildlife Service 1994). According to USFWS (2019a):

> "The specific physical and biological features of desert tortoise critical habitat are (1) sufficient space to support viable populations within each of the six recovery units and to provide for movement, dispersal, and gene flow; sufficient quality and quantity of forage species and the proper soil conditions to provide for the growth of these species; (2) suitable substrates for burrowing, nesting, and overwintering; (3) burrows, caliche caves, and other shelter sites; (4) sufficient vegetation for shelter from temperature extremes and predators; and (5) habitat protected from disturbance and human-caused mortality."

In California, federal critical habitat designation totals 19,239 km^2. Of this, 13,465 km^2 are Bureau of Land Management (BLM) land, 980 km^2 are military land, 538 km^2 are state land, and 4,255 km^2 are private land (U. S. Fish and Wildlife Service 1994) (Figure 5).



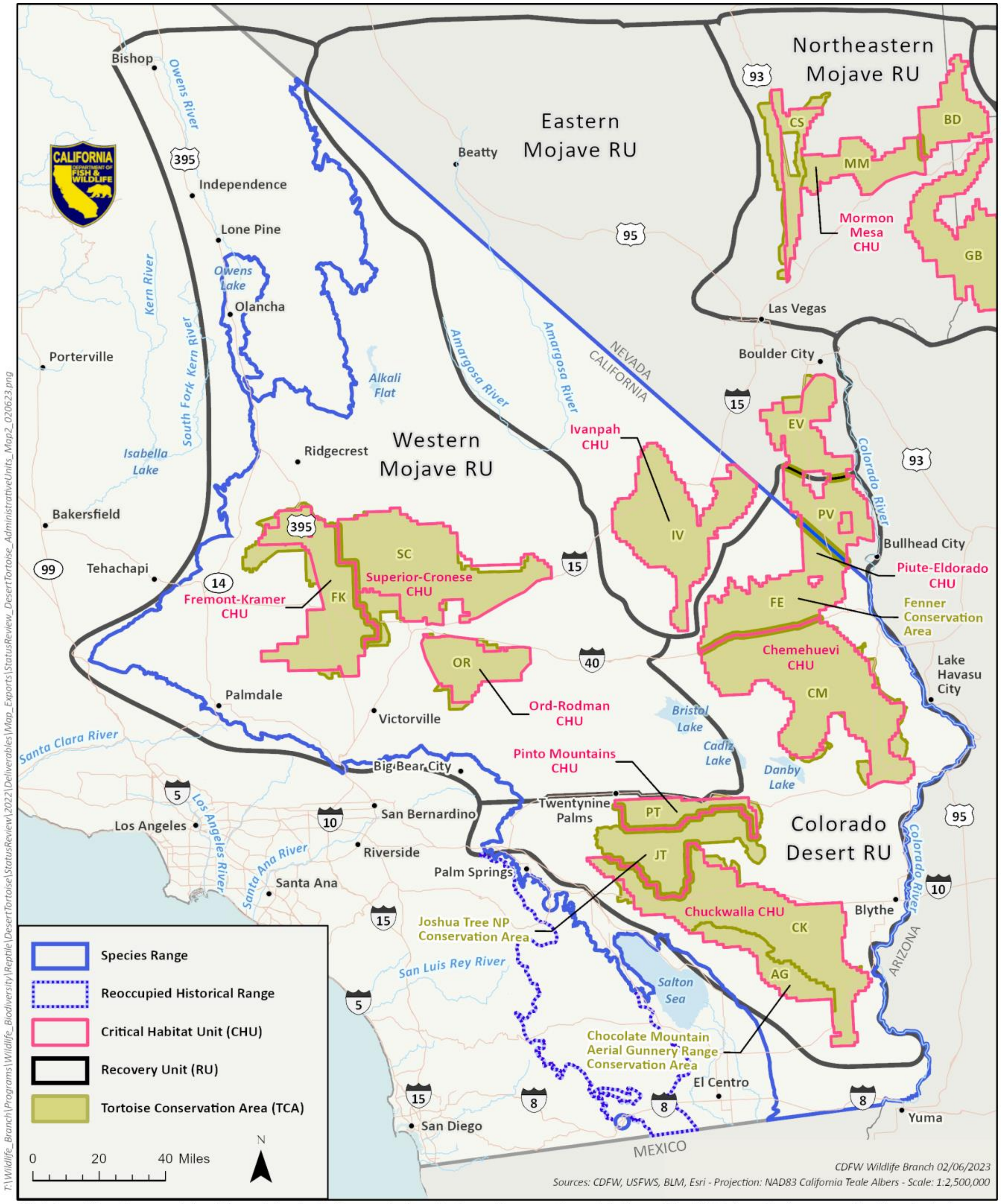
Disclaimer: Information presented on this map is for visual reference only. Consult primary data sources to ascertain the usability of this information for any use other than visual reference.

Figure 5. Landownership, RUs, and CHUs in the Mojave Desert Tortoise range in California.

Tortoise Conservation Areas (TCAs) are areas that mostly align with CHUs that the USFWS has designated for surveys to evaluate tortoise population status and recovery (see Figures 5, 6 and Table 1). They include “designated critical habitat as well as contiguous areas with potential tortoise habitat and compatible management” (U.S. Fish and Wildlife Service 2019*b*). The TCAs have the same name as the CHU they encompass, with a few exceptions where there are multiple TCAs within a CHU (Allison 2015), and Joshua Tree TCA which is not within a CHU. See Figure 6 for boundaries of CHUs and TCAs, and Table 1 for overall size and amount of habitat within the CHUs, and size of TCAs.

Table 1. Area of modeled desert tortoise habitat within California CHUs, and size of associated TCAs (U.S. Fish and Wildlife Service 2019a). Modeled habitat is suitable desert tortoise habitat per Nussear et al. (2009).

Recovery Unit	**Critical Habitat Unit**	**Area (km^2)**	**Modeled Habitat (km^2)**	**Tortoise Conservation Area**	**Area (km^2)**
Western Mojave	Fremont-Kramer	2,096	2,028	Fremont-Kramer	2,417
	Ord-Rodman	1,025	745	Ord-Rodman	1,124
	Superior-Cronese	3,104	2,934	Superior-Cronese	3,332
Eastern Mojave	Ivanpah	2,559	2,067	Ivanpah	2,567
Colorado Desert	Chuckwalla	4,130	3,275	Chuckwalla	3,509
	Chuckwalla			Chocolate Mountain Gunnery Range	755
	Chemehuevi	3,794	3,701	Chemehuevi	4,038
	Piute-El Dorado	3,928	3,764	Fenner	1,841
	Pinto Mountains	695	583	Pinto Mountains	751
				Joshua Tree	1,567



Disclaimer: Information presented on this map is for visual reference only. Consult primary data sources to ascertain the usability of this information for any use other than visual reference.

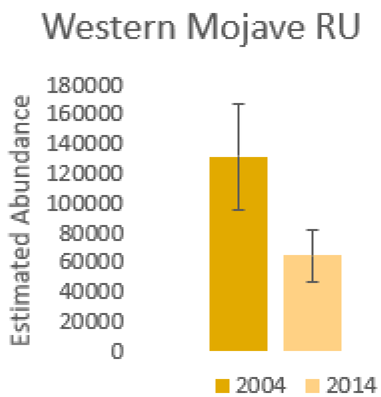
Figure 6. Mojave Desert Tortoise range, RUs, CHUs, and TCAs.

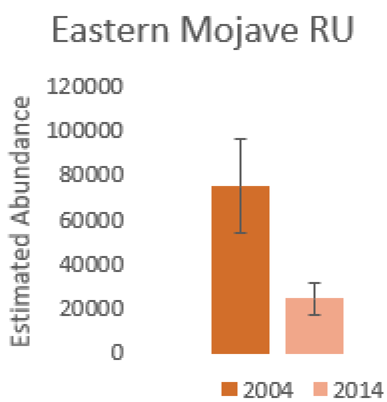
3.2 Trends in Density and Abundance

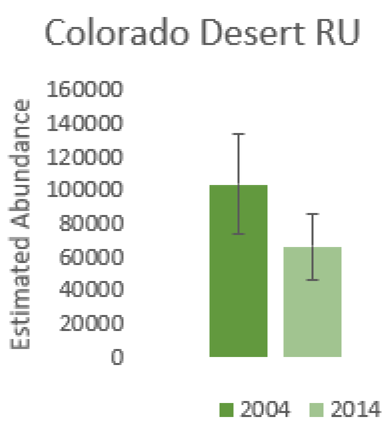
Tortoises are long lived, reach sexual maturity late, and have decades of reproductive life. These life history characteristics make it difficult to assess trends in tortoise populations. For such species, short- and medium-term studies (1–10 years) may not be long enough to adequately understand population trends (Tracy et al. 2004). Also, studies that cover only very small, localized portions of the tortoise's range have limited value in assessing the overall population status. This makes long-term studies with consistent methodology that cover large portions of the range in California key to understanding the extent to which tortoise populations are declining or recovering over time.

Since the species was listed as threatened under CESA in 1989, the most robust estimates of density over time come from long-term surveys of TCAs within each CHU using line distance sampling. Square transects with 3 km sides were set up to provide good coverage of each TCA, and a random selection of these transects are surveyed each year. Two surveyors walk line transects along the boundary of the square or as close to it as is feasible. They record the distance and bearing from the survey line to all tortoises seen and live tortoises are measured and sexed. In addition, data from tortoises carrying radio transmitters are used to estimate what portion of tortoises are above ground during the transects. Transects are scheduled in mid-March to May to maximize the chance tortoises will be active and above ground. Standard models are used to calculate density for the TCA from the line transect data in each sampling stratum. Funding for these efforts has varied, but in most years from 2001 to 2021 the USFWS has coordinated the distance sampling monitoring program for desert tortoises in the three recovery units that cover tortoise range in California (U.S. Fish and Wildlife Service 2015, 2019*b*, 2020*a*, 2022*b*, *c*). The years that each specific TCA was surveyed are presented in Table 2.

Despite the protections afforded though the federal ESA and CESA, tortoise populations have declined in recent decades. The 1994 USFWS Recovery Plan for desert tortoise identified 3.9 adult tortoises/km^2 as the minimum density necessary for population viability (U. S. Fish and Wildlife Service 1994, U.S. Fish and Wildlife Service 2011). Only one of the TCAs was below this threshold in 2004, but by 2014, 8 out of 10 were at or below it. Between 2004 and 2014, annual declines per year ranged from 3.3% in the Chocolate Mountain Gunnery Range to 10.8% in Chemehuevi (Allison and McLuckie 2018) (Figure 7). Joshua Tree was the only TCA in California where the population increased (6.2% annual rate of increase). However, Joshua Tree started with a very low estimated density of 1.9 tortoise/km^2 in 2004, most likely due to extended drought (Lovich et al. 2014, Allison and McLuckie 2018). These annual rates of decline are very high, and a species that reproduces as slowly as the desert tortoise will likely require a long time to recover from such losses.







Area	Annual Trend in Density 2004–2014
Fremont-Kramer TCA	-6.80%
Ord-Rodman TCA	-8.20%
Superior-Cronese TCA	-9.30%
Western Mojave RU	-7.10%
Ivanpah TCA	-7.40%
Eastern Mojave RU	-11.20%
Chocolate Mountain TCA	-3.30%
Chuckwalla TCA	-4.10%
Chemehuevi TCA	-10.80%
Fenner TCA	-7.30%
Joshua Tree TCA	6.20%
Pinto Mountains TCA	-8.30%
Colorado Desert RU	-4.50%

Figure 7. Estimated abundances (with standard errors) of adult Mojave Desert Tortoises (*Gopherus agassizii*) in 2004 and 2014 in the recovery units relevant to California (left). Estimated annual rates of change in density for recovery units and associated Tortoise Conservation Areas (right). Abundance estimates for recovery units are based on densities calculated from the model in Table 4 of Allison and McLuckie (2018) and applied to all areas of the associated recovery unit that meet criteria as modeled habitat. TCA annual trends in population are from U.S. Fish and Wildlife Service (2022a).

Allison and McLuckie (2018) estimated the abundance of desert tortoises in the three recovery units that fall within California in 2004 and 2014 from the density estimates in the TCAs (Figure 7). Abundance declined precipitously between 2004 and 2014 in the Western Mojave, Colorado Desert, and Eastern Mojave Recovery Units, with each of them losing between 35,000 and 65,000 adults. It should be noted that the Eastern Mojave and Colorado Desert Recovery Units each have one TCA outside of California so the abundance estimates are an over-estimate for California. Allison and McLuckie (2018) estimated that the Western Mojave Recovery Unit experienced a 51% decline in adults from 2004 to 2014.

Since 2014, densities have not declined as steeply as in the previous decade. Although no populations have reached pre-2014 highs, between 2015 and 2021, densities increased somewhat in Chemehuevi, Fenner, and Ivanpah. The declines continued in Chocolate Mountains, Ord-Rodman, Fremont-Kramer, and Superior-Cronese (U.S. Fish and Wildlife Service 2022*a*, *c*) (Figures 8 and 9, Table 2). The most recent surveys (2019–2021) show that in the Eastern and Western Mojave Recovery Units, all of the TCAs surveyed were below the 3.9 adult tortoises/km^2 threshold. In the Colorado Desert Recovery Unit, two were at the threshold, two were below it, and only one TCA (Fenner) was above (U.S. Fish and Wildlife Service 2022*a*) (Figures 8 and 9, Table 2). The declines in the TCAs occurred despite most of the land falling under federal land management agency ownership (Figure 5).

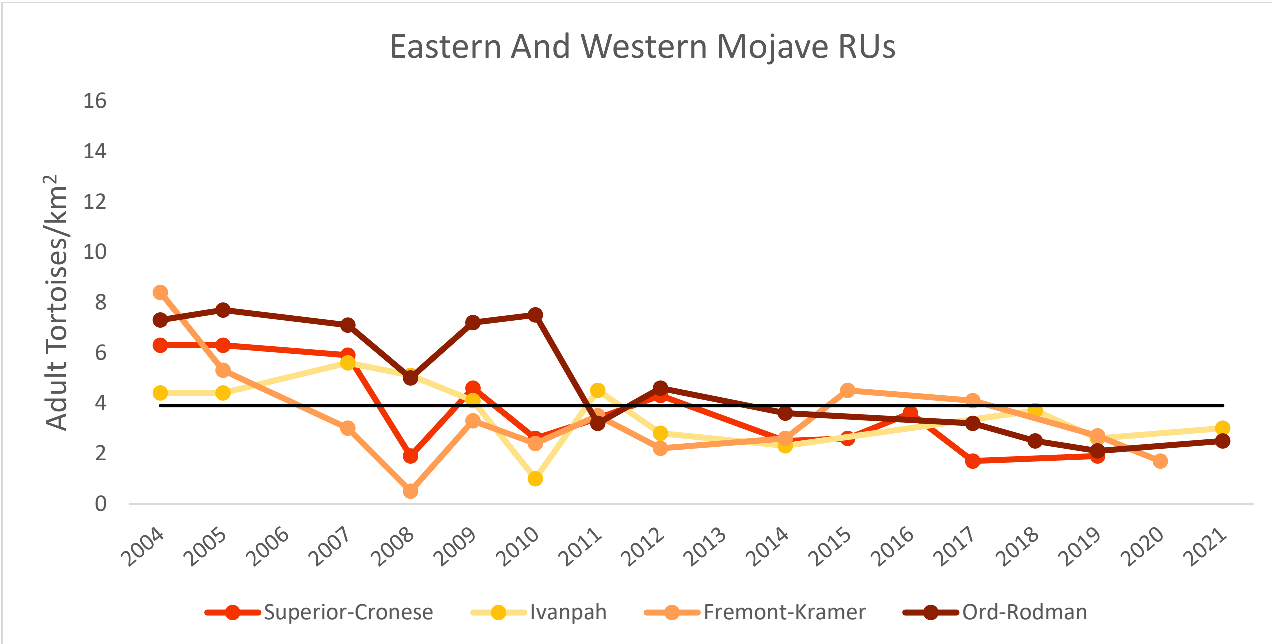


Figure 8. Estimated densities of adult tortoises (≥ 180 mm carapace length) in TCAs in the Eastern and Western Mojave RUs in California 2004–2021. Black horizontal line represents 3.9 adults/km^2, the estimated minimum density needed for population viability. For time series figures of individual TCAs including error bars, see Appendix A.

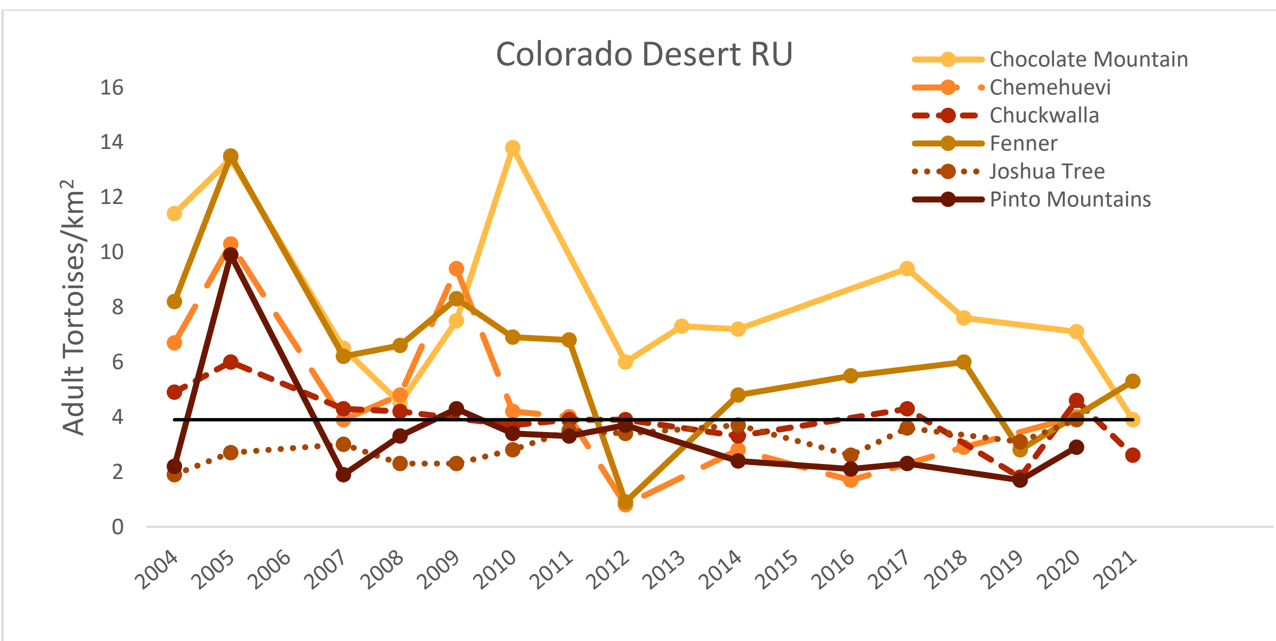


Figure 9. Estimated densities of adult tortoises (≥ 180 mm carapace length) in TCAs in Colorado Desert RU in California 2004–2021. Black horizontal line represents 3.9 adults/km^2, the estimated minimum density needed for population viability. For time series figures of individual TCAs including error bars, see Appendix A.

Table 2. Estimated densities of adult tortoises (≥ 180 mm carapace length) in Tortoise Conservation Areas in California. Estimates for 2004–2014 have standard errors (SE); estimates for 2015–2021 have coefficients of variation expressed as percentages. Data from (U.S. Fish and Wildlife Service 2015, 2016, 2018, 2019*b*, 2020*a*, 2022*c*, *b*, Allison and McLuckie 2018), and presented in Figures 8 and 9.

Estimated Density (number/km^2)

Recovery Unit	TCA	2004	2005	2007	2008	2009	2010	2011	2012	2013	2014	2015	2016	2017	2018	2019	2020	2021
Western Mojave	Fremont-Kramer	8.4 (2.31)	5.3 (1.28)	3.0 (1.46)	0.5 (0.51)	3.3 (1.13)	2.4 (0.60)	3.5 (1.11)	2.2 (1.07)		2.6 (0.3)	4.5 (28.0)		4.1 (22.01)		2.7 (24.0)	1.7 (27.6)	
	Ord-Rodman	7.3 (2.25)	7.7 (1.80)	7.1 (3.26)	5.0 (5.34)	7.2 (2.65)	7.5 (1.85)	3.2 (1.18)	4.6 (2.14)		3.6 (0.4)			3.9* (19.84)	3.4* (20.79)	2.5* (20.33)		2.5* (24.3)
	Superior-Cronese	6.3 (1.84)	6.3 (1.32)	5.9 (2.28)	1.9 (1.19)	4.6 (1.12)	2.6 (0.49)	3.4 (0.79)	4.3 (1.41)		2.5 (0.6)	2.6 (26.7)	3.6 (26.3)	1.7 (23.76)		1.9 (23.7)		
Eastern Mojave	Ivanpah	4.4 (1.19)	4.4 (2.46)	5.6 (1.95)	5.1 (2.92)	4.1 (1.86)	1.0 (0.48)	4.5 (1.72)	2.8 (1.79)		2.3 (0.2)			3.7 (23.62)	3.7 (23.62)	2.6 (24.9)		3.0 (24.5)
Colorado Desert	Chocolate Mountain	11.4 (3.55)	13.4 (4.31)	6.5 (1.50)	4.5 (2.56)	7.5 (2.74)	13.8 (3.52)		6.0 (1.84)	7.3 (1.96)	8.4 (0.8)			9.4 (14.8)	7.6 (32.46)		7.1 (22.1)	3.9 (31.8)
	Chuckwalla	4.9 (1.49)	6.0 (1.77)	4.3 (1.19)	4.2 (2.84)		3.7 (1.14)	3.9 (1.37)	3.9 (1.62)		3.3 (0.4)			4.3 (15.7)		1.8 (28.8)	4.6 (19.4)	2.6 (24.0)
	Chemehuevi	6.7 (1.27)	10.3 (3.10)	3.9 (1.71)	4.8 (3.07)	9.4 (5.98)	4.2 (1.40)	4.0 (1.51)	0.8 (0.90)		2.8 (0.3)		1.7 (30.6)		2.9 (24.21)		4.0 (15.2)	
	Fenner	8.2 (1.94)	13.5 (2.80)	6.2 (2.37)	6.6 (3.05)	8.3 (4.01)	6.9 (2.49)	6.8 (2.78)	0.9 (0.95)		4.8 (0.5)		5.5 (30.0)		6.0 (26.25)	2.8 (29.8)		5.3 (19.8)
	Pinto Mountains	2.2 (2.12)	9.9 (3.58)	1.9 (0.98)	3.3 (3.53)	4.3 (2.38)	3.4 (1.85)	3.3 (1.39)	3.7 (1.57)		2.4 (0.3)		2.1 (31.6)	2.3 (32.7)		1.7 (31.8)	2.9 (20.6)	
	Joshua Tree	1.9 (0.53)	2.7 (0.79)	3.0 (1.94)	2.3 (1.75)	2.3 (1.56)	2.8 (1.56)	3.5 (1.33)	3.4 (1.63)		3.7 (0.4)		2.6 (34.7)	3.6 (22.5)		3.1 (20.2)	3.9 (23.3)	

*724 adults were translocated into the Ord-Rodman TCA in 2017–2019 due to expansion at 29 Palms Marine Corps Air Gunnery Command Center. These are included in these density estimates.

The long-term surveys in the TCAs provide robust data on declines in density since 2004. However, tortoise populations had been in decline for decades previously, and estimates of densities from before the species was listed under CESA in 1989 are important for understanding the scale of long-term decline. While there were no large scale or frequent systematic population monitoring programs in the 20th century, multiple regional or short-term surveys give snapshots of density in certain areas pre and post listing. Collectively, these studies give a broad picture of the state of tortoise populations in the past several decades.

Estimates of tortoise densities in California before the species was listed under CESA can be found in Berry (1986*a*):

> "Berry and Nicholson (1984a) developed a more detailed map of relative tortoise abundance throughout an area of over 100,000 km^2 using data from 1,808 strip transects. Transects, which were 2.4 km by 9.1 m, provided counts of tortoise signs (live individuals, carcasses, scats, cover sites, tracks, drinking sites, and courtship rings). Counts of signs were calibrated against counts along transects in areas where tortoise densities had been estimated by repeated censuses. The map prepared by this method showed five relative density classes: 0–8, 9–19, 20–39, 40–97, and >97 tortoises/km^2. Four major tortoise population centers or crucial habitats with densities of >77 tortoises/km^2 were identified: (1) Fremont-Stoddard in the western Mojave Desert (4864 km^2), (2) Ivanpah in the eastern Mojave Desert (918 km^2), (3) Fenner-Chemehuevi in the eastern Mojave and northeastern Colorado deserts (3881 km^2), and (4) Chuckwalla (1333 km^2) in the southern Colorado Desert."

In addition, in the 1970s the BLM established 27 2.6 km^2 (1 mile^2) survey sites in California (Berry and Turner 1986). Using mark recapture methods, researchers surveyed the plots over 60-day periods in the spring every 2–10 years (Berry and Medica 1995). Berry (1986*a*) reports that of those 27 sites, "eight had estimated densities of ≤8 tortoises/km^2, six had 8–39 tortoises/km^2, and 13 sites supported 42–184 tortoises/km^2", though the years those estimates come from are not reported. Multiple of these sites are located within the current Tortoise Conservation Areas, with sites in the Ivanpah, Chuckwalla, Fenner, and Chemehuevi TCAs. Using data reported in Berry and Medica (1995), rough comparisons can be made between the estimated densities in 1979–1992 and the 2004–2014 surveys. The earlier surveys covered the whole of the plot and did mark recapture methods to estimate density, while the later USFWS surveys used line transects. In addition, the BLM density estimates are only for the single plot per TCA, while the more recent line transects use multiple line transects per TCA to estimate density across the whole TCA. However, the combined density estimates provide a benchmark of declines over the past 50 years. The Desert Tortoise Natural Area overlaps with the northern border of the Fremont-Kramer TCA. Estimates of densities in 1979–1980 vary from 36 adults/km^2 in Chemehuevi to a high of 73 adults/km^2 in Fenner and Chuckwalla (Figure 10). By the early 1990s, density of adults had not fallen particularly dramatically except in Chuckwalla which had a 57% decline from about 73 adults/km^2 to about 31 adults/km^2, and the Desert Tortoise Natural Area which saw a 93% decline to 3.7 adults/km^2 which is below the density needed for population viability (Figure 10). However, on the scale of multiple decades, all the surveyed areas experienced very steep declines. From 1979–1980 to 2020–2021, densities of adults in the corresponding TCAs fell 93% in Fenner, 96% in Chuckwalla, 89% in Chemehuevi, and 93% in Ivanpah (Table 2 and Figures 8, 9,10).

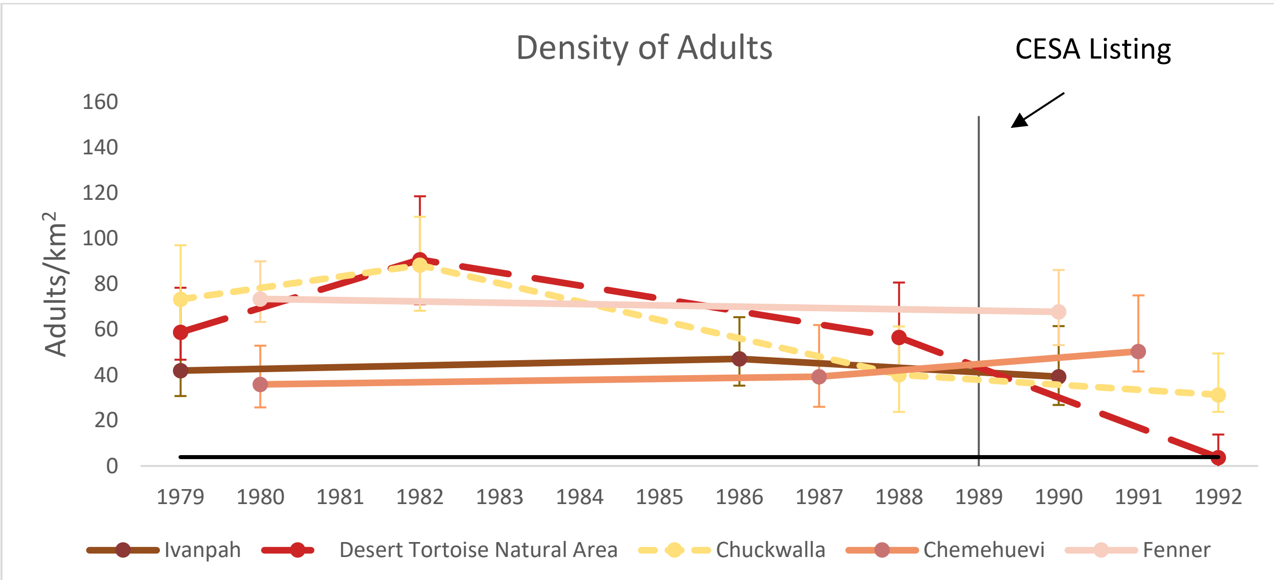


Figure 10. Estimated densities of adults/km^2 in plots surveyed 1979–1992 using mark recapture methods. The dot represents the midpoint of the density estimates, bars are 95% confidence intervals. Black horizontal line represents 3.9 adults/km^2, the estimated minimum density needed for population viability. Redrawn from figures in Berry and Medica (1995).

Berry et al. (2020b) continued the work of surveying tortoises at Desert Tortoise Research Natural Area in the western Mojave Desert for decades. Part of the site was fenced to keep out sheep, vehicles and humans but allow movement of tortoises, and surveys were done both inside and outside the fence. In 1979 when they started the surveys, estimated densities of all tortoises inside the fence were 103/km^2, and 79/km^2 outside the fence. In 2002 it had declined to 10.2/km^2 inside the fence and 4.17/ km^2 outside the fence. By 2012 densities had increased to 15.6/ km^2 inside the fence, and to 4.9/km^2 outside the fence. Counts of tortoises (from which densities were estimated) followed an estimated linear decline of 9.1% per year over the 30+ years of the study.

Other studies give rough estimates of historical density in other parts of the range. In the Pinto Basin of Joshua Tree National Park in 1991–1996, Freilich et al. (2000) used mark recapture methods to resurvey an area that had been surveyed in the 1970s. Their methods were designed to estimate abundance rather than density, and since they did not have a well-defined effective trapping area, their density estimates are rough. However, they report that in the 1970s the density estimates were 29–31 adults and juveniles/km^2, while their estimate for the early 1990s was 42 adults/km^2. Lovich et al. (2014) reports that surveys in the Pinto Basin in 1987–1988 estimated densities as high as 77 tortoises/km^2.

Medium-term tracking of densities did occur in four study sites in California at various times between 1977 and 1985 (Berry et al. 1986). At one site in the western Mojave Desert, Fremont Peak, sampling occurred three times (1977, 1980, and 1985) over a 9-year period and the population density declined from 27/km^2 in 1980 to 15/km^2 in 1985 (Berry et al. 1986). However, at three other sites there were no significant changes in density during those years. At the Kramer Hills site in the Western Mojave Desert there were an estimated 42 adults/km^2 in 1980 and 44 adults/km^2 in 1982. The Chemehuevi Wash site in the Colorado Desert was surveyed in 1979 and 1982 and saw a nonsignificant increase from 18 adults/km^2 to 22 adults/km^2. The Chuckwalla Bench study site also in the Colorado Desert had a non-significant increase in density from 75 adults/km^2 in 1979 to 87 adults/km^2 in 1982 (Berry et al. 1986), see Figure 10.

Although the density surveys in the 1970s and 1980s do not use the same methodology as later surveys and only cover small areas, they do give an idea of the range of tortoise densities in the decades before the start of the surveys in the TCAs, providing context for more recent density estimates.

Juveniles

Juvenile tortoises are easier to overlook during surveys than adults, and the U.S. Fish and Wildlife surveys in the TCAs do not report densities of juveniles (but see below). However, Berry and Medica (1995) report on the density of adults and all tortoises using mark recapture surveys in BLM plots from 1979 to 1992. From those we can roughly calculate historic density of juveniles (density of all tortoises minus density of adult tortoises) (Figure 11).

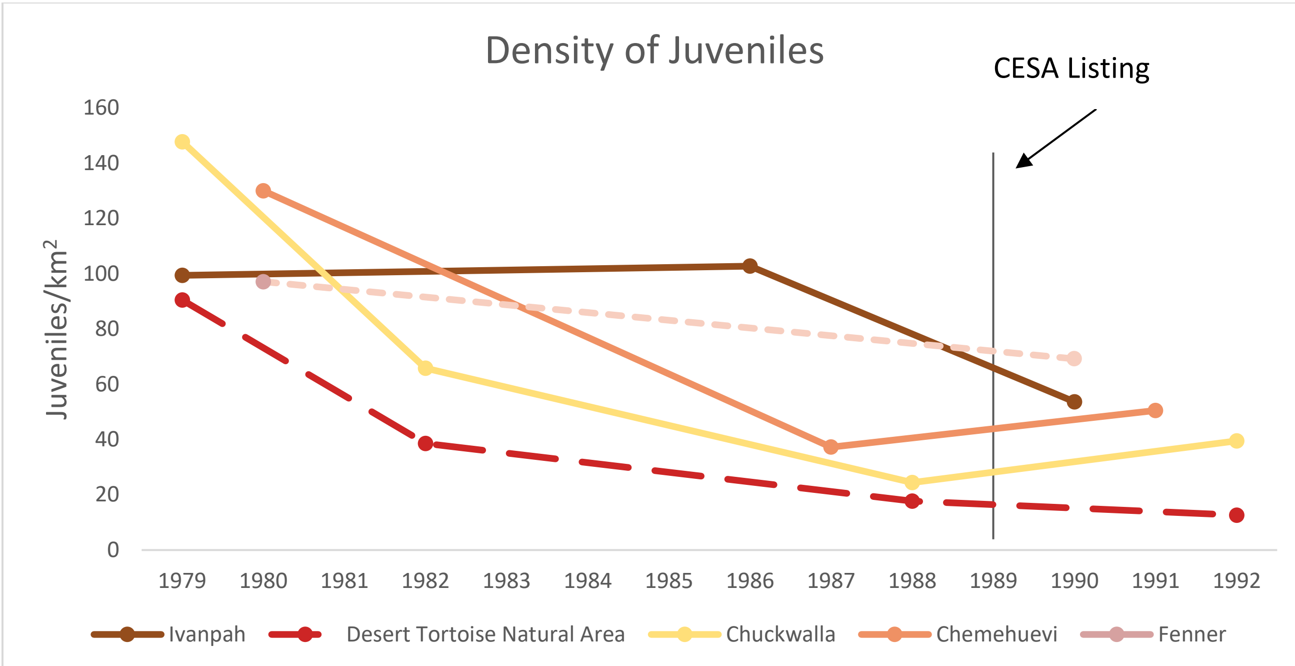


Figure 11. Density of juvenile tortoises in plots in California from 1979 to 1992. Juvenile density was calculated by subtracting density of adults from density of all tortoises presented in Berry and Medica (1995).

Between the late 1970s and early 1990s, the density of juveniles declined roughly 46% in Ivanpah, 86% in the Desert Tortoise Natural Area, 73% in Chuckwalla, 62% in Chemehuevi, and 29% in Fenner (Figure 11). While juvenile tortoises are expected to have low survival rates, this long-term loss of juveniles from the landscape is concerning, and there is evidence that it is continuing into recent years. In 2014 in the Western Mojave Recovery Unit, the density of adult tortoises was 49% of what it had been in 2004, and the proportion of juveniles in the population declined by 9% (Allison and McLuckie 2018). In the yearly transect surveys done in the TCAs, many fewer tortoises with midline carapace length <180 mm were found in 2007–2015 compared to 2001–2005 (Figure 12). In some areas, the youngest tortoises found in recent years were at least 30 years old (Holcomb 2022*a*). Even if conditions quickly improve for juveniles, such a long period with little recruitment of juveniles into the population will hinder population recovery significantly.

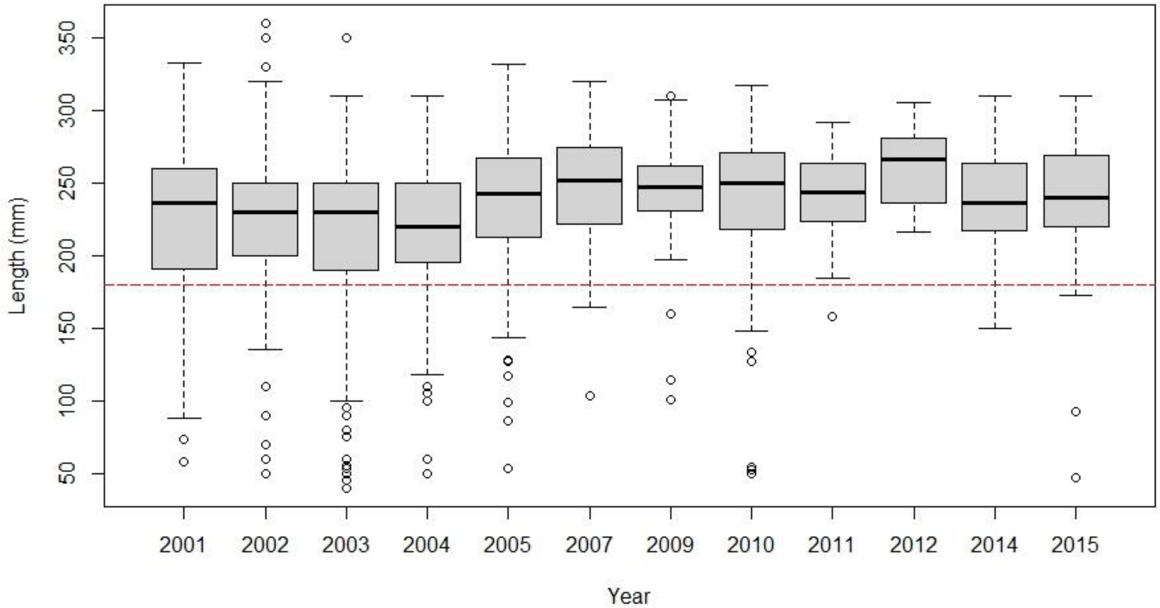


Figure 12. Midline carapace length of tortoises surveyed within the Western Mojave Recovery Unit Tortoise Conservation Areas, showing a reduction in observations of tortoises smaller than 180mm after about 2005. Described in Alison and McLuckie (2018), and figure made with USFWS unpublished data provided by K. Holcomb and used with permission. The horizontal dashed line at 180 mm represents the size over which tortoises are considered to be adults.

3.3 Mortality and Survival Rates

Adult and juvenile survival rates are important demographic factors that can affect whether a population is increasing, stable, or declining. Desert tortoises generally have low survival rates (i.e., high mortality rates) as hatchlings and juveniles, and relatively high adult survival rates (Berry and Murphy 2019). The adult survival rate needed for population stability depends on a number of factors, including population reproduction and/or recruitment rates, but the USFWS 1994 Recovery Plan estimated that an adult survival rate of 98% per year is needed for population growth of 0.5% per year. A more recent estimate that incorporated current adult densities and juvenile survival rates found that an adult survival rate of 93% per year was necessary for desert tortoise population stability (no growth or decline) (Holcomb 2022*a*). Estimates of survival/mortality rates come from a variety of studies within California, most of which were quite limited in geographic scale. When comparing survival rates to mortality/death rates, a broad rule of thumb is that mortality or death rate ≈ 1-(survival rate).

Adult tortoises are much easier to survey than juveniles, consequently most of the information about survival and mortality in the wild relates to adults. In the late 1970s and early 1980s, a study from four sites provided some limited information on annual mortality rates in stable and declining populations (Berry et al. 1986). At Fremont Peak in an area that became the Fremont-Kramer TCA, densities of adults and subadults declined significantly between 1977 and 1985, and the estimated annual mortality rate was 4.5% per year. In contrast, three other sites surveyed during that period that did not see significant declines in density had annual mortality rates of 2.2–2.9% (Berry et al. 1986). Berry et al. (2020b) estimated survival rates (1979–2012) of adults and juvenile tortoises inside and outside of the fenced portion of the Desert Tortoise Research Natural Area in the Western Mojave. As mentioned previously, in 1979 estimated densities of all tortoises was 103/km^2 inside the fence, and 79/km^2 outside the fence. By 2012 densities had decreased to 15.6/km^2 inside the fence, and to 4.9/km^2 outside the fence. During those years the population suffered an estimated 87.6% decline. Median annual survival probability (converted into percentages for ease of comparison) for adults inside and outside of the fenced area ranged from 79%–83% in 1979–1989, 71%–78% in 1989–2002, and 94%–96% in 2002–2012. These estimates are all well below the necessary survival rate identified in the USFWS 1994 Recovery Plan to achieve modest population growth. Juveniles had lower survival, their estimated median annual survival probability was 66%–73% in 1979–1989, 57%–65% in 1989–2002, and 90%-93% in 2002–2012.

In Eastern Joshua Tree National Park, tortoises were surveyed intermittently from 1978 to 2012 (Lovich et al. 2014). The authors tested the impact of rainfall on survival, and the best model of survival was based on the average estimated winter precipitation over the preceding three winters. They estimated a mean annual (apparent) survival rate of 0.87 (87%). Values below the mean occurred in 1991, 1997–2004 and 2008, which were years of lower rainfall (Lovich et al. 2014). Estimated survival was above the mean in 2010–2011. It should be noted that other factors that impact survival, such as predation and disease, were not tested independently. Instead, it was assumed that these factors would be mediated by rainfall (i.e., tortoises would be in poorer conditions in drier years and therefore they would be more susceptible to predation or disease).

Between 2002 and 2004, Berry and Keith (2008) evaluated the status of desert tortoise populations in Red Rock Canyon State Park in Kern County. Previous surveys had occurred in the 1970s, and density was estimated to be <8 tortoises/km^2. The death rate over four years was estimated at 67% for adults and subadults, and densities were between 2.7 and 3.6 tortoises/km^2.

In 2007–2008, Berry et al. (2020c) evaluated the status of a population of tortoises in the El Paso Mountains close to the Fremont-Kramer Critical Habitat Unit. Estimated density of adults was 4.8/km^2 and the annual death rate of adults in 2003–2008 was 6.9% (Berry et al. 2020*c*). The top causes of known death were mammalian and avian predators, gunshots, and vehicles. The authors concluded that “the high death rate of adults, low population density, high human visitor use, and ongoing decline in the adjacent critical habitat unit indicate that a viable population is unlikely to persist in the study area” (Berry et al. 2020*c*).

Esque et al. (2010) tracked several hundred adult tortoises before and after translocations from Fort Irwin National Training Center to neighboring public land in the Superior-Cronese Critical Habitat Unit. They monitored translocated tortoises, tortoises resident at the release sites, and control tortoises in nearby areas that were not affected by the translocations. In the first year (2008), 19% of control tortoises, 20% of resident tortoises, and 25% of translocated tortoises died. Most of the mortalities were thought to be due to coyote predation. As a comparison, at a different reference site in the Superior-Cronese Critical Habitat Unit, 8.3% of tracked tortoises died in 2008. At reference sites in other critical habitat units in California, percent mortality in 2008 ranged from 0% in Ivanpah and Ord-Rodman to 28–30% in Chemehuevi and Chuckwalla. Esque et al. (2010) also showed that mortality can vary greatly year to year in the same site. For example, at Soda Mountain outside of the Superior-Cronese Critical Habitat Unit, in 2006 at there was no mortality, in 2007 mortality was 17%, and in 2010 it was 43% (Esque et al. 2010).

In 2009, Berry et al. (2020a) surveyed about 93 km^2 of BLM land within the eastern Chemehuevi Valley, adjacent to the Chemehuevi Critical Habitat Unit. Based on the number of live and dead tortoises found, they concluded that the density of adults was 2.0/km^2 (+/- 1.0), and that the annual death rate in the four years prior to the survey was 13.1%/year. These data led them to conclude that the population was probably nonviable (Berry et al. 2020*a*).

Collectively, these data suggest that adult survival rates in most recently surveyed areas are too low to support stable populations and have been below the thresholds established by the USFWS 1994 Recovery Plan and by Holcomb (2022a) for some time (Table 3). Although survival rates have not been estimated systematically across the tortoise's range in California, rates appear to be particularly low outside of CHUs.

Table 3. Survival and mortality rates of adult and subadult tortoises in various studies.

Life stage	Survival vs Mortality	Rate	Location	Time scale	Reference
Adults	Median annual survival probability	79%-83%	Desert Tortoise Research Natural Area	1979-1989	Berry et al. 2020b
Adults	Median annual survival probability	71%-78%	Desert Tortoise Research Natural Area	1989-2002	Berry et al. 2020b
Adults	Median annual survival probability	94%-96%	Desert Tortoise Research Natural Area	2002-2012	Berry et al. 2020b
All	Mean annual survival	87%	Eastern Joshua Tree National Park	1978-2012	Lovich et al. 2014
Adults & subadults	Annual mortality	4.5%	Fremont -Kramer TCA	1977-1985	Berry et al. 1986
Adults & subadults	Annual mortality	2.2%-2.9%	Kramer Hills, Chemehuevi, Chuckwalla	1977-1985	Berry et al. 1986
Adults & subadults	Death rate over 4 years	67%	Red Rock Canyon State Park	2002-2004	Berry and Keith 2008
Adults	Annual death rate	6.9%	El Paso Mountains near Fremont-Kramer CHU	2003-2008	Berry et al. 2020c
Adults	Annual mortality	13%	Chemehuevi Valley	2005-2009	Berry et al. 2020a
Adults	Annual mortality	0%	Ivanpah	2006-2008	Esque et al. 2010
Adults	Annual mortality	0%	Ord-Rodman	2006-2008	Esque et al. 2010
Adults	Annual mortality	0%-31%	Chemehuevi	2006-2008	Esque et al. 2010
Adults	Annual mortality	9%-29%	Chuckwalla	2006-2008	Esque et al. 2010
Adults	Annual mortality	0%-44%	Soda Mountain	2006-2008	Esque et al. 2010

Adults	Annual mortality	6.3%-8%	Superior-Cronese	2007-2008	Esque et al. 2010

Juvenile Survival

In long-lived species like the tortoise, if adult survivorship drops, reproductive rates or juvenile survival would have to increase dramatically to keep populations stable. Analysis by the USFWS (1994) estimated that “a 10% increase in adult mortality can require a 300% increase in juvenile survivorship” to maintain a stable population. Many of the threats to adult survival affect juveniles, making it unlikely that juvenile survivorship can naturally increase to the levels needed to compensate for the decreasing adult survival documented above.

Several factors limit the number of hatchlings that are produced in the wild each year. Females lay a maximum of about 30 eggs per year, incubation success depends on temperature, and nest predation is common (Berry and Murphy 2019). After emerging from the egg, survival rates of wild hatchlings can be low. In the Ivanpah Valley between 2011 and 2014, Tuberville et al. (2019) compared survival and growth of free ranging hatchlings to those reared in pens under different rainfall scenarios. Both groups were hatched from eggs laid by wild females and brought into captivity for the study. Free ranging hatchlings were released into the wild between 0 and 18 months old. Estimated annual survival rates for the free ranging hatchlings was 48%–49% compared to 94% of those reared in pens.

We do not have much information on historical juvenile survival rates, but the impact of recent low survival rates can be seen in demographic information. As mentioned previously, in the yearly surveys performed in the Western Mojave TCAs, many fewer tortoises with midline carapace length <180 mm were found in 2007–2015 compared to 2001–2005 (Figure 12). One likely cause of juvenile mortality is raven predation. Holcomb et al. (2021) estimated that annual survival rates for 1–10-year-old tortoises in 5 CHUs averaged 63% when within 500m of a raven’s nest, and ~76% when the median distance to a nest was 1.72 km. See section 4.4 for more detail on predation.

One strategy to improve juvenile survival is to raise tortoises in captivity and then release them once they reach a certain size (referred to as head-starting; for more details see section 9.1). A study at the Fort Irwin National Training Center on head-started juvenile tortoises (Nagy et al. 2015*b*) found that in the two years after release, survivorship was 76–79%, but in the third year survivorship dropped to 53%, resulting in an overall three year survival rate of 32%. Survival was generally higher amongst tortoises with a carapace length of at least 100 mm (9 years old). Another study on head-starting found that found no significant difference in the survival rate of hatchlings released vs those reared indoors for 7 months vs those reared in outdoor pens for 7 months (Daly et al. 2019). Although the head-started tortoises grew quickly, the three groups combined annual survival after release was 44%, with the odds of survival increasing 51% for every 100m away from a raven’s nest. They predicted that survival would be near 100% if the nearest nest was more than 1.6 km away (Daly et al. 2019)

Even with head-starting, juvenile survival rates are often lower than the 59% average annual juvenile survival rate estimated by Holcomb (2022a) to be necessary for population stability if adult annual survival rates are 93% (Table 4). The available information suggests that low juvenile survival is one of the major reasons why there have been widespread declines in density.

Table 4. Survival and mortality rates of juvenile tortoises in various studies.

Life stage	Survival vs Mortality	Rate	Location	Time scale	Reference
Juveniles	Median annual survival probability	66%-73%	Desert Tortoise Research Natural Area	1979-1989	Berry et al. 2020b
Juveniles	Median annual survival probability	57%-65%	Desert Tortoise Research Natural Area	1989-2002	Berry et al. 2020b
Juveniles	Median annual survival probability	90%-93%	Desert Tortoise Research Natural Area	2002-2012	Berry et al. 2020b
Head started juveniles	Survivorship after 2 years	76-79%	Fort Irwin	2005-2007	Nagy et al. 2015
Head started juveniles	Survivorship after 3 years	53%	Fort Irwin	2005-2008	Nagy et al. 2015
Wild Hatchlings	Survival rate	48%-49%	Ivanpah Valley	2011-2014	Tuberville et al 2019
Head started juveniles	Annual survival after release	44%	Mojave National Preserve	2015	Daly et al. 2019
Juveniles	Annual survival close to ravens' nest	63%	Mojave Desert	2020	Holcomb et al. 2021
Juveniles	Annual survival far from raven's nest	76%	Mojave Desert	2020	Holcomb et al. 2021

For species like tortoise with slow growth, delayed maturation, and low reproduction rates (Shine 2005), factors that lower adult survival rates can have long-term negative impacts on abundance/density. Snapping turtles have similar life history traits as desert tortoises, and in a population in Ontario Canada, river otters killed about 50% of the adults over three years in the late 1980s (Keevil et al. 2018). Female annual survival rates fell from 94% to 76–86% during those years, and the population was reduced by about 40% (Keevil et al. 2018). Twenty-three years later, survival rates had returned to early 1980s level, but abundance did not rebound. This suggests that even if threats are removed, and survival rates increase, for a long-lived species like the desert tortoise, populations may not recover for several decades. The problem is magnified if juvenile survival is very low as is seen in multiple survey areas in California. Having breeding adults on the landscape is vital for population viability, and low rates of juvenile recruitment create an unstable demographic structure that will make it less likely for populations to recover and makes them vulnerable to any additional sources of mortality (Holcomb 2022*b*).

4 FACTORS AFFECTING THE ABILITY TO SURVIVE AND REPRODUCE

Desert tortoise life history traits, including delayed reproductive maturity, relatively low annual fecundity, and low survival rates of juvenile tortoises cause populations to be vulnerable to a multitude of threats (Berry et al. 2020*b*). Their vulnerability is increased because many of the threats are interactive and amplify each other. For clarity, this document focuses on individual threats, but also recognizes that many of them are fundamentally intertwined. Many of the threats described in the initial desert tortoise status review and the USFWS Recovery Plans (U.S. Fish and Wildlife Service 1994, U.S. Fish and Wildlife Service 2011) continue to affect the species.

4.1 Habitat Modification and Destruction

Mojave Desert Tortoise range in California occurs on a variety of public and private land jurisdictions, the top three being BLM (39,251 km^2), National Park Service (NPS) (17,035 km^2), and Department of Defense (DoD) (13,018 km^2). The type of habitat modification and destruction permitted on each of these land types varies. BLM land is managed for a wide range of uses and stakeholders, and permitted activities that may impact tortoises include off-highway driving, mining, and renewable energy projects. Activities on NPS land are much more restricted; off-highway driving, mining, and renewable energy projects are not allowed. DoD land is not generally open to the public and uses range from extremely low impact to high impact live artillery use. See Figure 5 for more details on land ownership.

In the large majority of tortoise habitat, at least some alteration is allowed which can impact tortoises. Across all states, an estimated 66% of Mojave Desert Tortoise habitat has some development within 1 km, where development is defined as “urban development, cultivated agriculture, energy development (e.g., oil and gas well pads, solar energy facilities), surface mines and quarries, pipelines and transmission lines, and transportation (e.g., roads and railroads” (Carter et al. 2020). The direct impacts of development include removal of soil and vegetation, destruction of burrows, and creation of roads and other infrastructure that can kill tortoises or hinder their movements (Boarman and Sazaki 1996, 2006). An important indirect impact of development is subsidization of predators (see section 4.4) (Boarman et al. 2006).

Tortoises are less likely to occur in areas that have even a low level of development. Carter et al. (2020) found that “encounter rates of both live and dead Mojave Desert Tortoises combined decreased significantly with development levels” and that when “10% of the area within 1 km of that location has been altered by development” (10% development), it was rare to find live or dead tortoises at a location. The authors estimated that encounter rates for both live and dead Mojave Desert Tortoises decreased an average of 4% for every 1% increase in the development index (Carter et al. 2020).

In the Western Mojave Recovery Unit (which is wholly within California) 47% of tortoise habitat has almost no development (<1% within 1 km), and 5% of habitat has >10% development (U.S. Fish and Wildlife Service 2022*a*). For the Eastern Mojave Recovery Unit, the proportion of habitat with <1% development within 1 km is 58%, and 5% is at 10% development. In the Colorado Desert Recovery Unit, it is 65% and 4% respectively (U.S. Fish and Wildlife Service 2022*a*). However, those two units extend outside of California (see Figure 6), and it is unclear whether those percentages are representative of the range in California. In their 2022 5-year review, the USFWS concluded that "space does not appear to be a limiting factor to tortoise recovery". However, these categories of development used above do not take into account unpaved roads and tracks for off-highway vehicles (OHVs) which are allowed on BLM land (see section 4.2).

Driven by a number of forces, the human population in the inland deserts of California has increased significantly in the past 30 years. Between 1990 and 2022, the number of housing units increased 58% in Imperial County, 79% in Riverside County, and 37% in San Bernadino County (numbers calculated from State of California Department of Finance 2023). Urban or suburban development typically expands along the edges of previously impacted habitats which generally contain few tortoises. Therefore, we focus discussion on other types of projects that are more likely to have large-scale impacts on areas with desert tortoise populations.

Department of Defense

The Department of Defense is a major landholder in desert tortoise range. Military bases in California deserts include Fort Irwin, Naval Air Weapons Station China Lake, Edwards Air Force Base, George Air Force Base, Chocolate Mountain Aerial Gunnery Range, Marine Corps Air Ground Combat Center Twentynine Palms, and Marine Corps Logistics Base Barstow. In total, these bases encompass over 3 million acres (14.78% of the total tortoise range in California, see Figure 4). A wide variety of land uses occur on DoD property, and some of those uses are very compatible with desert tortoises while others are not. Training areas are generally high impact and tortoises in training designated areas are translocated to other sites. For example, according to the USFWS (2022c), the "Department of the Army (Army) expanded training onto 18,197 acres (73.6 km^2) of designated critical habitat on the southern area of Fort Irwin that had previously been off-limits to training, thus requiring the translocation of approximately 650 adult desert tortoises. In addition, the Army plans to expand activities onto and displace tortoises from up to 62,045 acres (~250 km^2) of its western training area in the near future, which is designated critical habitat and currently off limits to training. The Department of the Navy (Navy) expanded training for the Marine Corps Air Ground Combat Center (MCAGCC) at Twentynine Palms into approximately 167,982 acres (680 km^2) of public and private land, which required translocating approximately 1,000 adult tortoises." Around 700 of those tortoises were translocated into the Ord-Rodman TCA (see section 9.1 on Translocation).

Along with translocation of tortoises, other strategies used by the DoD to offset the impact of converting large areas of habitat into training grounds include acquiring land (making it federal) within a CHU, buying out grazing allotments, increased law enforcement in tortoise habitat, predator monitoring and targeted control within translocation sites, rehabilitation of closed routes, installation of off-highway vehicle barriers and desert tortoise exclusion fencing, and constructing perimeter fences to prevent public trespass into tortoise habitat (U.S. Fish and Wildlife Service 2022*a*). For more discussion of efforts to conserve tortoises, see section 5.2 Current Management Actions.

Given the relatively large amount of DoD land with land use practices that require translocation of tortoises, it is of interest whether and how quickly that habitat might become suitable again for tortoises if and when the areas are no longer used for training. Recovery from disturbance can take a long time in desert ecosystems. This has been documented in soils and vegetation of the Desert Training Center which spans parts of southern California, southern Nevada, and western Arizona. This area was used for military training exercises in the 1940s and 1960s, and 40–60 years later the soil in tank tracks remained compacted and rain infiltration rates were low (Prose and Wilshire 2000). These soil differences led to increased plant density in the tracks, but those plants had restricted growth. In addition, grass species with shallow fibrous root systems increased in density in the tracks while species with long tap roots had reduced density and cover (Prose and Wilshire 2000). USFWS (1994) estimated that areas where camps, roads, and parking lots were built would take "decades or centuries to recover." Other documented direct negative impacts to tortoises on military property include "vandalism, predation, mycoplasmosis and shell diseases" with "significantly more tortoises with shell disease…found on plots with current and recent military use than on plots with no history of military use" (Berry et al. 2006). For more detail on shell disease see section 4.7.

Renewable Energy Projects

Renewable energy projects, namely solar farms and wind energy facilities are a major source of development in desert tortoise habitat. These facilities are regarded as key to reducing CO_2 emissions, and their development has been prioritized on public land (e.g., American Reinvestment and Recovery Act 2008; National Energy Policy Act 2005, Infrastructure Investment and Jobs Act 2021, Inflation Reduction Act 2022). Unlike urban or suburban development, energy projects tend to be sited in mostly undeveloped public land, thus leading to the potential degradation and fragmentation of relatively high-quality tortoise habitat (Lovich et al. 2011).

The impacts of wind and solar energy facilities generally differ from more typical forms of development, primarily due to the diffuse nature of the infrastructure. Data specifically evaluating the impacts of renewable energy facilities on desert tortoises remains limited, however two studies suggest that tortoise survival rates are relatively high. A study near Palm Springs in Riverside County estimated tortoise survival rate within a wind energy facility (WEF) and a nearby wilderness area (NWA) using data from 1997–2000 and 2009–2014 (Agha et al. 2015). They found "long-term tortoise survivorship within the WEF (96.7 %) was significantly higher than in the nearby NWA (92.1 %)" (Agha et al. 2015). This counter intuitive result may have been due to tortoises at the WEF benefiting from "edge enhancement of vegetation (food resources), turbine pads (artificial rain catchments), reduced subsidized predators and low traffic." (Agha et al. 2015).

Lovich et al. (2011) tracked tortoises at a wind energy facility near Palm Springs for six field seasons (1997–2000 and 2009–2010). The facility contained turbines, electrical transformers, and an extensive network of roads (Lovich et al 2011). Their estimated annual survivorship rate of 91.6% (confidence interval 90.5–93.5%) was based only on adult females, which is a much higher survival rate than has been reported in many areas across the range in California (see section 3.3). The authors suggested a few characteristics of the site that might have led to high survival rates including very restricted public access and fewer ravens. However, they cautioned that without before-and-after studies of the impact of energy facilities, of which there are very few, it is hard to draw conclusions about the long-term impacts of energy facilities on desert tortoise.

Development of a wind power project results in a variety of disturbances that are classified as temporary or permanent. Permanent impacts include land occupied by wind turbine pads, access roads, substations, and transmission lines. Temporary direct impacts include temporary roads, staging areas, and substation/transmission construction (Denholm et al. 2009). However, in desert ecosystems, ‘temporary’ disturbances may have decades-long impacts if sites are not actively rehabilitated. Denholm et al. (2009) collated data on the size of several wind projects in California including total size (land associated with the complete wind plant project) and area of direct (permanent and temporary) impact. Of the four projects with complete data, direct impacts accounted for 1.5–7% of the total area of the project.

Solar power plants have a different design and land use than windfarms. However, similar types of impact classifications occur. Direct impacts occur where land is occupied by solar arrays, access roads, substations, service buildings, and other infrastructure (Ong et al. 2013). Three types of solar power plants were evaluated in one study, and the percentage of total land that was directly impacted was between 38% and 100% of the project site (N=12 projects) (Ong et al. 2013). The impact of infrastructure to wildlife extends beyond the habitat that is directly modified, including fragmentation and barriers to gene flow, effects due to noise, vibration, and shadow flicker, electromagnetic field generation, macro- and micro-climate change, predator attraction, dust and dust suppressants, and increased fire risk (Lovich and Ennen 2011, 2013). A study in southern California compared wind farms with nearby areas and found that species richness, evenness, and diversity was lower on the farm sites for reptiles, birds, mammals, arachnids, and plants (Keehn and Feldman 2018). Renewable energy facilities are not sited within tortoise CHUs, however they can be close enough that the impacts listed above spill over into critical habitat (K. Berry USGS, pers. comm 2022).

Renewable energy projects that could potentially cause ‘take’ of desert tortoises must apply for incidental take permits (ITPs) from the Department or from the USFWS depending on jurisdiction (see section 5.1 for more detail). Between 2010 and 2021, the Department issued ITPs for desert tortoise for 49 renewable energy projects. In 2022, the Department completed ITP permitting for six renewable energy projects within San Bernadino and Riverside counties that would have a total footprint of about 10,600 acres (43 km^2). As of October 2022, the Department was in the process of reviewing or issuing ITPs for 14 more renewable energy projects in Riverside and San Bernadino counties that could potentially have footprints of up to 20,750 acres (84 km^2). Not all of these projects are necessarily sited within the recovery units or will end up receiving permits from the Department. However, it does show that there is increasing demand to use land within the Mojave Desert for renewable energy projects (for more information about ITPs, see Section 5.2).

Cannabis Operations

Illegal cannabis farms are an emerging threat to tortoises and their habitat in the Mojave Desert. Habitat is destroyed to put up greenhouses, and there are potential associated spillover effects like chemical leakage into stream beds, trash dumps, and other land disturbances beyond the footprint of the greenhouses. In addition, water and trash may attract and increase densities of predators like coyotes and ravens, and guard dogs are thought to kill tortoises (CDFW unpublished data, Holcomb 2022a, U.S. Fish and Wildlife Service 2022a). In the Department's Region 6, which includes the majority of desert tortoise range, as of 2022 there had been 3,065 acres (~12 km^2) of illegal cannabis cultivation visited by law enforcement. However, the Department acknowledges that there are vastly more illegal sites within tortoise range for which a law enforcement response has not been possible, therefore these numbers likely underestimate the true impacts. The presence of illegal cannabis farms can have additional indirect impacts on tortoise conservation. For example, according to USFWS (2022a), "illegal cannabis farms have already led to the cessation of raven monitoring and management efforts in the Fremont-Kramer Critical Habitat Unit in 2021, with the likelihood that tortoise monitoring in the same unit scheduled for 2022 will be cancelled due to safety concerns for field workers."

Legal cannabis cultivation also occurs within the desert tortoise range. Currently in Region 6 there are 2,394 acres (~9.5 km^2) of legal cannabis cultivation that have Streambed Alteration Agreements. The Department evaluates each development project individually for the purposes of the California Environmental Quality Act, and there has not been a robust analysis of the cumulative impacts to the species resulting from cannabis development in the area. Due to the newness of the threat, the overall impact on tortoises from illegal and legal cultivation has not been quantified. However, it a matter of increasing concern, and the current tools of permitting and law enforcement resources may not be sufficient to lessen the negative impacts on tortoises.

While the long-term impact of habitat modification and destruction resulting from all the land use types described above, along with any associated mitigation measures, is not fully known, the USFWS (2019a) states the impacts are "unlikely to be positive, despite the numerous conservation measures that have been (or will be) implemented as part of the actions." Although there are multiple science-based measures enacted to manage and mitigate threats, U.S. Fish and Wildlife Service (2019a) warns that they "have been unable, to date, to determine whether the expected benefits of the measures have yet been realized, at least in part because of the low reproductive capacity of the desert tortoise. Therefore, the conversion of habitat into areas that are unsuitable for this species continues the trend of constricting the desert tortoise into a smaller portion of its range".

Across the entire species range, it has been estimated that 7.4% of modelled tortoise habitat is now completely unsuitable for tortoise survival due to development and recent fire (Holcomb 2022*a*). Additionally, habitat is degraded in many additional areas as a result of factors such as off-highway vehicle use, wildfire, invasive plan species, and increased temperature due to climate change Therefore, focusing solely on the proportion of direct habitat loss in the desert tortoise range may be misleading and create an overly optimistic picture. With more than 90% of historical habitat still accessible, tortoise populations have declined severely in the past two decades.

4.2 Vehicle Strikes, Roads, and Fencing

Development of all types creates roads and other transport corridors that impact tortoises directly through vehicle strikes and as barriers to movement. Indirect impacts of transport corridors include habitat degradation including the spread of invasive species (Boarman et al. 1997, Brooks et al. 2005).

Desert tortoises are particularly susceptible to being killed on roads due to their slow rate of travel. Human behavior also plays a role. Boarman et al. (1997) anecdotally reported drivers intentionally swerving to hit turtles and tortoises. Even if drivers are not intentionally hitting tortoises, speeding on all types of roads can lead to unintentional but deadly strikes on tortoises (A. Ellsworth pers. comm. Nov 2022). Boarman and Sazaki (1996) estimated a kill rate of 1 tortoise per 2.4 km of road per year on Highway 58 in the western Mojave Desert, but warned their estimate was likely low because carcasses disappear quickly in the desert (likely due to scavenging). Anecdotal evidence from the Mojave Desert Preserve indicates an average of 5.3 tortoises are killed per year on the 216 km of paved road in the Preserve. Using 2008-2010 data from the Preserve, Hughson and Darby (2013) estimated that 31 female tortoises per year killed (on top of natural mortality) would be unsustainable, concluding that road mortalities may account for about ~9% of the excess mortality per year (assuming equal sex ratios). Juvenile dispersing tortoises are more likely to be killed on roads compared to adults (Boarman and Sazaki 1996).

Tortoises are often attracted to roads within their home ranges as places where appropriate forage plants grow and rain runoff collects (Boarman et al. 1997). However, impacts from direct mortality and increased access for predators near roads can result in the creation of reduced occupancy zones along roads, whose width can vary (Boarman et al. 1997). Two-lane paved roads in Mojave National Preserve had reduced occupancy up to 400 m away from the road (Hughson and Darby 2013). Boarman and Sazaki (1996) studied Highway 58 in California and found reduced occupancy up to 800m away. If the roads occur at a sufficient density, these zones could impact enough habitat to affect tortoise density across large scales. Although these results are only correlative, the TCAs that have road densities above 0.75 km/km^2 all had declines in tortoise densities between 2004 and 2014, while TCAs with less dense roads had both increases and declines in tortoise density (U.S. Fish and Wildlife Service 2022*a*).

Keeping tortoises off roads is a conservation priority (U.S. Fish and Wildlife Service 2022*a*). Well-constructed fencing designed to stop tortoises from accessing roads can lead to 93% fewer tortoise carcasses along highways as well as reducing road kills of other small vertebrates (Boarman and Sazaki 1996). Properly designed culverts under roads facilitate tortoise movements and help prevent fences from fragmenting tortoise populations (Boarman and Sazaki 1996). According to the USFWS (2022c):

> "Through 2011 approximately 1,660 km of highway roadside (including both sides of roads for those fenced on each side) had tortoise exclusion fencing installed to prevent road mortalities. Unfortunately, only approximately 43 km of roadside have been fenced in the decade since 2011. Almost 500 km of roadside have been identified as priorities for fencing based on our current understanding of road-effect zone area, relative habitat potential, and locations of extant populations (Holcomb 2019)."

Considerations that can slow or prevent fence building include cost, maintenance, visual disruption of the landscape, and loss of habitat during construction. At the October 2022 Desert Tortoise Management Oversight Group Meeting, the BLM reported that 3.5 miles of I-40 in the Ord-Rodman CHU will be fenced soon, and 5 miles of fence will be built soon in Mojave National Preserve. Other strategies to reduce tortoise mortalities on roads such as lowering speed limits, installing warning signs, and driver education have not been shown to be particularly effective (Hughson and Darby 2013).

Off-highway vehicles

Off-roading is a popular pastime in the California's deserts. According to the BLM, in 2008 there were four times the number of off-highway vehicles in the West than in 1998 (Bisson 2008). In Desert Wildlife Management Areas and CHUs, OHVs are legally required to stay on established roads and trails, while on the remainder of BLM land they can travel cross-country, although local BLM offices can enact further restrictions. OHVs and their associated unpaved trails lead to habitat degradation, but the impacts are thought to be generally less severe than paved roads.

OHV trails are typically <4m wide with a dirt surface, and are unimproved (i.e., they have never been bladed or filled) (Brooks et al. 2005). When the trails are created, it alters soils, vegetation, and some types of wildlife may potentially be killed. Tortoises can be run over on and off these trails and vehicles can crush burrows, depriving tortoises of refuge from extreme temperatures and drought. In areas of very frequent OHV use, multiple routes may merge into broad areas devoid of perennial vegetation 10–100 m or more across. These extremely high impact areas are rare, however there are large networks of OHV trails across the Mojave Desert which collectively can create significant changes to habitat and soils (Brooks et al. 2005). OHV trails change water runoff patterns especially on slopes and lead to greater erosion (Brooks et al. 2005). In addition, roads of all kinds can serve as pathways for invasive species. Inholding of private parcels within BLM land often are set aside for conservation, and OHV trails formally stop and restart at the boundaries. However, drivers often trespass across those private parcels, creating negative impacts for the tortoises even in areas that are designated as protected (A. Ellsworth, CDFW pers. comm. Oct 2022). The ecosystem or landscape-wide impact of OHV use can be hard to tease out in areas like the Mojave Desert that have multiple land uses, and Brooks et al. (2005) warned that “dispersed landscape effects … should be generalized very cautiously”.

The extent of OHV trails in desert tortoise habitat is hard to quantify, however the recent expansion of the Spangler, El Mirage, and Johnson Valley off-highway vehicle recreation areas under the 2019 John D. Dingell, Jr. Conservation, Management, and Recreation Act opened up an additional 60,000 acres (~242 km^2) of public land to cross country OHV use (U.S. Fish andWildlife Service 2022a). At the October 2022 Desert Tortoise Management Oversight Group Meeting, the BLM reported that there is a multi-year restoration project in Fremont-Kramer CHU to monitor and restore OHV routes.

4.3 Impacts from Invasive and Non-Native Species

Invasive Grasses and Forbs

Like many of the processes threatening desert tortoise, the impacts of invasive species are often tied to and synergistic with other factors such as livestock grazing, drought, and wildfire. Fueled in part by nitrogen pollution carried by wind from the Los Angeles Basin which enriches desert soils (Fenn et al. 2010), invasive Mediterranean grasses have spread through much of the Mojave Desert. These grasses create fuel for wildfires (Drake et al. 2015) and outcompete native annual plants (DeFalco et al. 2003). In 1995, 34 plots in the Mojave Desert near Barstow had frequencies of occurrence of 17% for *Bromus* and 38% for *Schismus* (both invasive grasses) (Brooks 1999). A more recent study sampled 718 plots across the Mojave Desert in 2009–2013 to investigate invasive grasses (*Bromus* spp. and *Schismus* spp.) and an invasive forb *(Erodium cictarium*). At least one of the invasive taxa occurred in 91% of the plots with herbaceous cover, and two or more of the species co-occurred in 77% (Underwood et al. 2019). Although these two methodologies are different, the general trend of increasing cover of invasive grass and forb species has occurred broadly across the Mojave Desert.

Berry et al. (2020b) summarized the impacts of invasive grasses on desert tortoise:

> “Tortoises avoid plants high in potassium and do not thrive on diets of native or non-native grasses. Both juveniles and adults lose mass and are out of nitrogen balance when consuming grasses (Barboza 1995a, b; Hazard et al. 2009, 2010; Drake et al. 2016). Grasses are high in fiber, contain less digestible energy, and little protein (Hazard et al. 2009), causing juveniles to lose phosphorus and potentially shell volume (Hazard et al. 2010). Because of numerous human activities, invasive, non-native, and fire-prone grasses became established in tortoise habitat and now contribute substantially to the biomass of annual plants in late winter and spring, the principal feeding time for the tortoise (Brooks and Berry 2006, Brooks and Matchett 2006, Brooks et al. 2006, Minnich 2008). These grasses compete with native forbs for nutrients (Brooks 2000a). A diet of grasses is insufficient in nutrients and leads to water loss during digestion (Hazard et al. 2009, 2010). In experimental studies, 32–37% of neonates and yearlings did not survive on a diet of grasses, whereas individuals in these size groups fed native

> forbs or a mix of native forbs and grasses had better body condition, immune functions, growth, and survival rates exceeding 95% (Drake et al. 2016)."

In contrast to grasses, the alien forb *Erodium* provided sufficient nitrogen and is of similar nutritional quality as a native forb (Nagy et al. 1998), allowing juvenile tortoises fed on forbs to gain weight (Hazard et al. 2009).

Livestock and other grazers

Grazing by livestock is a major part of the recent history of the desert. Until the 1990 listing of the desert tortoise as threatened under the ESA, grazing by livestock was allowed on BLM land in tortoise range (Berry et al. 2014). After listing, BLM banned livestock grazing in the CHUs. However, grazing is allowed on private inholdings within the CHUs, which are often unfenced. The documented impacts of livestock on tortoises include competition for food, trampling to death, and causing the collapse of burrows (see Berry and Murphy (2019)). Livestock also degrade habitat by creating or expanding trails via trampling which reduces annual cover and disrupts the soil surface, thus promoting wind erosion, and compacts the soil which slows future growth of annual plants (Webb and Stielstra 1979, Lovich and Bainbridge 1999). Livestock increase browsing pressure on the trees and shrubs tortoises require for shade and for establishing burrows (Berry et al. 2020a). Artificial watering sites set up for livestock concentrate activity of wild and domesticated large herbivores, potentially changing aspects of soil nutrients, compaction, seedbanks, and density of invasive species nearby. In a grazing allotment on BLM land in the west central Mojave Desert, cover of native plants decreased with increasing proximity to water site, while cover of alien (but not necessarily invasive) species increased (Brooks et al. 2006). This change in plant composition was observed up to 800m away from the watering site. Ninety-six percent of the alien plant cover was made up of three species, including the forb *Erodium cicutarium* and the alien grass *Schismus* spp. (Brooks et al. 2006).

4.4 Predation

Predation affects tortoises across age classes, with different species predating various age classes. While there have always been predators that target tortoises, the number of predators and their distribution on the landscape has increased in tandem with human development.

The best studied predators of tortoises are ravens and coyotes. These species are generalist predators which utilize a variety of habitats including human modified ones. Human presence in tortoise habitat provides food resources such as unsecured trash, water, and road-killed carcasses, and buildings and other structures that provide shelter (Boarman et al. 2006, Kristan and Boarman 2007). These 'resources bonanzas' (Kristan and Boarman 2007) allow raven and coyote populations to flourish, increasing predation pressure on native prey.

Raven populations have drastically increased in the Mojave Desert since the 20th century and have become a major predator of juvenile tortoises. This contrasts with population trends for many other bird species. Between the early 20th century and 2013–16, survey sites in the

Mojave Desert lost 43% of their bird species on average (Iknayan and Beissinger 2018). Ravens were the only species to substantially increase across survey sites. The probability that ravens would be detected at a survey site was on average 35% in the first half of the 20th century and 76% in 2013–2016 (Iknayan and Beissinger 2018). In 2020, surveys in Fenner, Ivanpah, Fremont-Kramer, Ord-Rodman, and Superior-Cronese CHUs found average densities of 0.63 ravens/km^2 in Fenner in the east to 2.44 ravens/km^2 in Fremont-Kramer in the west (Holcomb et al. 2021). This expansion of raven presence in extent and abundance is due at least in part to increased anthropogenic subsidies (Boarman and Berry 1995). Ravens spend their time near these subsidies (Boarman and Berry 1995, Boarman et al. 1995, 2006), which is one of the factors that leads to higher mortality for tortoises near human infrastructure than in open desert (Berry et al. 2006, Esque et al. 2010). As human infrastructure has increased in the Mojave Desert, the impact of raven predation on desert tortoise populations has likely increased. Nagy et al. (2015b) released 53 tortoises on Fort Irwin National Training Center in 2005, and 78% of the mortality of smaller tortoises (carapace 45–80 mm) was due to ravens, while coyotes were a major source of mortality for larger (111–175 mm) tortoises (Nagy et al. 2015*b*). High levels of raven predation on juveniles are thought to have led to far fewer juveniles being observed in the annual TCA surveys. In an area with a raven density of 2.4/km^2, the USFWS estimated survival of 0–12-year-old tortoises at 51%, which is much lower than in areas without ravens (Holcomb 2022*b*). Distance to the nearest raven nest impacts the survival rates of 0-10 year old tortoises. Using decoy tortoises, Holcomb et al. (2021) found that juvenile tortoises on average had an annual survival rate of 63% 500m from a raven's nest, while tortoises 1.72 km away had ~76% annual survival rates. They estimated that in areas where there were more than 0.89 ravens/km^2, and tortoises were less than 1.72 km from a nest, juvenile mortality would be great enough to cause population decline. If these criteria were applied to the Fremont-Kramer CHU, raven predation alone would likely have caused "inadequate" recruitment of juvenile tortoises across the majority of the CHUs over the past 20 years (Holcomb et al. 2021). Ivanpah and Fenner CHUs have fewer anthropogenic subsidies for ravens and therefore lower raven densities. However, the densities in those CHUs are high enough that predation pressure combined with drought, road mortality and invasive species together permit sustained recruitment of juvenile tortoises only in a few places. (Holcomb et al. 2021)

Predation pressure by ravens is not even across the tortoise range. In a study in the El Paso Mountains east of Bakersfield between 2008 and 2009, avian predators (mostly ravens) accounted for only 2.5% (on plot) and 3.7% (off plot) of observed mortalities (Berry et al. 2020*c*).

Coyotes are a major predator of adult tortoises. In a translocation study in the Superior-Cronese CHU, 158 tortoises were translocated from Ft. Irwin in 2008. Ten years later, 104 were dead, an estimated 60% of which were killed by coyotes (Mack and Berry 2023). Kelly et al. (2021) found that coyotes in the Mojave Desert predated more adult than juvenile tortoises while desert kit foxes focused on juveniles. In an examination of the dead tortoises found in the El Paso Mountains east of Bakersfield between 2008 and 2009, 20% of the carcasses found on the survey plots and about 52% of those found off plots were killed by mammalian predators including coyote, kit fox, and badger (Berry et al. 2020*c*).

There is also some evidence that canid predators focus more on females than males. In the Superior-Cronese CHU in 2008, Esque et al. (2010) found that tortoises suffered high levels of mortality (8.3–25% of tracked tortoises died in the year covered by the study), with the majority of tortoises found dead having been killed by predators (likely coyotes) and that females were more likely to be killed because they were smaller. They also looked at reference sites across the Mojave Desert and found that coyote predation on tortoises was strongly associated with the size of nearby human populations (Esque et al. 2010).

Other predators of tortoises include fire ants, white-tailed antelope squirrels, bobcats (Nagy et al. 2015*a,b*), red-tailed Hawks (Anderson and Berry 2019), rattlesnakes (Berry et al. 2016), domestic dogs (Berry and Murphy 2019), and badgers (Smith et al. 2016).

Like many threats facing desert tortoises, predation may be influenced by other factors including drought (Esque et al. 2010). The periods of extended drought may exacerbate coyote predation pressure due to low rodent and lagomorph numbers and coyotes switching to relying more on tortoises for food, however data on small mammal abundances that would provide direct evidence of this is lacking (Esque et al. 2010).

4.5 Climate Change and Drought

Anthropogenic climate change has led to higher annual average air temperatures in general as well as increased volatility of California’s climate. Extreme events like drought and heat waves are more frequent, rainfall is increasingly variable, and flow regimes of rivers are changing (Bedsworth et al. 2018). These changes have led to observable shifts in species distributions and timing of life history events (Office of Environmental Health Hazard Assessment 2018). In California, Mojave Desert Tortoises inhabit the relatively cooler high Mojave Desert, and the hotter low Sonoran Desert. The western part of the tortoise range in the Mojave Desert gets most of its precipitation in the winter with only about 15% from summer monsoons, whereas the monsoons account for about 30% of yearly precipitation in the eastern deserts (Hopkins 2018).

Impacts of Increased heat

In the inland deserts of California, daily maximum temperatures warmed by 0.4–0.7°F (0.2–0.38°C) when 1976–2005 was compared to a historical base line of 1961–1990 (Hopkins 2018). Annual average maximum daily temperatures are projected to rise 5.6–8.8°F (3.1–4.9°C) by 2100 across the state generally as compared to a historical average from 1976–2005. In the already hot inland deserts, maximum daily temperatures are projected to see increases of up to 8–14°F (4.4–7.7°C) by 2070–2100, depending on the future emission levels of greenhouse gases (Hopkins 2018). It is projected that there will up to 141 days a year in the Mojave Desert when the temperature exceeds 95°F (35°C), with minimum daily temperatures projected to rise 4–7°F (2.2–3.8°C) by 2070–2100 (Hopkins 2018).

Under warming scenarios described above, desert tortoises will have fewer areas where they can stay within their physiological limits. As habitat area shrinks, tortoises are already heading upslope in some areas to escape the heat of the valley bottoms, a distribution known as the ‘toilet bowl effect’ (W. Campbell pers. comm. May 2022). This type of movement may become more difficult as temperatures increase and suitable upslope areas shrink. Sadoti et al. (2017) found that tortoises restrict their movements when it is hotter. While this is not necessarily surprising, if there are more days when it is too hot for tortoises to move, they might find it harder to move to avoid those hot temperatures and will have limited opportunities to disperse or find mates. However, the degree to which increased heat in the summer will shift mating season or impact reproductive success is unknown. Increased temperatures will make burrows as refugia from the heat more critical. Since only certain types of soils and substrates allow for creation of adequately long tunnels, available tunnel sites may become a critical habitat concern in the future and should be taken into consideration in conservation efforts (Mack et al. 2015).

Impacts of drought

Desert tortoises are adapted to drought and heat. However, increasing levels of both are likely to cause physiological stress, alter the availability of edible vegetation, and increase the impact of predation. Barrows (2011) lists some of the physiological and behavioral impacts of drought:

> “Drought conditions result in reduced tortoise activity (Duda et al., 1999) and lower metabolic and reproductive rates (Peterson, 1996a; Henen, 1997; Henen et al., 1998) although some breeding activity occurs even during periods of water stress (Henen, 1997). Despite these behavioral and physiological adaptations, during droughts tortoises experience as much as 40% loss of body mass and a 60% loss of water volume relative to body mass as well as large variations in blood osmolarity (Peterson, 1996b) and can have higher levels of mortality (Turner et al., 1984).”

California has undergone extreme drought recently with the 2000–2021 span being the driest in the southwestern US in the past 1,200 years (Williams et al. 2022). Although there is significant uncertainty regarding projected precipitation changes, current models show that winter precipitation is likely to increase in the inland deserts, but the summer monsoon precipitation could decrease up to 40% (Hopkins 2018). Precipitation events are likely to be more intense and at the same time soils are predicted to be drier, leading to more flash flooding (Hopkins 2018). The projected warmer and periodically drier conditions during the 21st century may increase the risk for more severe drought (Hopkins 2018).

Long-term drought has caused die offs of perennial plants in desert tortoise habitat, likely driven by lack of winter rain (McAuliffe and Hamerlynck 2010). Die offs were extensive but not homogenous, and soil conditions likely played a role (McAuliffe and Hamerlynck 2010). Tortoises are selective herbivores that will feed from a wide variety of available plants if necessary but primarily focus their observed foraging effort on a small set of species, many of which are so rare on the landscape they were not detected during plant surveys (Jennings and Berry 2015). Given predictions that winters may become wetter but summers drier (Hopkins

2018), the impacts of future droughts on the vegetation that tortoises rely on is unclear. Some invasive species of *Bromus* grasses are successful in disturbed habitats, and their presence in desert habitat has helped alter the fire cycle (Brooks 1999, Bradley et al. 2016). However, germination, growth, and reproduction are limited by temperature and rainfall which makes it difficult to predict the relative success of invasive grasses vs. native forbs under predicted climate changes (Bradley et al. 2016). It is possible that tortoises will also face increased nutritional stress if preferred plants die off and more nutrient poor grasses like *Bromus* remain available.

Lovich et al. (2014) used surveys in Joshua Tree NP from 1979 to 2012 to estimate the impact of persistent and recurrent drought on tortoise survival. Estimated population size decreased dramatically from 1996 to 2012, with high survival in 1978–1996, and lower survival in 1997–2002. The lower survival rates were concurrent to persistent drought, and estimated survival rates were best explained by winter precipitation. Being in a national park, tortoises in Joshua Tree should be sheltered from many anthropogenic impacts including large scale habitat modification and degradation and direct killing by humans. In addition, in 2012, many of the dead tortoises showed signs consistent with death by dehydration and starvation. Therefore, the authors concluded the decline was likely the result of reduced survival rates due to drought (Lovich et al. 2014). Other populations of desert tortoises have also shown a negative impact of drought on survival and abundance. Populations in Arizona of *G. agassizii* and *G. morafkai* were surveyed multiple times between 1990 and 2017 and experienced very low survival (30% in the Black Mountains and 34% in the Hualapai Mountains) during a drought, which led to a drop in adult abundances of about 50% (U.S. Fish and Wildlife Service 2022*a*).

Another potential source of indirect stress from increasing drought comes from predators. Under drought conditions, the rodents and lagomorphs that coyotes regularly prey on tend to be depleted, and it is likely that this leads to increased predation pressure on tortoises (Esque et al. 2010, Nagy et al. 2015*b*). Ravens particularly target juvenile tortoises, but since they are heavily subsidized by human activities, drought may have less of an impact on their predation behavior.

A major question is how much desert tortoise habitat will become unsuitable in the future due to heat and drought. Species have shifted altitude and/or latitude as climate has changed (Vanderwal et al. 2013, Wolf et al. 2016), but species that are not nimble dispersers may have trouble accessing new areas, and those areas may not contain the full suite of conditions necessary for survival. However, within current habitats, local refugia may persist in future climatic conditions and allow species to persist. Barrows et al. (2016) evaluated potential habitat refugia on US Marine Corps Air Ground Combat Center (MCAGCC) at Twentynine Palms and found that 33% of the study area (283,900 ha) supported desert tortoise habitat at the time. With a simulated 1°C (1.8°F) of warming, the amount of habitat shrunk by 25%, with remaining habitat occurring at higher elevation. Under a simulated 3°C warming, habitat area shrunk by 56% (to 127,650 ha). Of the remaining available habitat, 91% overlapped with current tortoise habitat, suggesting that climate refugia would be relatively easy for tortoises to access. However, it should be noted that while Barrows et al. (2016) considered 3°C (5.4°F) to be an end of century level of warming, California's 4th Climate Change Assessment from 2018 predicts that level of warming to occur in the inland deserts by 2039 (Bedsworth et al. 2018). In Joshua Tree National Park, desert tortoises are found in both the Mojave and Sonoran desert portions. Modelling by Barrows (2011) predicts that under 2°C (3.6°F) of warming with 50 mm decrease in precipitation, habitat area will decrease by about 88% in the Sonoran Desert portion and by about 66% in the Mojave Desert portion.

4.6 Fire

Desert tortoise habitat historically experienced few fires due to low plant productivity and sparse fuel loads, and those that did occur tended to burn in a patchy mosaic pattern (Esque et al. 2003). Consequently, desert tortoise are not well adapted to fire, although use of burrows can prevent mass casualties in fires (Esque et al. 2003). The expansion of invasive plants (primarily grasses like *Bromus*) has increased fuel loads in the Mojave Desert (Brooks 1999), and fire frequency in the California portion of the Mojave Desert increased between 1980 and 1995 (Brooks and Esque 2002). However, longer term studies looking at fires in 1980–2004 (Brooks and Matchett 2006) and 1992–2011 (Hegeman et al. 2014) in the Mojave Desert show no clear increase in numbers of fires or acres burned per year, though 2005 stood out since "the amount of area burned in the Mojave Desert was 385,357 ha (952,238 acres) (M. Brooks unpublished data), representing 132% of the total area that burned during the previous 25 years (Brooks and Matchett 2006). However, those time series do not include the 2020 Dome Fire in Mojave National Preserve which burned 43,273 acres (175 km^2) of higher elevation tortoise habitat (U.S. Fish and Wildlife Service 2022*a*). Fire-caused tortoise death is summarized in Berry and Murphy (2019)):

> "Woodbury and Hardy (1948) reported deaths of about 14 tortoises from a fire covering ca. 5.2 km^2 on part of the Beaver Dam Slope south of Bunkerville in 1942. In a post-fire study, Lovich et al. (2011c) described a fire in the western Sonoran Desert that killed an adult female tortoise and injured five other adult tortoises. Nussear et al. (2012) reported that three of 30 tortoises died from fire during a comparative study of translocated and resident tortoises. In the Red Cliffs Desert Reserve and critical habitat in Utah, 687 tortoises died in 2005 in a fire that burned ca. 23% of the approximately 251 km^2 habitat (A. McLuckie, pers. comm.). Drake et al. (2012) described a tortoise recovering from burns three years post-fire."

The effects of wildfire on vegetation can negatively impact tortoises. A study in the low elevation Mojave Desert shrubland found that invasive *Bromus* cover increased after one fire but did not continue increasing after additional fires (Brooks 2012). However, native vegetation cover decreased with multiple fires, with percentage cover dropping from about 25% to about 1% when fire frequency increased from one every ten years to three every ten years. Given the poor nutritional content of *Bromus*, increasing fire frequency threatens tortoises' ability to find sufficient and adequate food. Tortoises tend to remain in same areas after fire (Lovich et al.

2018), foraging for annuals in the burned areas, while using the cover of perennial shrubs only found in unburned areas (Drake et al. 2015).

The effects of a changing climate on wildfire size and frequency in desert tortoise habitat are uncertain. Increased winter rain could promote biomass growth that dries out in the hotter summers and increases fuel load (Tagestad et al. 2016). Alternately, the predicted increase in drought like conditions may keep fuel loads low. Another variable is the cause of ignitions. In the past 40 years, human caused fires were more prevalent in areas with high visitation levels such as low to mid elevation and desert montane zones, while lightning caused fires were more common in the central and eastern areas that get summer monsoons (Brooks and Matchett 2006). There are widespread campaigns and regulations aimed at reducing the chances that visitors will cause fires in the desert, and the efficacy of these campaigns may influence fire frequency and spatial distribution in the future. Overall, Hopkins (2018) suggests that strong temporal and spatial variability in precipitation and fuel load across the desert makes long-term and widespread trends in fire regime hard to predict.

4.7 Disease and Parasites

Desert tortoises are susceptible to a variety of diseases, some of which are likely to have caused or contributed to population declines. Upper respiratory tract disease (URTD) has been cited as a cause of population declines in desert tortoise and was a reason for listing under the ESA in 1990 (U.S. Fish and Wildlife Service 1990).

The disease can be caused by the bacteria *Mycoplasma agassizii* and *Mycoplasma testudineum*, while herpesviruses can cause similar symptoms (Johnson et al. 2005, Jacobson et al. 2014). The disease presents as lesions in the nasal cavity and inflammation of mucosa of the upper respiratory tract, mucal discharge from the nares, damaged nasal scales due to chronic mucal discharge, wheezing breath, swollen and watery eyes, and extreme lethargy (Jacobson et al. 1995, 2014, Johnson et al. 2005, Sandmeier et al. 2013). Tortoises that do not show clinical signs of infection can still serve as a reservoir for the disease and likely can transmit it to healthy tortoises (Jacobson et al. 1995). Transmission is most likely through direct contact that happens during courtship, mating, and fighting, and aerosol transmission is not likely (U.S. Fish and Wildlife Service 1990, Jacobson et al. 2014). The disease both directly kills tortoises and can interfere with their sense of smell and therefore their ability to forage for food and can potentially negatively affect their reproductive fitness (Germano et al. 2014, Jacobson et al. 2014). Sandmeier et al. (2013) found evidence that longer and colder winters correlated positively with the proportion of tortoises exhibiting URTD, possibly because time spent underground depresses the tortoise immune system or allows the bacteria to flourish.

Outbreaks of the disease occurred in the Desert Tortoise Natural Area in Kern County in 1989 when 627 dead tortoises were recovered during a survey, and 43% of 468 live tortoises had signs of the disease (Jacobson et al. 1991). The population declined by 90% between 1979 and 1992 (Berry and Medica 1995). In 1990–1995, Christopher et al. (2003) sampled tortoises in three sites in the Mojave Desert:

> “Of 108 tortoises, 68.5% had clinical signs of upper respiratory tract disease consistent with mycoplasmosis at least once during the study period. In addition, 48.1% developed moderate to severe shell lesions consistent with cutaneous dyskeratosis. Ulcerated or plaque-like oral lesions were noted on single occasions in 23% of tortoises at Goffs and 6% of tortoises at Ivanpah. Tortoises with oral lesions were significantly more likely than tortoises without lesions to have positive nasal cultures *for Mycoplasma agassizii* (P=0.001) and to be dehydrated (P=0.0007)”(Christopher et al. 2003).

More recent studies have found much lower prevalence of URTD. In the central Mojave Desert in 2005–2008, Berry et al. (2015) found only 1.49% of sampled tortoises were antibody positive, and a study in a similar area in 1997–2003 found 2.2% antibody positivity rate.

It is thought that the high prevalence of the disease in wild populations in the 1970s–1990s was due in part from infected captive tortoises being released into the wild. A number of factors are correlated with outbreaks of the disease, mainly factors that increase physiological stress in tortoises such as drought, heavy metal pollution, and human disturbance (Jacobson et al. 2014). Berry et al. (2015) pointed out that many of the stressors that increase tortoise vulnerability to disease, especially drought and proximity to human populations, are increasing in desert tortoise range. However, there have not been any large outbreaks documented in California recently, and in the Desert Tortoise Natural Area the disease has “evolved from an acute, epizootic disease with high mortality to a chronic endemic disease with variable morbidity, low mortality”(Jacobson et al. 2014). Reflecting the decreased level of threat currently posed by the disease, in their 2022 5-year review the USFWS stated that “direct disease management of wild tortoise populations is less important (other than in translocations of tortoises between populations) than managing factors that affect their habitat and its capacity to support healthy tortoises” (U.S. Fish and Wildlife Service 2022*a*).

Being captured by humans for research and/or translocation can stress tortoises and make them more susceptible to URTD. Therefore, official handling protocols have strict guidelines in place to minimize stress as much as possible (U.S. Fish and Wildlife Service 2020*b*, *a*). In addition, translocating sick individuals runs the risk of spreading URTD, so translocation protocols involve health assessments and quarantine to minimize disease transfer between populations (U.S. Fish and Wildlife Service 2020*b*). However, disease can be transferred by tortoises naturally dispersing, and reservoirs of the disease in populations outside of California should be considered in discussions of connectivity (Burgess et al. 2021).

Shell diseases like cutaneous dyskeratosis also affect tortoises and present as “abnormal conformation and loss of normal integrity of the horny layer (scute) of the shell and cutaneous scales. Deep shell defects may expose dermal bone” (Homer et al. 2001). Shell lesions were associated with high mortality rates of desert tortoises in Chuckwalla Bench in 1982–1988 (Figures 10 and 11, Jacobson et al. 1994). In 1979, 56% of the tortoises surveyed had shell lesions. The proportion of effected tortoises increased to 65% in 1982, to 90% in 1988, and remained high in 1990 at 87%. During those years the density of all tortoises (adults and juveniles) fell from 221/km^2 to 71/km^2, a 68% decline (Berry and Medica 1995). While the declines in population cannot be definitively tied to shell lesions, they could be a sign of a deficiency disease or toxicosis (Jacobson et al. 1994). There has been very little reported on shell disease in wild tortoises in California since the mid-1990s.

4.8 Overexploitation

Under the California Fish and Game Code, desert tortoises have had some legal protection from take or collection since 1961 (Fish & G. Code, § 5000). However, vandalism (gunshots) and collecting for pets were listed as reasons for population declines in the USFWS's 1990 decision to list the desert tortoise as threatened (U.S. Fish and Wildlife Service 1990). Before tortoises were listed, Berry (1986*b*) found that percentage of tortoise deaths from gunshots in California deserts (1972–1982) ranged from a low of 1.8% at Chuckwalla Bench to a high of 28.9% in the Fremont Valley. Overall, 14.3% of carcasses found had evidence of gunshots, with the areas with the highest percentage in the Western Mojave. In a 2008–2009 study in the El Paso Mountains in Kern County, 6 of 67 carcasses had evidence of gunshots (Berry et al. 2020*c*). Direct take of tortoises has been illegal since the species was listed under the ESA and CESA, however shooting of tortoises still occurs. Berry and Murphy (2019) reported gunshot deaths subsequent to listing in Fort Irwin National Training Center (1997-2003), Red Rock State Park (2002-2004), and the Desert Research Natural Area (2011).

Despite legal protection, Berry et al. (1996) (reported in Berry and Murphy (2019)) estimated that more than 2,000 tortoises were removed from four study areas over a 10-year period from the mid-1980s to the mid-1990s. It is likely some tortoises are still being taken from the wild, with those near roads most vulnerable. A study in the Sonoran Desert of Arizona in 2008–2009 placed decoy tortoises on roads and found 1.4% of drivers stopped and tried to collect the decoy by placing it in their vehicle. Drivers were more likely to notice the tortoises on maintained gravel roads compared to paved roads or unmaintained gravel roads. However, road type did not influence the probability a driver would try to collect the tortoise (Grandmaison and Frary 2012).

4.9 Other Human-related Activities

Mining and pollution

Although Spanish colonizers panned for gold in the Chocolate Mountains in the late 1700s, commercial mining in California deserts began in the 1800s. Prospectors and miners dug shafts to extract gold, tungsten, silver, copper, and other valuable materials (Shumway et al. 1980). Some of these shafts remain open and unfenced, and tortoises can fall in and become trapped (Berry and Murphy 2019). Mining also leaves behind pollutants of various types including mercury, arsenic, and lead that impact soil and plants (including those favored by tortoises) up to 15 km from mining sites (Chaffee and Berry 2006). These pollutants can enter tortoises via breathing, ingestion of impacted plants, or absorption through skin, and there is some concern that exposure to these toxins may make tortoises more susceptible to disease (Berry et al. 2015, Berry and Murphy 2019). Tortoises collected from the Kelly Rand Ming District northeast of California City and from Edwards Airforce Base had bioaccumulated arsenic in their shell plates compared to tortoises from areas with minimal land disturbance (Foster et al. 2009). However, Cohn et al. (2021) analyzed the blood of tortoises in the Ivanpah Valley and found that heavy metal levels in the blood were generally low (0%–7%), heavy metal levels in the soil did not exceed soil health guidelines, and there was no relationship between metal concentrations and body health or disease prevalence suggesting that tortoises were not negatively impacted by mining pollution in that area.

Deliberate Releases

Based on public comments received by the Department, well-meaning individuals may release captive tortoises, believing it will help wild populations. People may also release animals they no longer wish to keep as pets. The deliberate release of captive tortoises presents several issues. Captive tortoises can have high prevalence of respiratory diseases which could be passed on to wild tortoises if they are released (Berry et al. 2015). Releasing animals of unknown genetic origin, or even different species like *G. morfaka* or the Texas tortoise (*G. berlandieri*), could result in hybridization with wild *G. agassizii* (U. S. Fish and Wildlife Service 1994). The release of diseased captive tortoises was a large enough concern to be mentioned as reason for population declines in the 1994 Recovery Plan (U. S. Fish and Wildlife Service 1994), but we lack robust recent data on the current prevalence of releases and their effects. A public education campaign highlighting the downsides to freeing captive tortoises may help address this threat. Translocations of captive tortoises into the wild are also discussed in section 9.1.

4.10 Vulnerability of Small Populations

Desert tortoises occupy a large range in California, and even at very low densities, populations in conservation areas can still number in the thousands. However, the various factors described above have nonetheless led to dramatic declines in density and abundance across the surveyed critical habitat units (Figure 7, Tables 2 and 5. The most recent estimates of abundance in the Tortoise Conservation Areas are from 2014. In 2014, tortoise density in all the TCAs except Chocolate Mountain and Fenner was below the estimated 3.9 tortoises per km^2 needed for population viability (Table 2). Estimated abundances ranged from 1,241 in the Pinto Mountains TCA to 10,469 individuals in Chemehuevi TCA (Table 5). Although these estimates remain in the thousands, most of these areas encompass hundreds to thousands of square kilometers (see Table 1).

Table 5. Estimated abundance in the Tortoise Conservation Areas within California in 2014. Reported in U.S. Fish and Wildlife Service (2022a) using data from Allison and McLuckie (2018).

Recovery Unit	Tortoise Conservation Area	Estimated Abundance in 2014
Western Mojave	Fremont-Kramer	6,196
	Ord-Rodman	3,064
	Superior-Cronese	7,398
Eastern Mojave	Ivanpah	5,578
Colorado Desert	Chocolate Mountain	5,146
	Chuckwalla	9,304
	Chemehuevi	10,469
	Fenner	8,517
	Pinto Mountains	1,241
	Joshua Tree	4,319

Since 2014, estimated densities have declined in all the TCAs in the Western Mojave, Chuckwalla, and dramatically in the Chocolate Mountains. Ivanpah and Pinto Mountains TCAs have increased in density since 2014 but are still below the 3.9 adults/km^2 threshold. Chemehuevi and Fenner have both increased in density since 2014 and are above the viability threshold, while Joshua Tree has increased slightly in density and was at the 3.9 adults/km^2 threshold in 2020. We do not have estimated abundances that are based on these most recent density estimates, and the 2014 abundance estimates are based on amount of potential habitat in Nussear et al. (2009). Given all of the factors mentioned in the previous sections, it is likely that some suitable habitat has been lost since then due to destruction and degradation, meaning that in the TCAs where densities have gone up, abundances may not have increased concordantly. Systematic surveys of populations are not conducted outside of the TCAs, but Berry et al. (2020a, c) concluded densities and survival rates in the El Paso Mountains and the Chemehuevi Valley were so low that the populations were unviable.

Desert tortoise populations are currently vulnerable to demographic pressures that are likely to exacerbate declining trends if not addressed. Foremost is the lack of recruitment. Low reproductive output and high predation pressure on juveniles has led to a worrying lack of young tortoises (Figure 12). Even with thousands of adults in a population, if sufficient juvenile tortoises are not surviving to breeding age, the population will decline without interventions like head-starting.

The threshold density for population viability of 3.9 adults/km^2 assumes equal sex ratios in the population (U.S. Fish and Wildlife Service 2011). Unequal sex ratios are thought to lower effective population size which in small populations with limited connectivity could exacerbate inbreeding (Frankham 1995). Unfortunately, there are no published data on sex ratios in the 17 TCAs (Berry and Murphy 2019), and the recent data we have are from very limited short term sampling efforts elsewhere. Berry and Keith (2008) surveyed a ~4 km^2 plot in Red Rock Canyon

State Park, and in 2004 they found three males and one adult female. Five subadult or adult females and four subadult or adult males had died 2–4 years previously, and the authors point out that if those animals had survived, the sex ratio of the population would have been much more balanced. In a 1 mi^2 study plot in Joshua Tree NP, “Sex ratios, defined as the number of live males divided by the number of females, ranged from unity, to male biased (5:1), to female biased (0.22:1) across years with no trend in any one direction” (Lovich et al. 2014). As mentioned in the section on life history, the sex of the hatchling is heavily influenced by incubation temperature. As temperatures rise and heat extremes become more common due to anthropogenic climate change, it is likely that sex ratios at hatching will skew to be more female dominated, however the degree to which this will impact adult sex ratios is unknown. Increased reporting of the sex ratios during surveys in the TCAs would illuminate the severity of this issue and allow detection the predicted skew toward females if it were to occur.

5 EXISTING MANAGEMENT

5.1 Regulatory Status and Legal Protections

Federal

<u>Federal Endangered Species Act</u>

In August 1989, the USFWS listed the Mojave population of desert tortoise as endangered on an interim basis. Eight months later in April 1990, it issued a final rule to list it as threatened (U.S. Fish and Wildlife Service 1990). In July 2002, the USFWS received a petition to reclassify the species from threatened to endangered. In 2017, the USFWS announced a 90-day finding that the petition did not present substantial scientific or commercial information indicating that reclassifying the Mojave population of the desert tortoise may be warranted, and no status review was initiated in response to the petition. The USFWS has published status reviews in 2010 and 2022, both recommending that the threatened status be retained (U.S. Fish and Wildlife Service 2010, U.S. Fish and Wildlife Service 2022a). The 2022 status review uses much of the same data presented here and acknowledges that “the status of the Mojave Desert Tortoise had not improved by 2014 and most threats to the species persist at or above 2010–2011 levels. These conditions portend further status deterioration in the absence of concerted efforts by land managers to meaningfully reduce predator subsidies, vehicle-caused tortoise mortalities, and invasive annual plants in important tortoise habitats” (U.S. Fish and Wildlife Service 2022*a*). The recommendation to retain the threatened status was based on finding about a dozen *G. agassizii* in Arizona, east of the Colorado River and outside the boundaries of the recovery units, recognition that the range-wide population of tortoises is in the hundreds of thousands, and optimism that conservation actions will eventually result in population improvements (U.S. Fish and Wildlife Service 2022*a*).

<u>National Environmental Policy Act</u>

The National Environmental Policy Act (NEPA) requires federal agencies to assess the environmental effects of their proposed actions prior to making certain decisions. Using the NEPA process, agencies evaluate the environmental and related social and economic effects of their proposed actions. Agencies also provide opportunities for public review and comment on those evaluations. Title I of NEPA contains a Declaration of National Environmental Policy. This policy requires the federal government to use all practicable means to create and maintain conditions under which man and nature can exist in productive harmony. Section 102 in Title I of the Act requires federal agencies to incorporate environmental considerations in their planning and decision-making through a systematic interdisciplinary approach. Specifically, all federal agencies are to prepare detailed statements assessing the environmental impact of and alternatives to major federal actions significantly affecting the environment. These statements are commonly referred to as Environmental Impact Statements and Environmental Assessments.

5.1.2 State

California Law/Fish and Game Code

California law has long included protections for Mojave Desert Tortoise. In 1939, California state law prohibited purchase or sale of the species. In 1961, and additional law was passed to prohibit shooting, harming, or possessing the species (Fish & G. Code, § 5000). In 1972, the Fish and Game Code was amended to allow possession of tortoises as long as the tortoise was legally acquired (Fish & G. Code, § 5001).

California Endangered Species Act

On August 3, 1989, the Commission listed the desert tortoise as a threatened species under CESA. CESA prohibits the import, export, take, possession, purchase, or sale of Mojave Desert Tortoise, or any part or product of Mojave Desert Tortoise, except as otherwise provided by the Fish and Game Code, such as through a permit or agreement issued by the Department under the authority of the Fish and Game Code (Fish & G. Code, § 2080 *et seq.*). For example, the Department may issue permits that authorize the incidental take of listed and candidate species if the take is incidental to an otherwise lawful activity, the impacts of the authorized take are minimized and fully mitigated, the activity will not jeopardize the continued existence of the species, and other conditions are met (Fish & G. Code, §§ 2081, subd. (b).). The Department may also authorize incidental take through voluntary local programs and safe harbor agreements (Fish & G. Code, §§ 2086 and 2089.2 et. *seq.*) and for scientific, educational, or management purposes (Fish & G. Code, § 2081, subd. (a).). If the species is listed under both the federal ESA and CESA, a project that has received a federal incidental take statement or incidental take permit that is consistent with CESA can receive a consistency determination (CD) from the Department (Fish & G. Code, § 2080.1.).

Given the predominance of federal land in desert tortoise range, it should be noted that federal agencies undertaking federal projects on federal land are usually not subject to CESA and instead must typically consult with the USFWS to “ensure that actions they fund, authorize, permit, or otherwise carry out will not jeopardize the continued existence of any listed species or adversely modify designated critical habitats” (U.S. Fish and Wildlife Service 2022). However, non-federal entities working on federal lands are subject to CESA. For example, timber companies with permission to harvest timber on U.S. Forest Service lands must comply with both federal and state wildlife laws.

In 2000 and 2005, the Department prepared summary status reports describing the status of desert tortoise as declining (California Department of Fish and Wildlife 2000, California Department of Fish and Wildlife 2005). These reports summarize the status of all species listed as endangered, threatened, or candidate under CESA (Fish and G. Code § 2079), and are made available to the public on the Department's website. The 2005 report described the desert tortoise as severely threatened by population losses and further stated that tortoise populations were extremely low in some areas and may not have been viable (California Department of Fish and Wildlife 2005).

California Environmental Quality Act

State and local agencies must conduct environmental review under the California Environmental Quality Act (CEQA) for discretionary projects proposed to be carried out or approved by the public agency unless the agency properly determines the project is exempt from CEQA (Pub. Resources Code, § 21080). If a project has the potential to substantially reduce the habitat, decrease the number, or restrict the range of any rare, threatened, or endangered species, the lead agency must make a finding that the project will have a significant effect on the environment and prepare an environmental impact report (EIR) or mitigated negative declaration as appropriate before proceeding with or approving the project (Cal. Code Regs., tit. 14, §§ 15065(a)(1), 15070, and 15380.). An agency cannot approve or carry out any project for which the EIR identifies one or more significant effects on the environment unless it makes one or more of the following findings: (1) changes have been required in or incorporated into the project that avoid the significant environmental effects or mitigate them to a less than significant level; (2) those changes are in the responsibility and jurisdiction of another agency and have been, or can and should be, adopted by that other agency; or (3) specific economic, legal, social, technological, or other considerations make infeasible the mitigation measures or alternatives identified in the environmental impact report (Pub. Resources Code, § 21081; Cal. Code Regs., tit. 14, §§ 15091 and 15093.). For (3), the agency must adopt a statement of overriding considerations finding that the overriding benefits of the project outweigh the significant effects on the environment. CEQA establishes a duty for public agencies to avoid or minimize such significant negative effects where feasible (Cal. Code regs., tit. 14, § 15021.). Impacts to Mojave Desert Tortoise, as a CESA-threatened species, must be identified, evaluated, disclosed, and mitigated or justified under the Biological Resources section of an environmental document prepared pursuant to CEQA.

Nonregulatory Status

Natural Heritage Program Ranking and IUCN Red List

Natural heritage ranking does not provide any regulatory protections but is often considered during the CEQA process (Hammerson, G.A. et al. 2008). All Natural Heritage Programs, such as the CNDDB, use the same ranking methodology originally developed by The Nature Conservancy and now maintained by NatureServe. This ranking methodology consists of a global rank describing the rank for a given taxon over its entire distribution, and a state rank describing the rank for the taxon over its state distribution. Both global and state ranks reflect a combination of rarity, threat, and trend factors. The ranking methodology uses a standardized calculator that uses available information to assign a numeric score or range of scores to the taxon, with lower scores indicating that a taxon is more vulnerable to extinction, and higher scores indicating that a taxon is more stable (Faber-Langendoen et al. 2012). The rank calculation process begins with an initial rank score based on rarity and threats, with rarity (multiplied by 0.7) factored more heavily into the calculator than threats (multiplied by 0.3). The combined rarity and threat rank is then either raised or lowered based on trends. When there is a negative trend, the rank score is lowered, and when there is a positive trend the rank score is raised. Short-term trends are factored more heavily into the calculator than long-term trends. International Union for Conservation of Nature (IUCN) and NatureServe assess extinction risk for species using a time period of 10 years or 3 generations, whichever is longer, up to a maximum of 100 years (Faber-Langendoen et al. 2012).

Mojave Desert Tortoise has been assigned a global rank of G3 indicating the species is "vulnerable and at moderate risk of extinction or collapse due to a fairly restricted range, relatively few populations or occurrences, recent and widespread declines, threats, or other factors". This species has been assigned a state rank of S2 indicating the species is locally imperiled and "at high risk of extirpation in the jurisdiction due to restricted range, few populations or occurrences, steep declines, severe threats, or other factors". The factors cited for this rank include widespread habitat loss, degradation, and fragmentation, and human-associated factors that cause mortality (NatureServe 2022).

The IUCN Red List provided a global scope assessment of Mojave Desert Tortoise in October 2021 (Berry et al. 2021) resulting in a designation of critically endangered. This Red List category represents the highest risk of extinction and is assigned when a taxon has been evaluated against the ranking criteria and is not yet designated Extinct in the Wild, but qualifies above endangered, vulnerable, and near threatened. The species was originally assessed as vulnerable in 1996 and its designation has steadily increased in severity (Berry and Murphy 2019).

5.2 Management Efforts

Due to its large range and the decades since it was formally protected under the ESA and CESA, a diverse suite of government and other entities are involved in land ownership and management within the range of Mojave Desert Tortoise (Table 6). The majority of land is managed by federal agencies, but the range also includes a substantial portion of private lands. The BLM is responsible for managing nearly 11,000 km^2 of Mojave Desert Tortoise critical habitat and is the largest landowner within the species range. The NPS is responsible for the next largest section of the range, most of which is congressionally designated Wilderness Areas where motorized vehicles are prohibited. Private lands and DoD lands comprise most of the remaining land ownership within the species range.

Table 6. Land ownership within the entire range of Mojave Desert Tortoise and within designated critical habitat.

Land Management Entity	Landownership in Species Range (Km^2)	Percent of Landownership in Species Range (%)	Landownership in Critical Habitat (Km^2)	Percent of Landownership in Critical Habitat (%)
United States Bureau of Land Management	37,960	42.5	10,917	56.6
United States National Park Service	18,418	20.6	3,702	19.2
Private Lands	15,147	17	1,730	9.0
United States Department of Defense	13,018	14.6	2,270	11.8
State of California	2,018	2.3	485	2.5
Cities, Counties, Non-Profits, Special Districts	995	1.1	114	0.6
Other Public or Private Lands	391	0.4	30	0.2
Other Federal	79	0.1	19	0.1
United States Bureau of Indian Affairs	689	0.8	NA	NA
United States Forest Service	242	0.3	NA	NA
United States Bureau of Reclamation	181	0.2	NA	NA
United States Fish and Wildlife Service	89	0.1	NA	NA

Partnerships and Working Groups

The Desert Tortoise Management Oversight Group (MOG), formed in 1994, is comprised of senior managers from USFWS, BLM, state transportation agencies, state wildlife agencies, county governments, and non-governmental organizations (NGOs) that work in the tortoise range in Arizona, Nevada, and California. This group identifies regional recovery priorities, addresses issues common to multiple agencies, and shares information and updates about tortoise status and their recovery activities.

The Recovery and Sustainment Partnership (RASP) is comprised of DoD and Department of Interior agencies and is intended to provide increased flexibility for the use of land for military operations (i.e., make it easier to conduct training in areas with tortoise populations) in return for developing recovery initiatives. Under this partnership, agencies contribute to a pooled funding source to implement recovery actions such as raven management in California. Pooled funding and the Memorandum of Understanding between RASP partners allows for increased flexibility and reduced regulatory hurdles for implementation of broad, regional scale recovery actions.

The California Desert Conservation Act (Fish & G. Code, § 1450 et seq.) became effective on January 1, 2022, and establishes a California Desert Conservation Program within the California Wildlife Conservation Board with the goals of protecting habitat in California's Mojave and Colorado deserts by planning and implementing land acquisition and restoration projects. The California Desert Conservation Program could result in increased conservation or restoration of Mojave Desert Tortoise habitat in California.

United States Fish and Wildlife Service

The USFWS has developed and revised range-wide Recovery Plans for Mojave Desert Tortoise that encourage collaboration, identify research priorities, and encourage management actions for the benefit of the species. In 1994, the USFWS published the first Recovery Plan and designated more than 25,000 km^2 of critical habitat, most of which is in California (U.S. Fish and Wildlife Service 1994). The plan identified Desert Wildlife Management Areas and included management recommendations such as landscape-level management and monitoring, public education, and habitat protection (U.S. Fish and Wildlife Service 1994). In 2008 and 2011, the USFWS published revisions to the Recovery Plan which identified research priorities and recovery actions, including facilitation of recovery partnerships, protection of existing populations and habitat, supplementing populations, and implementing adaptive management (U.S. Fish and Wildlife Service 2011). In 2010, the USFWS published its first 5-year review for Mojave Desert Tortoise across its multi-state range, in which they assigned a recovery priority number indicating that the species faces a moderate degree of threat, has a low potential for recovery, and faces conflict with construction or other development projects or other forms of economic activity. The USFWS recommended no change in status from threatened to endangered, in part because implementation of the 2008 Revised Recovery Plan was expected to resolve key uncertainties and improve recovery potential. In 2022, the USFWS published another 5-year review reporting the continuing declines in density in all of the California Tortoise Conservation Areas except Joshua Tree in 2004–2014 (see Table 2), but also recommended no change in the listing status of the Mojave Desert Tortoise (U.S. Fish and Wildlife Service 2022*a*). For more detail see section 5.1.

As part of the revised 2011 Recovery Plan, Recovery Implementation Teams were developed, which are “composed of representatives from government agencies and non-profit organizations. Participants in these teams prepare proposals for recovery actions, seek funding to support the proposals, and assist with implementation when funding becomes available” (Berry and Murphy 2019). Recovery Implementation Teams have focused on restoration of habitat burned and/or denuded by livestock, trash management to subsidize predators, invasive plant control, roadway fencing, and other conservation and management actions (Berry and Murphy 2019).

Bureau of Land Management

The 2016 Desert Renewable Energy and Conversation Plan (DRECP) Land Use Plan Amendment to the California Desert Conservation Act Plan of 1980 guides management of 10 million acres (~40,469 km^2) of BLM lands, some of which is Mojave Desert Tortoise habitat. The entire DRECP Plan Area covers approximately 22.5 million acres (~91,054 km^2) of federal and non-federal land. Phase I of the DRECP focused on the BLM lands and was released as a Land Use Plan Amendment (LUPA). Phase II will focus on county-level planning designed to work in conjunction with the LUPA. Along with many other agencies and stakeholders, the Department was involved in the development of the DRECP but is not a signatory to the 2016 LUPA.

Under the DRECP, 11,290 acres (~46 km^2) of modeled desert tortoise habitat would eventually be developed for renewable energy, with a streamlined permit review process (Bureau of Land Management 2016). The LUPA contains numerous conservation and management actions, including establishment of a cumulative limit (no more than 1%) on ground-disturbing activities within BLM-owned portions of TCAs and mapped linkages. The plan amendment further prohibits long-term habitat removal in high density tortoise areas (more than five tortoises at least 160 mm carapace length per square mile, or more than 35 individuals in total), but gives an exception for transmission projects. Outside of the development focus areas intended for renewable energy, the plan amendment includes actions that are more protective of desert tortoises than direction contained in the previous land use plan (U.S. Fish and Wildlife Service 2022*a*).

National Park Service

Management of the Mojave Desert Tortoise on NPS lands is guided by the NPS Organic Act of 1916, the ESA of 1973, the Wilderness Act of 1964, the 2006 NPS Management Policies, and each unit's General Management Plan (GMP), Superintendent's compendiums, and Resource Stewardship Strategies. Broad conservation actions are outlined in GMPs and specific closures and updates to prohibited actions are contained in the Superintendent's compendium. Examples include prohibitions on use of Unmanned Aircraft Systems (drones), limits on use of artificial lights to view wildlife, requirements for food storage and trash management, and commitments for restoration of disturbed areas and/or mitigation of direct vegetation impacts.

In desert tortoise range, the NPS administers Joshua Tree National Park, Death Valley National Park, and Mojave National Preserve. The majority of lands across these three units are congressionally designated Wilderness, including nearly 50% of lands in Mojave National Preserve, approximately 85% of lands in Joshua Tree National Park, and roughly 93% of lands in Death Valley National Park. The Wilderness Act of 1964 is intended to preserve places "where the earth and its community of life are untrammeled by man, where man himself is a visitor who does not remain" (Wilderness Act section 2, subd. I). Most notably, use of offroad vehicles and motorized equipment is prohibited in Wilderness areas.

The NPS Organic Act of 1916 (39 Stat. 535, 16 U.S.C. 1, as amended), states that the NPS "shall promote and regulate the use of the Federal areas known as national parks, monuments, and reservations…to conserve the scenery and the national and historic objects and the wildlife therein and to provide for the enjoyment of the same in such manner and by such means as will leave them unimpaired for the enjoyment of future generations." The NPS Management Policies indicate that Parks will "meet its obligations under the National Park Service Organic Act and the Act to both pro-actively conserve listed species and prevent detrimental effects on these species." This includes working with other agencies and partners to implement management programs which inventory, monitor, restore, and maintain listed species habitats. The Mojave Desert Inventory & Monitoring Network of the NPS regularly implements monitoring programs at all three NPS units focused on desert spring riparian vegetation and water quality as well as upland vegetation and soil characteristics that might influence the survival of Mojave Desert Tortoise.

United States Department of Defense

The Sikes Act was established in 1960 to ensure conservation and protection of natural resources used by the DoD. The U.S. Congress amended the Sikes Act in 1997 requiring the DoD to develop and implement Integrated Natural Resources Management Plans (INRMPs). These plans outline how each military installation will manage its significant natural resources holistically while maintaining military readiness. Since these lands are often protected from access and use by the general public, they may contain some of the more significant remaining large tracts of habitat and play important roles for species conservation and habitat connectivity.

Under the ESA, the DoD is responsible for managing and protecting the threatened and endangered species found on its installations. DoD is required to consult with the USFWS and National Oceanic and Atmospheric Association (NOAA) Fisheries to manage their threatened and endangered species efforts (Dalsimer 2016).

DoD facilities within the Mojave Desert Tortoise range include Naval Air Weapons Station China Lake, Edwards Air Force Base, Fort Irwin, the Marine Corps Air Ground Combat Center, and the Chocolate Mountain Aerial Gunnery Range. DoD is an active collaborator in the MOG and RASP partnerships and contributes funding to many recovery actions. Unlike most other federal land, tortoise habitat under DoD jurisdiction is “subject to more dramatic changes in management or use than other Federal lands depending on the changing national security situation” (U.S. Fish and Wildlife Service 2011). This means that large tracts of desert tortoise habitat can relatively quickly be converted to uses that are incompatible with desert tortoise, requiring translocation of large number of tortoises (see section 4.1 for more details). To offset these losses of tortoise habitat, the DoD undertakes a variety of actions such as purchasing land in critical habitat units, increasing law enforcement, predator control and monitoring, rehabilitation of closed roads, and installation of fencing.

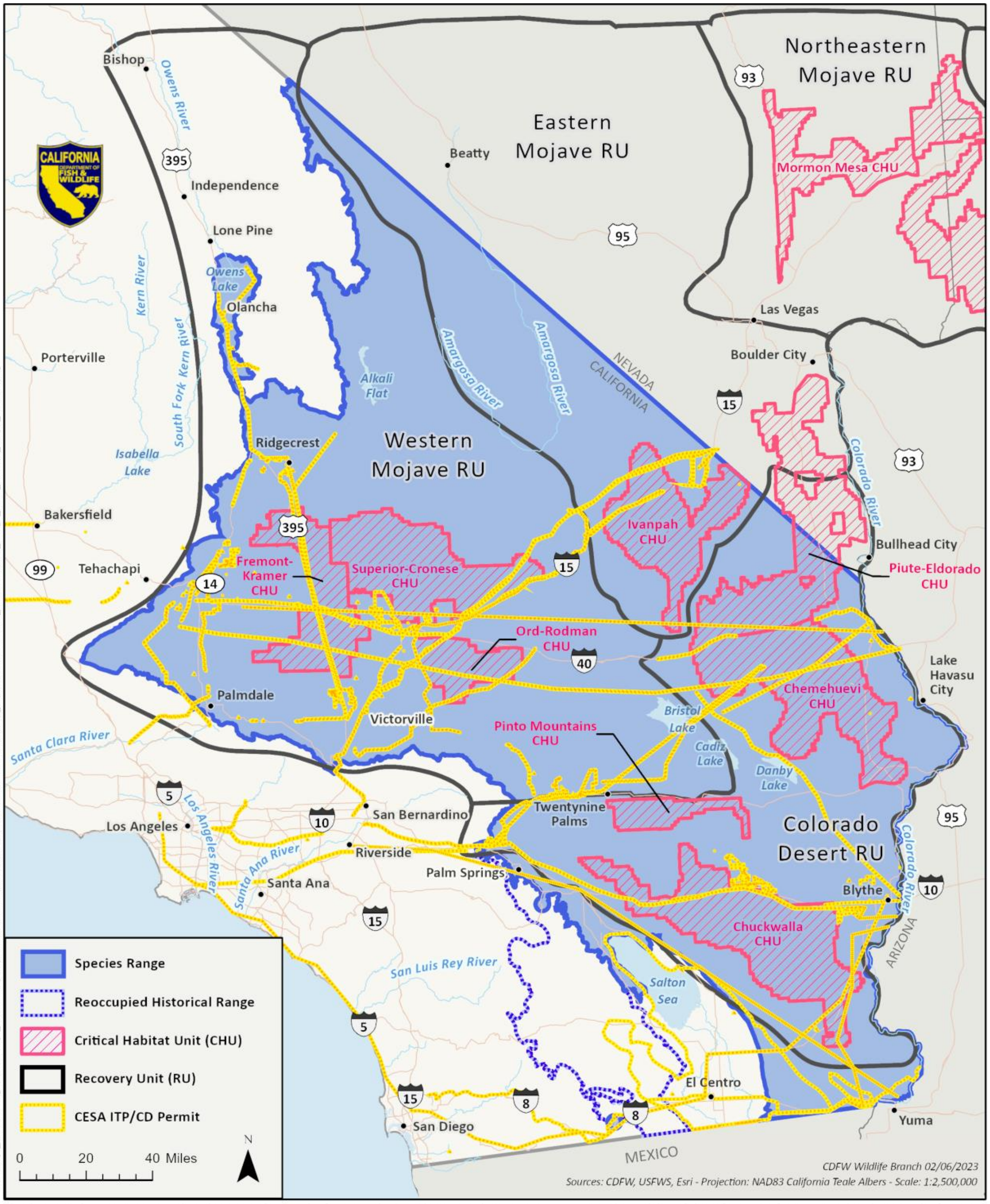
California Department of Fish and Wildlife

CESA prohibits the unauthorized take of desert tortoise, but the Department may permit take that is incidental to otherwise lawful activities if the impacts of the take are minimized and fully mitigated. These permits are commonly called incidental take permits.

The Department is required to determine what qualifies as "full mitigation" for each permit on a case-by-case basis. As a practical matter, perpetual protection and management of habitat mitigation lands has often been the type of mitigation required. In addition, projects may have to implement a variety of measures to minimize take of tortoises including but not limited to surveying and monitoring for their presence, fencing to keep tortoises out of the project site, relocating of nests to safe offsite locations, translocating tortoises on the project site, and managing ravens on the site.

Since 1989, CDFW has issued 192 ITPs and 49 CDs covering incidental take of Mojave Desert Tortoise; the most common project types include renewable energy, transportation, and utility infrastructure (for locations of permitted projects see Figure 13). The Department's records are not complete; however, at minimum these permits authorize 62,131 acres (~250 km^2) of permanent impacts and 14,672 acres (~59 km^2) of temporary impacts (based on data available about temporary acres from 36% of ITPs and 79% of ITPs for permanent impacts). The ratio at which projects have to protect and manage mitigation habitat varies on a project-by-project basis, however projects sited in federally designated Critical Habitat are generally mitigated at a 5:1 ratio and other habitats at around a 3:1 ratio depending on quality. Permit holders have multiple options when choosing mitigation lands but must typically provide for permanent protection and perpetual management of habitat for the listed species either on the project site or at another location approved by the Department. This requires transfer of fee-title and/or recordation of a conservation easement, to which the Department must be at least a third-party beneficiary, funding of short-term management practices and a long-term management endowment, and monitoring to ensure compliance with the conservation easement. Alternatively, permittees may purchase credits at conservation and mitigation banks.

The desert tortoise is addressed in several Natural Community Conservation Plans (NCCPs) and Habitat Conservation Plans (HCPs) in California, including the West Mojave Plan, the Coachella Valley Multi Species Habitat Conservation Plan (MSHCP), and the California Energy Commission's Habitat and Species Protection Research Project. The Coachella Valley MSHCP area supports a small, but significant population of desert tortoise in Riverside County (CDFW 2005). This MSHCP includes all federally designated critical habitat within the plan area as part of the Desert Tortoise and Linkage Conservation Area.



Disclaimer: Information presented on this map is for visual reference only. Consult primary data sources to ascertain the usability of this information for any use other than visual reference.

Figure 13. Map of Incidental Take Permits (ITPs) and Consistency Determinations (CD) in the general area of Mojave Desert Tortoise range in California. The linear permit areas are for energy transmission lines, pipelines, fiber optic lines, and other linear features. Other types of projects are represented as polygons.

6 SUMMARY OF LISTING FACTORS

The preceding sections of this status review describe the best scientific information available to the Department, with respect to the key factors identified in the regulations. This section considers the significance of any threat to the continued existence of Mojave Desert Tortoise for each of the factors.

6.1 Present or Threatened Modification or Destruction of Habitat

Like many species, habitat loss and degradation are major concerns for desert tortoise. Tortoises are sensitive to habitat alteration by development and an estimated 66% of Mojave Desert Tortoise habitat has some development within 1 km (Carter et al. 2020). The direct impacts of development include removal of soil and vegetation, destruction of burrows, and creation of roads and other infrastructure that can kill tortoises or hinder their movements (Boarman and Sazaki 1996, 2006). Large amounts of desert tortoise habitat are open to renewable energy development, off road driving, or is under DoD jurisdiction and could be used for training or associated infrastructure development. For example, in the past 10 years, a net of ~150,000 acres of the ~3,000,000 acres (~607 km^2 of ~12,140 km^2) of viable desert tortoise habitat under DoD jurisdiction have been eliminated (U.S. Fish and Wildlife Service 2022*a*).

Tortoises are less likely to utilize areas that have even a low level of development. Carter et al. (2020) found that "encounter rates for both live and dead Mojave desert tortoises combined decreased significantly with increased development levels" and that when "10% of the area within 1 km of that location has been altered by development", it was rare to find live or dead tortoises at that location. To date, models show that only 5% of Mojave Desert Tortoise habitat falls into that category (Carter et al. 2020). However, as the demands for housing and renewable energy facilities increase in the desert, it is likely that the amount of development within or near tortoise habitat will continue to increase.

Currently there are about 62,000 acres (about 250 km^2) permitted to be permanently impacted by renewable energy projects within desert tortoise range in California. Wind and solar farms alter the habitat in permanent and temporary ways (though some alterations considered to be temporary can have impacts lasting decades in the desert. Studies of the impacts of wind farms on tortoises indicate that tortoises can survive on some farm sites, and that in some cases their survivorship may be higher on farms than in surrounding areas. However, such studies are few and the impacts of wind and solar farms on tortoises remain uncertain. Roads and OHV routes are a direct threat to tortoises through roadkill, as well as habitat degradation and fragmentation. The proliferation of such features in desert tortoise habitat adversely impacts tortoises, especially since the installation of exclusion fencing has been limited over the past decade. Other factors that degrade habitat include increasing temperatures and potential drought frequency, which are expected to reduce the ability of current habitat areas to support tortoise populations in the future.

Invasive grasses have caused widespread impacts to desert tortoise habitat. These grasses, mostly *Bromus* and *Schismus* species, are outcompeting native grasses and forbs that tortoises preferentially eat. The invasive grasses lack sufficient levels of the nutrients that tortoises need to survive and consuming them leads to increased water loss. The impact seems especially acute on juvenile tortoises and is likely being a factor in the low survival rates for juveniles seen in some areas. The grasses also intensify the fire cycle which in turn decreases the amount of native vegetation that is an important food source for tortoises.

Loss of habitat is traditionally considered to be one of the major drivers of species declines worldwide. However, direct loss of habitat may be less of an issue for desert tortoises than habitat degradation. Although current estimates indicate more than 90% of historical habitat still available (only 7.4% of modelled habitat is currently considered completely unsuitable (Holcomb 2022*a*)), tortoise populations have declined severely in the past two decades. Habitat degradation through road construction and off-vehicle vehicle use, fire, invasive species outcompeting native plants, and increasing temperatures due to climate change have likely reduced the quality of much of the remaining habitat. Therefore, focusing solely on the proportion of habitat loss in the desert tortoise range as a means of measuring population impacts may be misleading and create an overly optimistic picture.

6.2 Overexploitation

People still shoot and collect desert tortoises but seemingly not at the frequencies seen in the late 20th century. This may have to do with changing human behavior patterns or because there are simply fewer tortoises on the landscape for humans to encounter. Overexploitation is not currently considered a major threat to Mojave Desert Tortoise.

6.3 Predation

Predation, especially by ravens and coyotes, is a significant factor in desert tortoise population decline. Ravens (and to lesser extent coyotes) are subsidized by the infrastructure, water, and food around human development, and their populations have dramatically increased in recent decades. Ravens preferentially target juvenile tortoises, and since clutch sizes are low and tortoises can take 12–20 years to become sexually mature, decreased juvenile survival is likely an important factor in many areas with declining tortoise densities. Given the slow life history traits of tortoises, lower juvenile survival will be a long-term issue for the population, impacting populations for decades. Coyotes can kill older tortoises, and in some areas are a significant cause of death meaning that even in the unlikely scenario where the threat from ravens is eliminated quickly, predation could remain an issue and recovery is unlikely to be swift.

6.4 Competition

There is some direct competition with livestock for food however there is not much recent data on the severity of the impacts specifically in California. In a recent paper on anthropogenic stressors to desert tortoises, livestock grazing is listed as a threat in Nevada but not California (Tuma et al. 2016).

6.5 Disease

Upper respiratory tract disease has been cited as a cause of population declines in desert tortoise and was a reason for listing under the ESA in 1990. It is thought that its high prevalence in wild populations in the 1970s through 1990s was due in part to infected captive tortoises being released into the wild. Drought, heavy metal pollution, and human disturbance increase physiological stress in tortoises and are correlated with outbreaks of the disease (Jacobson et al. 2014). Berry et al. (2015) points out that many of the stressors that increase tortoise vulnerability to disease, especially drought and proximity to human populations, are increasing in desert tortoise range. However, there have not been any large outbreaks causing mortality documented in California since the 1990s. There is not currently significant concern about the disease in wild populations, although great care still needs to be taken during translocations to prevent any accidental spread.

6.6 Other Natural Occurrences or Human-related Activities

Climate Change

Climate change is a major threat which will also intensify other threats. The predicted increase in heat and periodically drier conditions increase the chances drought in California through the end of the century will increase the amount of time tortoises experience physiological stress, decrease the amount of suitable habitat, and likely negatively alter the vegetation they rely on. Climate change in general is causing governments to invest in the expansion of wind and solar farms, and the number of proposed renewable energy projects in desert tortoise habitat are increasing. The DoD considers climate change a major threat to global stability (U.S. Department of Defense 2021) and predicts that global climate change will intensify political unrest worldwide. This makes it possible that training activity in the many military bases in desert tortoise habitat will increase in the future, converting more land from suitable tortoise habitat to training areas, and requiring large scale translocations of resident tortoise as mitigation.

Fire

Desert tortoise habitat historically experienced few fires due to low plant productivity and sparse fuel loads, and those that did ignite generally burned at low severity in a patchy mosaic pattern. Consequently, desert tortoise and the vegetation they rely on are not well adapted to fire. Tortoises have some direct protection from fire as they spend much of their time underground. The expansion of invasive plants (primarily invasive *Bromus* species) has increased fuel loads, though over the long-term fires have not become more common in the desert. Fire directly causes some tortoise death and further changes the vegetative community making it more difficult for tortoises to find nutritious foods.

Mining

Mining has a long legacy in desert tortoise habitat. Some mining shafts remain open and unfenced, and tortoises can fall in and get trapped inside. Mining leaves behind pollutants of various types including mercury, arsenic, and lead that impact soil and plants (including those favored by tortoises) up to 15 km from mining sites. Tortoises can absorb the pollutants via breathing, eating impacted plants, or absorption through skin, and exposure to these toxins may make tortoises more susceptible to disease. Though there is evidence pollution from mining has negative impacts on tortoise health, it does not appear to be a major threat to tortoise populations.

6.7 Summary of Key Findings

Historical and current conservation efforts have not proven sufficient to halt the population declines of desert tortoise. The most robust estimates of densities come from annual systematic surveys done in the Tortoise Conservation Areas, which include the Critical Habitat Units and contiguous areas with potential tortoise habitat and compatible management. These surveys began in 2004 and cover large areas of the best tortoise habitat. Taken as a whole, these surveys provide strong evidence that most tortoise populations in California have declined rapidly over the past two decades. Estimated rates of annual decline in density in the TCAs for 2004–2014 were between 3.3% and 10.8% per year, which is unsustainable for most species, but especially for such a long-lived and slow-reproducing species as the desert tortoise. Sixty percent of the TCAs currently have densities below 3.9 adult tortoises/km^2 which is the density considered necessary for population viability, while another 30% are at the threshold. Only one TCA currently has density above the 3.9/km^2 population viability threshold. While we do not have estimates of density in all the TCAs prior to the desert tortoise being listed as threatened, densities in the early 1980s in select TCAs varied between 35 and 90 adults/km^2, and between 35 and 70 adults/km^2 when they were listed as threatened under CESA in 1989. It is estimated that densities of adults in certain TCAs fell between 89% and 97% from the early 1980s to 2020–2021. Since the late 1970s, the number of juveniles detected on surveys has also fallen sharply, to the point that in recent surveys in the Western Mojave almost no juveniles were found. Overall, the population data available from the last 20 years continue to document tortoise declines in most sampled areas populations in in many TCAs, which represent much of the best habitat, are no longer considered viable.

Due to the slow components of tortoise life history, if past and current management is successful at mitigating threats and adverse impacts to tortoises, it would still take at least 25 years of positive population growth to reach the USFWS Recovery Criteria (U.S. Fish and Wildlife Service 2022*a*). For example, in the USFWS 1994 Recovery Plan they estimate that when adult survivorship is 98%, population growth would be less than 0.5% per year, and would take 140 years to double in size. Annual survival rates for both adults and juveniles in many areas are much lower than 98%, making population stability, let alone growth, unlikely. Collectively, the available data show that despite 30 years of state and federal protection, in the critical habitat units (which are considered to be the best tortoise habitat), most tortoise populations have continued to decline and do not show consistent signs of recovery. In most regularly surveyed areas, tortoise densities are below the thresholds considered to represent population viability.

The dramatic declines in Mojave Desert Tortoise populations have likely resulted from the extensive number and interconnected nature of the threats facing tortoises in California. The important threats fall in two categories, those that directly kill adults and juveniles, and changes in habitat suitability that make it less likely to support healthy populations.

Particularly in long-lived species that are slow to reproduce, decreased survival has long lasting impacts on the population and can alter demographic patterns for decades. Predation pressure from ravens and coyotes reduce the survival of juvenile and adult tortoises respectively. Increasing development removes or reduces habitat suitability and creates roads and increased traffic that can endanger tortoises. Extensive networks of trails for off-highway vehicles on public lands increase the chance that tortoises will be run over even in areas without paved roads. Well-designed fences and culverts can help prevent tortoises and other wildlife being killed by vehicles along major roads, but many primary roads remain unfenced and little fencing has been built since 2011.

Habitat modification and destruction reduces the amount of habitat that can support tortoises in the long-term. Development in the desert will likely continue and possibly speed up given California's need for housing and renewable energy (Office of Governor Gavin Newsom 2021). The Department of Defense is a large landowner in desert tortoise range and frequently expands the areas that it uses for training, requiring translocation of hundreds of tortoises. Large scale tortoise translocations do not tend to have high survival rates. It is hard to predict the amount of land the DoD will convert into training areas in the future, but given the increases of the federal defense budget over the past 20 years (Wikipedia 2023), military training needs are not likely to decrease.

Additional factors have direct and indirect impacts on tortoises and their habitat. Climate change, which is likely to make desert tortoise range hotter and drier, will increase tortoise physiological stress and change activity patterns. The nutritious native plants tortoises preferably feed on are being outcompeted by nutritionally poor invasive grasses, which can lower tortoise survival rates. Fires fueled by invasive grasses are becoming more common, which decreases the amount of native vegetation available for tortoises to feed on.

Some threats appear to be declining. Upper respiratory tract diseases were a major concern when tortoises were listed as threatened. Encouragingly, the prevalence of diseased tortoises is lower than in previous decades, and it does not currently appear to be an acute threat to wild populations. The prevalence of gunshot deaths also decreased in the past several decades, but it is unclear if this is due to change in human behavior or simply reflects a lower tortoise encounter rate due to declining tortoise density.

There is still a large amount of available habitat and even at low densities, in 2014 there were estimated to be more than 61,000 adult tortoises within the TCAs. However, that is a decrease from an estimated ~310,000 adults in 2004, and as densities have continued to fall since 2014, current abundance is likely lower than 60,000 adult tortoises, and in 60% of the TCAs the populations are below the densities needed for viability. Given that there are multiple interacting threats that are reducing the amount and quality of viable habitat and lowering survival rates of adults and juveniles, the available information suggests that tortoise populations will continue to decline for the foreseeable future. However, several of the major threats like raven predation on juveniles and the lack of fencing on highways can be minimized with the appropriate resources and policy changes. Implementing these actions where appropriate to improve survival in the short term is critical to give desert tortoises the resilience to be able to weather longer term habitat and climactic effects.

7 PROTECTION AFFORDED BY LISTING

It is the policy of the state to conserve, protect, restore and enhance any endangered or any threatened species and its habitat (Fish & G. Code, § 2052). If listed as an endangered rather than a threatened species pursuant to CESA, unauthorized "take" of Mojave Desert Tortoise will remain prohibited and its conservation, protection, and enhancement will remain a statewide priority. As the Mojave Desert Tortoise is already listed as threatened, public agency environmental review is required under the California Environmental Quality Act (CEQA) and its federal counterpart, the National Environmental Policy Act (NEPA). There are no changes in legal protections under CESA for species changed from threatened to endangered.

However, if the status of the Mojave Desert Tortoise is changed to endangered under CESA, it may increase the likelihood that state and federal land and resource management agencies will prioritize and allocate more funds towards protection and recovery actions. The federal and state listings of the desert tortoise as threatened stimulated a great deal of interest and funding in addressing basic questions about the species, with expanded research into status and distribution of populations, ecology, genetics, and diseases, as well as collaborations to minimize conflict among the many users of desert tortoise habitats. It also triggered the creation of a federal Recovery Plan and the numerous conservation and management measures outlined in the Existing Management Section. However, funding for species recovery and management is limited, and there is a growing list of threatened and endangered species. Therefore, while a status change pursuant to CESA will highlight the urgency of tortoise conservation needs, the management effects of such a change are uncertain.

8 RECOMMENDATION FOR THE COMMISSION

CESA requires the Department to prepare this report regarding the status of Mojave Desert Tortoise in California based upon the best scientific information available to the Department (Fish & G. Code, § 2074.6). CESA also requires the Department to indicate in this status review whether the petitioned action is warranted (Fish & G. Code, § 2074.6; Cal. Code Regs., tit. 14, § 670.1, subd. (f)). Based on the criteria described above, the best scientific information available to the Department indicates that Mojave Desert Tortoise is in serious danger of becoming extinct in California due to one or more causes including present or threatened degradation and loss of habitat, predation, and other natural occurrences and human-related activities.

The Department recommends that the Commission find the petitioned action to change the status of Mojave Desert Tortoise from threatened to endangered to be warranted.

9 MANAGEMENT RECOMMENDATIONS

CESA directs the Department to include in its status review recommended management activities and other recommendations for recovery of Mojave Desert Tortoise (Fish & G. Code, §

2074.6; Cal. Code Regs., tit. 14, § 670.1, subd. (f).). The USFWS created a Recovery Plan for desert tortoise in 1994 which was revised in 2011. This is currently the most comprehensive framework of actions needed to recover the desert tortoise, and many of the recommendations are still very relevant. For our recommendations we borrow heavily from the framework in the 2011 revised Recovery Plan, include examples of recent progress, and point out specific areas where the Department could engage more. We also focus on specific actions like translocation and head-starting that have been in use for multiple years to examine what evidence there is that they have been effective.

9.1 Actions

This document is not a Recovery Plan; however, it is useful to identify the conservation goals that the management recommendations are meant to achieve.

In brief, the USFWS Recovery Plan includes the following objectives:

1. Maintain self-sustaining populations of desert tortoises within each Recovery Unit into the future.
   - Criteria: Rates of population change (λ) for desert tortoises are increasing (i.e., $\lambda > 1$) over at least 25 years (a single tortoise generation)
2. Maintain well-distributed populations of desert tortoises throughout each recovery unit.
   - Criteria: Distribution of desert tortoises throughout each tortoise conservation area is increasing over at least 25 years (i.e., ψ [occupancy] > 0)
3. Ensure that habitat within each recovery unit is protected and managed to support long-term viability of desert tortoise populations.

The major elements of the USFWS Recovery Plan strategy to achieve these objectives are:

1. Develop, support, and build partnerships to facilitate recovery.
2. Protect existing populations and habitat, instituting habitat restoration where necessary.
3. Augment depleted populations in a strategic manner.
4. Monitor progress toward recovery.
5. Conduct applied research and modeling in support of recovery efforts within a strategic framework.
6. Implement a formal adaptive management program.

For each of the strategies in the Recovery Plan, the USFWS includes specific measures to contribute to those strategies. We do not list all of these specific measures here, but instead discuss the strategies and measures that are most relevant and important to recovery in California and highlight those which the Department may have a role in implementing.

1. Develop, support, and build partnerships to facilitate recovery.

There are multiple existing partnerships to facilitate recovery of desert tortoise (see section 5.2 Management Efforts). The Department could become more active in the MOG, participate in Recovery Implementation Teams, and strengthen maintain relationships with state and federal agencies to collaboratively address priorities such as highway fencing and translocation.

2. Protect existing populations and habitat, instituting habitat restoration where necessary.

Here we focus on the issues most relevant to California.

a. Conserve intact desert tortoise habitat
The majority of land (63.1%) in the tortoise range is under stewardship of the BLM or the NPS and receives some level of protection (see Table 6). Future habitat conservation efforts should consider how habitat suitability will change in the coming decades under predicted climate change and ways in which habitat can be restored and made more resilient and/or habitat degradation can be ameliorated.

b. Secure lands/habitat for conservation.
Projects that will potentially result in incidental take of tortoises may apply for an ITP from the Department. As a condition of the ITP, the Department must require any impacts to the desert tortoise to be fully mitigated. This requirement is most often met through the perpetual protection and management of off-site habitat. CDFW should continue to focus on securing high quality habitats through the ITP process and through other means (e.g., facilitating recovery land acquisitions through grants, facilitating conservation easement, etc.). The USFWS also issues take authorizations that ask for mitigation in the form of land protection. For more detail see section 5.2 Management Efforts.

As mentioned previously, “the Army acquired approximately 100,000 acres (~405 km^2) of nonfederal land within the Superior-Cronese Critical Habitat Unit for conservation management of desert tortoises. It also purchased the base property of three cattle allotments on which the Bureau subsequently re-allotted the forage to wildlife” (U.S. Fish and Wildlife Service 2022*a*).

c. Connect functional habitat
Low genetic differentiation among desert tortoise populations in California (Hagerty and Tracy 2010) suggests that historically there were few barriers to movements and mixing, aside from large mountain ranges and other significant climatic or vegetative barriers. However, this is effectively no longer the case, and instead there is what is more accurately described as a metapopulation (Berry and Murphy 2019, Desert Tortoise Council 2022) where habitat patches are separated by roads, housing, agriculture, industry, energy projects, and military activities.

The strategy outlined in the 1994 Recovery Plan suggests that habitat patches of at least 2590 km^2 (1,000 mi^2) are needed in each recovery unit to “contain a viable population of desert tortoises that is relatively resistant to extinction processes” (U.S. Fish and Wildlife Service 1994). Multiple TCAs are smaller than 2,590 km^2, therefore protecting corridors between TCAs so that tortoises can disperse is key for conservation of metapopulations. Tortoises within isolated patches are at higher risk of extirpation due to the usual risks to small populations—

stochastic catastrophes like drought and fire, reduction in genetic variation, and potential associated losses of fitness (Boarman et al. 1997, Berry and Murphy 2019, U.S. Fish and Wildlife Service 2022*a*). While many of the patches share the same threats, given the differences in land use and management across the desert tortoise's range, individual patches should be managed to minimize the most severe threats for that patch. The USFWS (2019a) points out that the current fragmented nature of desert tortoise habitat (e.g., urban and agricultural development, highways, freeways, military training areas) will make "recolonization of extirpated areas difficult, if not impossible."

Land is not equally protected across CHUs, creating potential barriers between areas of functional habitat. We recommend focusing the compensatory habitat purchases and other types of land acquisitions on connecting functional habitat. The BLM is acquiring several thousand acres of checkerboard inholding in Chuckwalla Critical Habitat Unit which will improve connectivity to Joshua Tree National Park.

d. *Fence, restrict, designate, close roads and routes*

In order for functional habitat to be connected, tortoises need to be able to move and not be isolated in patches. A major action to achieve this is to erect tortoise fencing and crossings along roads.

Erecting tortoise exclusion fencing along major roadways and funneling them into well designed crossings is a key recovery action. There are 500 kms (~310 mi) of road identified as priority for fencing (U.S. Fish and Wildlife Service 2022*a*). Currently, the regulations on highway fencing have made it extremely difficult and expensive to install tortoise fencing and are a major reason that there was very little tortoise exclusion fencing installed between 2011 and 2022. Under current practice, when an applicant applies for an ITP for a road project that includes tortoise exclusion fencing and culverts for crossing, the area of land inside of the fence including the median between lanes of traffic is considered to be habitat that is impacted and the impacts need to be fully mitigated through land acquisition. The costs of procuring land adds substantial costs to fencing projects, to the point that much needed fencing is not getting built. To speed up the building of fences, the Department can work with CalTrans and other agencies to reduce cost and administrative burden of building tortoise exclusion fencing. Having more flexibility in the measures that are used to fully mitigate the impacts of road projects will help speed up progress on recovery actions. At the moment there are some fencing projects in process, including the first phase of a BLM effort to build 3.5 miles of fencing along I-40 in the Rod-Ordman Critical Habitat Unit. In the Mojave National Preserve there is a road rebuilding project that includes 5 miles of tortoise fencing.

In addition to fencing paved roads, we recommend closing and restoring unauthorized OHV routes in CHUs.

e. Minimize excessive predation on tortoises

Implementing multiple actions simultaneously is necessary to slow the expansion of predator populations. The DoD and the USFWS have active programs to reduce anthropogenic subsidies to ravens and coyotes by securing trash and water sources and reducing the number of nesting and roosting sites created by infrastructure. The USFWS has a program to reduce raven populations via egg oiling with a goal of no raven nests in areas that are a priority for tortoise recruitment (K. Holcomb, USFWS Raven Management in CA. MOG April 16 2022).

f. Restore desert tortoise habitat

Restore closed OHV trails, and work to reduce non-native invasive grasses from desert tortoise habitat. Areas degraded by off road vehicles in Fremont Kramer Critical Habitat Unit are being restored by the BLM and Marine Corps Air Ground Combat Center Twentynine Palms is restoring habitat as part of implementing RASP.

g. Minimize factors contributing to disease (particularly upper respiratory tract disease)

Continue to discourage the release of pet tortoises into the wild. Monitor and quarantine translocated tortoises to make sure they are not diseased before relocation following recommendations in U.S. Fish and Wildlife Service (2020b).

h. Establish/continue environmental education programs

Environmental education is a preventative action that has been shown to effectively change learned behavior and can be used to reduce stakeholder conflict before it happens (Hungerford and Volk 1990). An educated public is more likely to be aware of the consequences they can have on desert tortoises and to be more willing to take responsibility for their actions than those with less knowledge (Vaske and Donnelly 2007). Aggressive and widespread efforts in museums, hunting clubs, and in BLM and NPS visitor centers and interpretive sites are needed to inform the public about the status of the desert tortoise and its recovery needs (U.S. Fish and Wildlife Service 2011).

Interpretive kiosks or visitor centers should be used to disseminate information about the desert tortoise and the need for regulated access and use of habitat. Education programs should include such subjects as husbandry and adoption programs for captive tortoises, the importance of discouraging unauthorized breeding of desert tortoises in captivity, and the illegality under State laws of releasing captive tortoises into wildlands. Education efforts should be focused on groups that use the desert on a regular basis, such as rock-hounds and off-highway vehicle enthusiasts. Additional educational tools include public service announcements, news releases, informational videos, brochures and newsletters, websites, and volunteer opportunities (U.S. Fish and Wildlife Service 2011).

i. Increase law enforcement.

Increase efforts to enforce rules banning off-roading by OHVs in Desert Wildlife Management Areas and CHUs.

3. Augment Depleted Populations through a Strategic Program

Population augmentation is currently accomplished through two types of projects, translocation and head-starting. Translocation involves moving tortoises from a site where they would be harmed and into an appropriate recipient site. Head-starting is a strategy to reduce predation mortality on juvenile tortoises by hatching and rearing juveniles in captivity until they are large enough to avoid most predators.

a. Translocation

Proposed projects that could result in incidental take of tortoises may apply for an ITP. As part of the minimization measures, tortoises in the project area are translocated to pre-approved recipient sites.

There are a number of considerations that need to be taken into account when tortoises are translocated as laid out in the USFWS Plan Development Guidelines (U.S. Fish and Wildlife Service 2020*b*). Major concerns include the habitat suitability of potential translocation sites and the possibility of disease transfer from transplants to resident tortoises. The Department requires that ITP holders monitor any tortoises translocated, and has teams carefully examine recipient sites for soil and vegetation communities that are suitable for all life stages of tortoise, evaluate the presence and abundance of predators, and make sure there are sufficient burrows of appropriate size so that translocated tortoises can quickly find shelter. Most of the tortoises translocated under ITPs granted by the Department are placed within 4 miles of the donor site and the number of tortoises translocated for any project is usually less than 50. Due to the consistent efforts to find suitable recipient sites, deaths from translocation via dehydration or predation are rare (CDFW unpublished data, W. Campbell pers comm Jan 2023). However longer-term success of those translocations is not known.

However, there is evidence that larger scale translocations are not very successful. This is likely because it is much more difficult to find recipient sites that are suitable for larger numbers of tortoises. If donor sites are chosen because resident populations are depleted or have low densities, they may not have the capacity to maintain higher densities of tortoises in general and might not be able to support large numbers of translocated animals (U.S. Fish and Wildlife Service 2011). For example, sites with a depleted population due to habitat modification or degradation may currently be at a low carrying capacity and not be able to support many transplants because the site lacks sufficient food or burrows to support more individuals, or it simply is too hot. In the spring of 2008, 570 tortoises (184 females, 293 males, 93 juveniles) were translocated from the southern edge of Fort Irwin National Training Center to neighboring public land in the Superior-Cronese Critical Habitat Unit. Esque et al. (2010) tracked the survival of the translocated tortoises and within a year, 25% of them died. In the same translocation event, (Mulder et al. 2017) found that the males that survived were not fathering hatchlings. Even though translocated males made up 46% of the males they genotyped in the population, all hatchlings that could be assigned fathers were sired by resident males. A different study examined drivers of survival when 158 adult tortoises were translocated from Ft. Irwin to release sites 7.36–42.54 km from their home sites (Mack and Berry 2023). The tortoises were tracked for 10 years. Thirty-nine percent died in the first year, more than 50% were dead by the end of the third year, and after 10 years about 66% were confirmed dead and another 15% missing. Most of the dead tortoises were killed by coyotes. After 10 years, survival was highest in the site closest to the site they had been taken from, and across the study males were more likely to survive. Low survival is not limited to the translocated tortoises; in the same time period the density of resident tortoises also declined. Supplementation of the resident population by translocated individuals does not appear to stabilize populations, as explained by (Mack and Berry (2023):

> "In 2004–2005, prior to translocation, the USFWS (2015) estimated densities of resident adult tortoises at 6.4 adults/km2 for the Superior-Cronese critical habitat unit where the translocation later occurred. In contrast, densities of adults on release plots at the time of release were approximately 40/plot or 15.5/km2, more than two times that of the surrounding resident population. Several decades ago, habitat may have supported ≥15 adult tortoises/km2 in the region (USFWS 1994, Berry and Murphy 2019). Declines in abundance occurred prior to, during, and after the release; the USFWS (2015) reported a 61.5% decline in adult tortoises in the Superior-Cronese critical habitat unit between 2004 and 2014 to 2.4 adults/km2, despite additions of several hundred tortoises from the NTC translocation project in 2008. By 2017, the density of adults had declined further to 1.7 adults/km2 (USFWS 2018)."

Further evidence that translation has not necessarily increased the recipient populations in California comes from Ord-Rodman Critical Habitat Unit. In 2014, the estimated density of tortoises in Ord-Rodman was 3.6 adults/km^2 with an estimated abundance of about 3000 adults (Tables 2 and 5). Between 2017 and 2019, 724 adult tortoises were translocated into the Ord-Rodman TCA due to expansion at 29 Palms Marine Corps Air Gunnery Command Center. From 2017 on, the surveys kept track of the densities of all adults and of residents adults only (Figure 14) (U.S. Fish and Wildlife Service 2018, 2019*b*, 2020*a*, 2022*c*, *b*). Although the initial influx of a large number of translocated adults pushed the population back up to 3.9 adults/km^2 in 2017, in subsequent years the density of residents and all adults fell and has stayed below the threshold for population viability since.

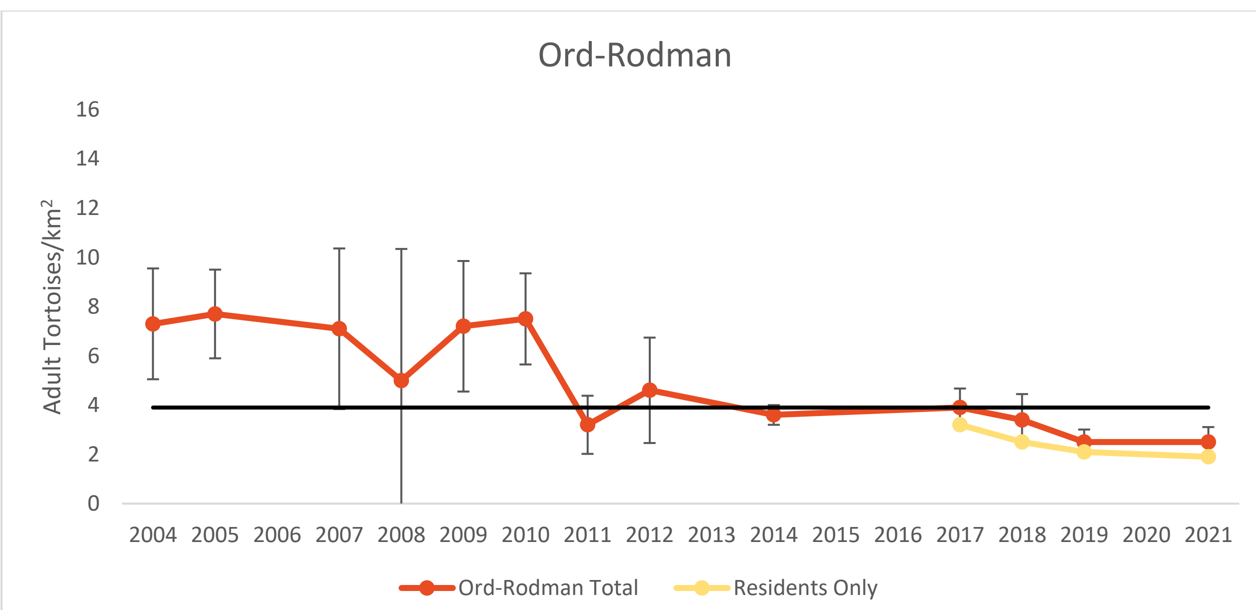


Figure 14. Estimated densities of adult tortoises (≥ 180 mm carapace length) in the Ord-Rodman TCA in the Western Mojave Recovery Unit 2004–2021. Black horizontal line represents 3.9 adults/km^2, the estimated minimum density needed for population viability. Error bars are standard errors calculated from reported coefficients of variation. The Residents Only density is for adults that were not translocated, the Ord-Rodman Total is the density of residents plus the translocated tortoises starting in 2017.

Nor has translocation been successful just across the Nevada border from the Ivanpah Critical Habitat Unit. As Scott et al. (2020) reported:

> "In 1996, the 100-km^2 Large-Scale Translocation Site (LSTS) was established. The LSTS is located in the Ivanpah Valley near Jean, Nevada, within the natural range of the tortoise, and is surrounded by either a tortoise-barrier fence or relatively inhospitable mountains….Between 1997 and 2014, ~9,105 tortoises (~50.2% of which were adults) of unknown provenance were translocated to the LSTS, where they intermingled with an estimated 1450 adult local tortoises that were natural residents at the site. Most native and translocated tortoises in the LSTS have since died, consistent with steep declines in neighboring populations and likely furthered by high post-translocation densities and less comprehensive health screening during the first decade of the translocation program. However, roughly 350 adults were estimated by line-distance surveys to be alive in 2015"

The failure of these large and long-term translocations to either keep translocated tortoises alive or the resident population stable suggests translocation may often not be an effective management strategy. The majority of the tortoises translocated into LSTS came from captivity and were likely not well adapted to surviving in the wild, which is likely a factor in their high death rates. Most official translocations in California involve moving wild tortoises from a project site to a nearby area, and so may not face the same difficulties in survival that releasing captive tortoises appear to create. However, the evidence from Ord-Rodman suggests that even an addition of large numbers of new adults to a nearby area can slow but does not prevent population declines. The low survival rates of translocated adults and the lack of genetic integration of males suggest that large scale translocation may not provide much recorded benefit to recipient populations and does not necessarily remove the translocated tortoises from harm's way. Thus, identification of the reasons for the depleted population in the recipient site is important to ensure translocation is conducted in a manner appropriate to facilitate survival, and to prevent its failure as a minimization measure.

An additional consideration is how far to translocate individuals. When tortoises must be translocated from large tracts of land such as on military bases, translocating individuals close to their home ranges is not feasible. Long distance translocation involves potential mixing of genetic subunits and possible maladaptation to the environment, and investigations into the genetic makeup of the source and recipient populations can help mangers make appropriate decisions (Weeks et al. 2011). Averill-Murray and Hagerty (2014) used microsatellite loci and concluded that "releasing tortoises at recipient sites within a straight-line distance of 200 km from the source population would most conservatively maintain historic genetic population structure.” However more recent work by Sánchez-Ramírez et al. (2018) using Single Nucleotide Polymorphisms (SNPs) suggests that there are there are three genetic subunits within the Western Mojave Recovery Unit and translocating them at distances of 200 km away could mix individuals from different genetic units.

Given the long-term decline of tortoise populations, understanding the population impacts of translocation across the state is critical. ITP holders monitor translocated tortoises for 5 years and submit reports to the Department. These data should be organized and analyzed in order to understand long-term survival rates of translocated individuals and the impacts of potential population fragmentation (see section 9.3). Increased collaboration should occur between agencies that perform translocations to understand the landscape and population impacts of short- and long-range translocations and coordinate research on disease dynamics, recruitment rates, and gene flow (U.S. Fish and Wildlife Service 2020*b*).

b. Head starting

Head-starting is a strategy to try to circumvent the high mortality of juvenile tortoises in the wild (see sections on Survival and Predation). Population modeling suggests that increased juvenile survival can improve population growth rates and is a factor managers can manipulate relatively easily (Berry and Murphy 2019). Eggs are hatched in captivity and juveniles are reared until they reach a certain size and then released. There is some evidence that this strategy appears to be effective at least in the short term (Nagy et al. 2015*a,b*, Tuberville et al. 2019), however, mortality is high for juveniles smaller than 100 mm in length. When Daly et al. (2019) monitored head started tortoises after release in the Mojave National preserve, annual survival was 44% and short-term survival was better if tortoises were more than 1.6 km from a raven’s nest. Daly et al. (2019) points out that by itself, head-starting is unlikely to lead to population recovery if larger issues such as raven density and habitat degradation are not addressed. Nagy et al. (2015*a*) recommends not releasing head-started tortoises until they are over 100 mm, which requires keeping them in captivity for about 9 years and is a considerable investment of time and resources. There is currently a head-starting program at the Ivanpah Desert Tortoise Head-starting Facility in Mojave National Preserve, a joint project between the University of Georgia and UC Davis. They have produced more than 675 hatchlings, released 324 which have been radio-tracked following release, with another approximately 275 for upcoming releases (Tuberville 2022). Another head-start program is on Edwards Air Force Base and involves San Diego Zoo, the U.S. Geological Survey, Cadiz Inc., and the BLM (San Diego Zoo Wildlife Alliance 2018).

7. Monitor progress toward recovery.

The USFWS does yearly surveys of the Tortoise Conservation Areas which are used to generate estimates of density, abundance, and annual rates of change. The results of this monitoring are summarized in section 3.2 Trends in Density and Abundance. Along with the data and estimates that are currently published in the report, making sex ratio data public would help stakeholders better understand demographic trends, especially as they are influenced by climate change.

The USFWS (2011) has more detailed recommendations on how to monitor populations on the scale of recovery units.

The Department collects a variety of data on tortoises from holders of ITPs and Scientific Collecting Permits. Improving the capacity of the Department to summarize and analyze these data to identify the cumulative impacts of permitted projects on tortoise populations will help expand the geographic scope of monitoring and is key to developing criteria for decisions on potential limits to take for desert tortoise. Sharing this information with other state and federal agencies through the MOG will help bring a broader and more comprehensive understanding of the state of tortoise populations in California. In addition, the Department should continue to engage with the USFWS and other partners to address high priority monitoring needs through the Cooperative Endangered Species Conservation Fund (Traditional Section 6) Grant Program See sections 9.2 and 9.3 for more detail.

5. Conduct applied research and modeling in support of recovery efforts within a strategic framework.

The 2011 USFWS Revised Recovery Plan includes many specific research and modeling actions that are needed to address recovery of desert tortoise. Funding for continued long term monitoring at sites outside of TCAs such as the Desert Tortoise Natural Area would expand our understanding long term trends in areas with different types of management. The Department should continue to engage with the USFWS and other partners to address high priority research needs through the Cooperative Endangered Species Conservation Fund (Traditional Section 6) Grant Program and other funding opportunities.

6. Implement a formal adaptive management program.

The USFWS Recovery Plan includes steps to

1. Revise and continue the development of a recovery decision support system.
2. Develop and revise recovery action plans.
3. Amend land use plans, habitat management plans, and other plans as needed to implement recovery actions.
4. Incorporate scientific advice for recovery through the Science Advisory Committee.

The Department has authority to develop and implement non-regulatory Recovery Plans and recovery criteria for CESA-listed species with the goal of improving the status of species and managing threats to the point where CESA listing may no longer be appropriate or necessary. The Department should consider whether adoption of the federal Recovery Plan, potentially with amendments, is warranted.

9.2 Regulations and Policy

Due to the number of interacting threats facing the desert tortoise, there is an opportunity to be more flexible with what is considered appropriate mitigation for ITPs. Acquiring land is an important measure, but it only addresses a few of the recovery actions for the desert tortoise. The Department should consider all available actions that meet the “fully mitigated” standard for offsetting project impacts. All measures that support and improve populations should be considered as mitigation, including installing tortoise fencing along highways, habitat enhancement, management and control of raven populations, and measures that improve connectivity. Focusing on land acquisition at the expense of other measures could result the protection of high-quality habitat but limited reductions in broader factors causing direct mortality or restricting movement between protected areas.

Another useful step would be to review the ITPs issued and the implementation of mitigation measures since CESA listing and assess their impact on tortoise populations in general. Section 2081 c) states “No permit shall be issued …if issuance of the permit would jeopardize the continued existence of the species.” Given the long-term decline of desert tortoise populations, the Department should include evaluations of the success of mitigation measures as a part of assessments of the cumulative impacts that inform the Department’s decisions about issuing permits. See section on Capacity Building below.

9.3 Capacity Building CDFW

a) Personnel

For these Management Recommendations to be most consistently implemented and successful, staffing and/or funding capacity that can be devoted to developing, supporting, and building partnerships to facilitate recovery of the Mojave Desert Tortoise is needed. Adequate staffing facilitates internal coordination, continuity of institutional knowledge, and coordination with other agencies and organizations to address the most important issues. If CDFW had staffing dedicated to tortoise recovery, there could be a primary point of contact for desert tortoise permitting and better coordinate collaborate internally and externally with those working on tortoise conservation and management.

b) Upgrading Systems

Currently, much of the CDFW review and issuing of ITPs for Mojave Desert Tortoise is done on a project-by-project basis, with some take permitted through Natural Community Conservation Plans and Habitat Conservation Plans like the Coachella Valley Multi Species Habitat Conservation Plan. Projects that apply for ITPs are required to collect data and submit compliance reports to the Department. If a project is required to translocate tortoises, they need to be monitored for five years and data reported to the Department. There is currently no central location for those types of data and reports at the Department. Much of the old data, reports, and information is in paper form and is stored in various Department offices and is functionally inaccessible. Data on project locations, recipient sites, release points, disease testing locations with test results, and mitigation lands need to be stored digitally and made available in compliance with relevant CDFW scientific data policies. Without a central repository for data and platforms where it can be accessed and used by staff it is difficult to understand the scope and extent of impacts of development on tortoises. Consequently, the Department does not have a complete view of how many acres have been impacted, or the amount and location of habitat that has been conserved as mitigation and the success of that mitigation. However, a permitting system is currently in development that is intended to centralize and streamline the issuing of ITPs and other permits that will make it easier for the Department to make informed decisions on future incidental take permits and jeopardy determinations.

LITERATURE CITED

The following sources were used during the preparation of this Status Review report:

Agha, M., J. E. Lovich, J. R. Ennen, B. Augustine, T. R. Arundel, M. O. Murphy, K. Meyer-Wilkins, C. Bjurlin, D. Delaney, J. Briggs, M. Austin, S. v. Madrak, and S. J. Price. 2015. Turbines and terrestrial vertebrates: variation in tortoise survivorship between a wind energy facility and an adjacent undisturbed wildland area in the desert Southwest (USA). Environmental Management 56:332–341.

Allison, L. J., and A. M. McLuckie. 2018. Population trends in Mojave desert tortoises (*Gopherus agassizii*). Herpetological Conservation and Biology 13:433–452.

Andersen, M. C., J. M. Watts, J. E. Freilich, S. R. Yool, G. I. Wakefield, J. F. McCauley, and P. B. Fahnestock. 2000. Regression-tree modeling of desert tortoise habitat in the central Mojave Desert. Ecological Applications 10:890–900.

Anderson, K. M., and K. H. Berry. 2019. *Gopherus agassizi* (Agassiz's Desert Tortoise) predation. Herpetological Review 50.

Averill-Murray, R. C., and B. E. Hagerty. 2014. Translocation relative to spatial genetic structure of the Mojave desert tortoise, *Gopherus agassizii.* Chelonian Conservation and Biology 13:35–41.

Barrows, C. W. 2011. Sensitivity to climate change for two reptiles at the Mojave-Sonoran Desert interface. Journal of Arid Environments 75:629–635.

Barrows, C. W., B. T. Henen, and A. E. Karl. 2016. Identifying climate refugia: a framework to inform conservation strategies for Agassiz's desert tortoise in a warmer future. Chelonian Conservation and Biology 15:2–11.

Bedsworth, L., D. Cayan, F. Guido, L. Fisher, and S. Ziaja. 2018. California's Fourth Climate Change Assessment Statewide Summary Report. California's Fourth Climate Change Assessment.

Berry, Kristin H. 1986*a*. Desert tortoise (*Gopherus agassizii*) research in California, 1976-1985. Herpetologica 42:62–67.

Berry, Kristin H. 1986*b*. Incidence of gunshot deaths in desert tortoise populations in California. Wildlife Society Bulletin 14:127–132.

Berry, K. H., L. J. Allison, A. M. McLuckie, M. Vaughn, and Murphy R.W. 2021. *Gopherus agassizii*, Mojave Desert Tortoise. The IUCN Red List of Threatened Species.

Berry, K. H., T. Y. Bailey, and K. M. Anderson. 2006. Attributes of desert tortoise populations at the National Training Center, Central Mojave Desert, California, USA. Journal of Arid Environments 67:165–191.

Berry, K. H., A. A. Coble, J. L. Yee, J. S. MacK, W. M. Perry, K. M. Anderson, and M. B. Brown. 2015. Distance to human populations influences epidemiology of respiratory disease in desert tortoises. Journal of Wildlife Management 79:122–136.

Berry, K. H., and K. Keith. 2008. Status of the desert tortoise in Red Rock Canyon State Park. California Fish and Game 94:98–118.

Berry, K. H., L. M. Lyren, J. L. Yee, and T. Y. Bailey. 2014. Protection benefits desert tortoise (*Gopherus agassizii*) abundance: The influence of three management strategies on a threatened species. Herpetological Monographs 28:66–92.

Berry, K. H., and P. Medica. 1995. Desert tortoise in the Mojave and Colorado deserts. Pages 135–137 in E. T. LaRoe, editor. Our Living Resources: A Report to the Nation on the Distribution, Abundance, and Health of U.S. Plants, Animals, and Ecosystems. U.S. Department of the Interior, Washington D.C.

Berry, K. H., and R. W. Murphy. 2019. *Gopherus agassizii* (Cooper 1861) – Mojave Desert Tortoise. Chelonian Research Monographs 5.

Berry, K. H., L. Nicholson, S. Juarez, and A. P. Woodman. 1986. Changes in Desert Tortoise populations at four study sites in California. Pages 60–80 in. Desert Tortoise Council Proceedings of the 1986 Symposium.

Berry, K. H., T. A. Shields, and E. R. Jacobson. 2016. Gopherus agassizi (Agassiz's Desert Tortoise) probable rattlesnake envenomation. Herpetological Review 47:652–653.

Berry, K. H., and F. B. Turner. 1986. Spring activities and habits of juvenile desert tortoises, *Gopherus agassizii*, in California. Copeia 1986:1010–1012.

Berry, K. H., J. L. Yee, and L. M. Lyren. 2020a. Feral burros and other influences on desert tortoise presence in the Western Sonoran Desert. Herpetologica 76:403–413.

Berry, K. H., J. L. Yee, T. A. Shields, and L. Stockton. 2020b. The catastrophic decline of tortoises at a fenced Natural Area. Wildlife Monographs 205:1–53.

Berry, K. H., J. Yee, L. Lyren, and J. S. Mack. 2020c. An uncertain future for a population of desert tortoises experiencing human impacts. Herpetologica 76:1–11.

Bisson, H. 2008. Off-Highway vehicle management on public lands. Washington D.C.

Bjurlin, C. D., and J. A. Bissonette. 2004. Survival during early life stages of the desert tortoise (*Gopherus agassizii*) in the south-central Mojave desert. Journal of Herpetology 38:527–535.

Boarman, W. I., and K. Berry. 1995. Common Ravens in the southwestern United States, 1968–92. Pages 73–75 in E. T. Laroe, editor. Our living resources: a report to the nation on the distribution, abundance, and health of U.S. plants, animals, and ecosystems. U.S. Department of the Interior, National Biological Survey, Washington DC, USA.

Boarman, W. I., R. J. Camp, F. Collins, M. Hagan, and W. Deal. 1995. Raven abundance at anthropogenic resources in the Western Mojave Desert, California National Biological Service Riverside, California.

Boarman, W. I., M. A. Patten, R. J. Camp, and S. J. Collis. 2006. Ecology of a population of subsidized predators: Common ravens in the central Mojave Desert, California. Journal of Arid Environments 67:248–261.

Boarman, W. I., and M. Sazaki. 1996. Highway mortality in desert tortoises and small vertebrates: success of barrier fences and culverts. Orlando, FL, USA.

Boarman, W., and M. Sazaki. 2006. A highway's road-effect zone for desert tortoises (*Gopherus agassizii*). Journal of Arid Environments 94–101.

Boarman, W., M. Sazaki, and B. Jennings. 1997. The effect of roads, barrier fences, and culverts on desert tortoise populations in California, USA. Pages 54–58 in. Proceedings: Conservation, Restoration, and Management of Tortoises and Turtles — An International Conference.

Bradley, B. A., C. A. Curtis, and J. C. Chambers. 2016. *Bromus* response to climate and projected changes with climate change. Pages 257–274 in. Exotic brome-grasses in arid and semiarid ecosystems of the western US.

Brattstrom, B. H. 1965. Body temperatures of reptiles. American Midland Naturalist 73:376.

Brooks, M. 1999. Alien annual grasses and fire in the Mojave Desert. Madroño 46:13–19.

Brooks, M. L. 2012. Effects of high fire frequency in creosote bush scrub vegetation of the Mojave Desert. International Journal of Wildland Fire 21:61–68.

Brooks, M. L., and T. C. Esque. 2002. Alien annual plants and wildfire in desert tortoise habitat: status, ecological effects, and management. Chelonian Conservation and Biology 4:330–340.

Brooks, M. L., B. Lair, F. Station, and N. S. St. 2005. Ecological effects of vehicular routes in a desert ecosystem. Conservation Biology.

Brooks, M. L., and J. R. Matchett. 2006. Spatial and temporal patterns of wildfires in the Mojave Desert, 1980-2004. Journal of Arid Environments 67:148–164.

Brooks, M. L., J. R. Matchett, and K. H. Berry. 2006. Effects of livestock watering sites on alien and native plants in the Mojave Desert, USA. Journal of Arid Environments 67:125–147.

Bureau of Land Management. 2016. Land Use Plan Amendment, Desert Renewable Energy Conservation Plan.

Burgess, T. L., J. Braun, C. L. Witte, N. Lamberski, K. J. Field, L. J. Allison, R. C. Averill-Murray, K. Kristina Drake, K. E. Nussear, T. C. Esque, and B. A. Rideout. 2021. Assessment of disease risk associated with potential removal of anthropogenic barriers to Mojave desert tortoise (*Gopherus agassizii*) population connectivity. Journal of Wildlife Diseases 57:579–589.

California Department of Fish and Wildlife. 2000. The Status of Rare, Threatened, and Endangered Animals and Plants of California 2000.

California Department of Fish and Wildlife. 2005. The Status of Rare, Threatened, and Endangered Plants and Animals of California 2000-2004.

California Department of Fish and Wildlife. 2014. CWHR version 9.0 personal computer program. California Interagency Wildlife Task Group, Sacramento, CA, USA.

Carter, S. K., K. E. Nussear, T. C. Esque, I. I. F. Leinwand, E. Masters, R. D. Inman, N. B. Carr, and L. J. Allison. 2020. Quantifying development to inform management of Mojave and Sonoran desert tortoise habitat in the American southwest. Endangered Species Research 42:167–184.

Chaffee, M. A., and K. H. Berry. 2006. Abundance and distribution of selected elements in soils, stream sediments, and selected forage plants from desert tortoise habitats in the Mojave and Colorado deserts, USA. Journal of Arid Environments 67:35–87.

Christopher, M. M., K. H. Berry, B. T. Henen, and K. A. Nagy. 2003. Clinical disease and laboratory abnormalities in free-ranging desert tortoises in California (1990-1995). Journal of Wildlife Diseases 39:35–56.

Cohn, B., B. Wallace, C. Grouios, B. Dickson, R. Scherer, A. Kissel, M. E. Gray, and T. G. Jackson. 2021. Heavy metal concentrations in Mojave desert tortoises (*Gopherus agassizii*) related to a mitigation translocation project, Ivanpah Valley, California, USA. Herpetological Conservation and Biology 16:128–141.

Curtin, A. J., G. R. Zug, and J. R. Spotila. 2009. Longevity and growth strategies of the desert tortoise (*Gopherus agassizii*) in two American deserts. Journal of Arid Environments 73:463–471.

Dalsimer, A. 2016. Threatened and Endangered Species on DoD Lands. DoD Natural Resources.

Daly, J. A., K. A. Buhlmann, B. D. Todd, C. T. Moore, J. M. Peaden, and T. D. Tuberville. 2019. Survival and movements of head-started Mojave desert tortoises. Journal of Wildlife Management 83:1700–1710.

Davy, C. M., T. Edwards, A. Lathrop, M. Bratton, M. Hagan, B. Henen, K. A. Nagy, J. Stone, L. S. Hillard, and R. W. Murphy. 2011. Polyandry and multiple paternities in the threatened Agassiz's desert tortoise, *Gopherus agassizii*. Conservation Genetics 12:1313–1322.

DeFalco, L. A., D. R. Bryla, V. Smith-Longozo, and R. S. Nowak. 2003. Are Mojave Desert annual species equal? Resource acquisition and allocation for the invasive grass *Bromus madritensis* subsp. *rubens* (*Poaceae*) and two native species. American Journal of Botany 90:1045–1053.

Denholm, P., M. Hand, J. Maddalena, and S. Ong. 2009. Land-use requirements of modern wind power plants in the United States. National Renewable Energy Laboratory.

Desert Tortoise Council. 2022. Response by the Desert Tortoise Council to California Department of Fish and Wildlife's May 27, 2022 Notification of Status Review for Mojave Desert Tortoise under the California Endangered Species Act.

Drake, K. K., L. Bowen, K. E. Nussear, T. C. Esque, A. J. Berger, N. A. Custer, S. C. Waters, J. D. Johnson, A. K. Miles, and R. L. Lewison. 2016. Negative impacts of invasive plants on conservation of sensitive desert wildlife. Ecosphere 7.

Drake, K. K., T. C. Esque, K. E. Nussear, L. A. Defalco, S. J. Scoles-Sciulla, A. T. Modlin, and P. A. Medica. 2015. Desert tortoise use of burned habitat in the Eastern Mojave desert. Journal of Wildlife Management 79:618–629.

Esque, T. C., K. E. Nussear, K. K. Drake, A. D. Walde, K. H. Berry, R. C. Averill-Murray, A. P. Woodman, W. I. Boarman, P. A. Medica, J. Mack, and J. S. Heaton. 2010. Effects of subsidized predators, resource variability, and human population density on desert tortoise populations in the Mojave Desert, USA. Endangered Species Research 12:167–177.

Esque, T. C., C. R. Schwalbe, L. A. Defalco, R. B. Duncan, and T. J. Hughes. 2003. Effects of desert wildfires on desert tortoise (*Gopherus agassizii*) and other small vertebrates. Southwestern Naturalist 48:103–111.

Faber-Langendoen, D., J. Nichols, L. Master, K. Snow, A. Tomaino, R. Bittman, G. Hammerson, B. Heidel, L. Ramsay, A. Teucher, and B. Young. 2012. NatureServe conservation status assessments: methodology for assigning ranks. NatureServe, Arlington, VA.

Fenn, M. E., E. B. Allen, S. B. Weiss, S. Jovan, L. H. Geiser, G. S. Tonnesen, R. F. Johnson, L. E. Rao, B. S. Gimeno, F. Yuan, T. Meixner, and A. Bytnerowicz. 2010. Nitrogen critical loads and management alternatives for N-impacted ecosystems in California. Journal of Environmental Management 91:2404–2423.

Frankham, R. 1995. Effective population size/adult population size ratios in wildlife: A review. Genetics Research 89:491–503.

Freilich, J. E., K. P. Burnham, C. M. Collins, and C. A. Garry. 2000. Factors affecting population assessments of desert tortoises. Conservation Biology 14:1479–1489.

Germano, J., V. E. van Zerr, T. C. Esque, K. E. Nussear, and N. Lamberski. 2014. Impacts of upper respiratory tract disease on olfactory behavior of the Mojave desert tortoise. Journal of Wildlife Diseases 50:354–358.

Grandmaison, D. D., and V. J. Frary. 2012. Estimating the probability of illegal desert tortoise collection in the Sonoran Desert. Journal of Wildlife Management 76:262–268.

Hagerty, B. E., and C. R. Tracy. 2010. Defining population structure for the Mojave desert tortoise. Conservation Genetics 11:1795–1807.

Hammerson, G.A., D. Schweitzer, L. Master, and J. Cordeiro. 2008. Ranking species occurrences- a generic approach. NatureServe.

Harless, M. L., A. D. Walde, D. K. Delaney, L. L. Pater, and W. K. Hayes. 2009. Home range, spatial overlap, and burrow use of the desert tortoise in the West Mojave desert. Copeia 378–389.

Hazard, L. C., D. R. Shemanski, and K. A. Nagy. 2009. Nutritional quality of natural foods of juvenile desert tortoises (*Gopherus agassizii*): Energy, nitrogen, and fiber digestibility. Journal of Herpetology 43:38–48.

Hegeman, E. E., B. G. Dickson, and L. J. Zachmann. 2014. Probabilistic models of fire occurrence across National Park Service units within the Mojave Desert Network, USA. Landscape Ecology 29:1587–1600.

Holcomb, K. L. 2022a. Status Review of the Mojave Desert Tortoise (2012-2022). Desert Tortoise Management Oversight Group Meeting October 11, 2022.

Holcomb, K. L. 2022b. Fall 2022 Raven Management Update. Desert Tortoise Management Oversight Group Meeting October 11, 2022.

Holcomb, K. L., P. S. Coates, B. S. Prochazka, T. Shields, and I. Boarman, William. 2021. A desert tortoise – common raven viable conflict threshold. Human–Wildlife Interactions 15:405–421.

Homer, B. L., C. Li, K. H. Berry, N. D. Denslow, E. R. Jacobson, R. H. Sawyer, and J. E. Williams. 2001. Soluble scute proteins of healthy and ill desert tortoises (*Gopherus agassizii*). American Journal of Veterinary Research 62:104–110.

Hopkins, Francesca. 2018. Inland Deserts Summary Report. California’s Fourth Climate Change Assessment.

Hughson, D. L., and N. Darby. 2013. Desert tortoise road mortality in Mojave National Preserve, California. California Fish and Game 99:222–232.

Hungerford, H. R., and T. L. Volk. 1990. Changing learner behavior through environmental education. Journal of Environmental Education 21:8–21.

Iknayan, K. J., and S. R. Beissinger. 2018. Collapse of a desert bird community over the past century driven by climate change. Proceedings of the National Academy of Sciences of the United States of America 115:8597–8602.

Jacobson, E. R., M. B. Brown, I. M. Schumacher, B. R. Collins, R. K. Harris, and P. A. Klein. 1995. Mycoplasmosis and the desert tortoise (*Gopherus agassizii*) in Las Vegas Valley, Nevada. Chelonian Conservation and Biology 1:279–284.

Jacobson, E. R., M. B. Brown, L. D. Wendland, D. R. Brown, P. A. Klein, M. M. Christopher, and K. H. Berry. 2014. *Mycoplasmosis* and upper respiratory tract disease of tortoises: A review and update. Veterinary Journal 201:257–264.

Jacobson, E. R., C. H. Gardiner, M. B. Brown, H. P. Adams, J. M. Gaskin, J. L. Lapointe, R. K. Harris, and C. Reggiardo. 1991. Chronic upper respiratory tract disease of free-ranging desert tortoises (*Xerobates agassizii*). Journal of Wildlife Diseases 27.

Jacobson, E. R., T. J. Wronski, J. Schumacher, C. Reggiardo, and K. H. Berry. 1994. Cutaneous Dyskeratosis in free-ranging desert tortoises, *Gopherus agassizii*, in the Colorado Desert of southern California. Journal of Zoo and Wildlife Medicine 25:68–81.

Jennings, W. B., and K. H. Berry. 2015. Desert tortoises (*Gopherus agassizii*) are selective herbivores that track the flowering phenology of their preferred food plants. PLoS ONE 10.

Johnson, A. J., A. P. Pessier, J. F. X. Wellehan, R. Brown, and E. R. Jacobson. 2005. Identification of a novel herpesvirus from a California desert tortoise (*Gopherus agassizii*). Veterinary Microbiology 111:107–116.

Keehn, J. E., and C. R. Feldman. 2018. Disturbance affects biotic community composition at desert wind farms. Wildlife Research 45:383–396.

Keevil, M. G., R. J. Brooks, and J. D. Litzgus. 2018. Post-catastrophe patterns of abundance and survival reveal no evidence of population recovery in a long-lived animal. Ecosphere 9.

Kelly, E. C., B. L. Cypher, and T. L. Westall. 2021. Predation on desert tortoises (*Gopherus agassizii*) by desert canids. Journal of Arid Environments 189.

Kristan, W. B., and W. I. Boarman. 2007. Effects of anthropogenic developments on common Raven nesting biology in the west Mojave Desert. Ecological Applications 17:1703–1713.

Lovich, J., M. Agha, J. R. Ennen, T. R. Arundel, and M. Austin. 2018. Agassiz's desert tortoise (*Gopherus agassizii*) activity areas are little changed after wind turbine-induced fires in California. International Journal of Wildland Fire 27:851–856.

Lovich, J. E., and D. Bainbridge. 1999. Anthropogenic degradation of the southern California desert ecosystem and prospects for natural recovery and restoration. Environmental Management 24:309–326.

Lovich, J. E., and J. R. Ennen. 2011. Wildlife conservation and solar energy development in the desert southwest. BioScience 61.

Lovich, J. E., and J. R. Ennen. 2013. Assessing the state of knowledge of utility-scale wind energy development and operation on non-volant terrestrial and marine wildlife. Applied Energy 103:52–60.

Lovich, J. E., C. B. Yackulic, J. Freilich, M. Agha, M. Austin, K. P. Meyer, T. R. Arundel, J. Hansen, M. S. Vamstad, and S. A. Root. 2014. Climatic variation and tortoise survival: Has a desert species met its match? Biological Conservation 169:214–224.

Lovich, J., J. Ennen, S. Madrak, K. Meyer, C. Loughran, C. Bjurlin, T. Arundel, W. Turner, C. Jones, and G. Groenendaal. 2011. Effects of wind energy production on growth, demography and survivorship of a desert tortoise (*Gopherus agassizii*) population in southern California with. Herpetological Conservation and Biology 6:161–174.

Mack, J. S., and K. H. Berry. 2023. Drivers of survival of translocated tortoises. Journal of Wildlife Management 1–27.

Mack, J. S., K. H. Berry, D. M. Miller, and A. S. Carlson. 2015. Factors affecting the thermal environment of Agassiz's desert tortoise (*Gopherus agassizii*) cover sites in the central Mojave desert during periods of temperature extremes. Journal of Herpetology 49:405–414.

Manning, J. A. 2018. Genetic origins and population status of desert tortoises in Anza-Borrego Desert State Park, California: Initial steps towards population monitoring. Borrego Springs, CA, USA.

McAuliffe, J. R., and E. P. Hamerlynck. 2010. Perennial plant mortality in the Sonoran and Mojave deserts in response to severe, multi-year drought. Journal of Arid Environments 74:885–896.

Mulder, K. P., A. D. Walde, W. I. Boarman, A. P. Woodman, E. K. Latch, and R. C. Fleischer. 2017. No paternal genetic integration in desert tortoises (*Gopherus agassizii*) following translocation into an existing population. Biological Conservation 210:318–324.

Nagy, K. A., S. Hillard, S. Dickson, and D. J. Morafka. 2015*a*. Effects of artificial rain on survivorship, body condition, and growth of head-started desert tortoises (*Gopherus agassizii*) released to the open desert. Herpetological Conservation and Biology 10:535–549.

Nagy, K. A., S. Hillard, M. W. Tuma, and D. J. Morafka. 2015*b*. Head-started desert tortoises (*Gopherus agassizii*): Movements, survivorship and mortality causes following their release. Herpetological Conservation and Biology 10:203–215.

Nagy, K. A., B. T. Henen, and D. B. Vyas. 1998. Nutritional quality of native and introduced food plants of wild desert tortoises. Journal of Herpetology 32:260–267.

Nussear, K. E., T. C. Esque, R. D. Inman, L. Gass, K. a Thomas, C. S. A. Wallace, J. B. Blainey, D. M. Miller, and R. H. Webb. 2009. Modeling habitat of the desert tortoise (*Gopherus agassizii*) in the Mojave and parts of the Sonoran Deserts of California, Nevada, Utah, and Arizona. US Geological Survey open-file report. Volume 1102.

Nussear, K. E., C. R. Tracy, P. A. Medica, D. S. Wilson, R. W. Marlow, and P. S. Corn. 2012. Translocation as a conservation tool for Agassiz's desert tortoises: Survivorship, reproduction, and movements. Journal of Wildlife Management 76:1341–1353.

O'Connor, M. P., L. C. Zimmerman, D. E. Ruby, S. J. Bulova, and J. R. Spotila. 1994. Home range size and movements by desert tortoises, *Gopherus agassizii*, in the eastern Mojave Desert. Herpetological Monographs 8:60–71.

Office of Environmental Health Hazard Assessment. 2018. Indicators of Climate Change in California.

Office of Governor Gavin Newsom. 2021. Governor Newsom Signs Historic Legislation to Boost California's Housing Supply and Fight the Housing Crisis | California Governor. <https://www.gov.ca.gov/2021/09/16/governor-newsom-signs-historic-legislation-to-boost-californias-housing-supply-and-fight-the-housing-crisis/>. Accessed 8 Feb 2023.

Oftedal, O., S. Hillard, and D. Morafka. 2002. Selective Spring Foraging by Juvenile Desert Tortoises (*Gopherus agassizii*) in the Mojave Desert: Evidence of an Adaptive Nutritional Strategy. Chelonian Conservation and Biology 4:341–352.

Ong, S., C. Campbell, P. Denholm, R. Margolis, and G. Heath. 2013. Land-use requirements for solar power plants in the United States (No. NREL/TP-6A20-56290).

Peterson, C. C. 1996. Ecological energetics of the desert tortoise (*Gopherus agassizii*): Effects of rainfall and drought. Ecology 77:1831–1844.

Prose, D. v, and H. G. Wilshire. 2000. The lasting effects of tank maneuvers on desert soils and intershrub flora. Open-File Report OF 00-512.

Rostal, D. C., J. Grumbles, V. A. Lance, and J. R. Spotila. 2002. Chronology of sex determination in the Desert Tortoise (*Gopherus agassizii*). Chelonian Conservation and Biology 4:313–318.

Sadoti, G., M. E. Gray, M. L. Farnsworth, and B. G. Dickson. 2017. Discriminating patterns and drivers of multiscale movement in herpetofauna: The dynamic and changing environment of the Mojave desert tortoise. Ecology and Evolution 7:7010–7022.

San Diego Zoo Wildlife Alliance. 2018. Head-starting Program for California Desert Tortoises Begins. <https://stories.sandiegozoo.org/2018/07/03/head-starting-program-for-california-desert-tortoises-begins/#:~:text=Radio tracking of more than 30 female tortoises,returned to the wild into their original territory.>.

Sánchez-Ramírez, S., Y. Rico, K. H. Berry, T. Edwards, A. E. Karl, B. T. Henen, and R. W. Murphy. 2018. Landscape limits gene flow and drives population structure in Agassiz's desert tortoise (*Gopherus agassizii*). Scientific Reports 8.

Sandmeier, F. C., C. R. Tracy, B. E. Hagerty, S. Dupré, H. Mohammadpour, and K. Hunter. 2013. Mycoplasmal upper respiratory tract disease across the range of the threatened Mojave Desert tortoise: Associations with thermal regime and natural antibodies. EcoHealth 10:63–71.

Scott, P. A., L. J. Allison, K. J. Field, R. C. Averill-Murray, and H. B. Shaffer. 2020. Individual heterozygosity predicts translocation success in threatened desert tortoises. Science 370:1086–1098.

Shine, R. 2005. Life-history evolution in reptiles. Annual Review of Ecology, Evolution, and Systematics 36:23–46.

Shumway, G., L. Vredenburgh, and R. Hartill. 1980. Desert Fever: An Overview of Mining History of the California Desert Conservation Area.

Smith, A. L., S. R. Puffer, J. E. Lovich, L. A. Tennant, T. R. Arundel, M. S. Vamstad, and K. D. Brundige. 2016. A potential predator-prey interaction of an American badger and an Agassiz's desert tortoise with a review of badger predation on turtles. California Fish and Game 102:131–144.

State of California Department of Finance. 2023. Demographics | Department of Finance. <https://dof.ca.gov/forecasting/Demographics/>. Accessed 8 Feb 2023.

Tagestad, J., M. Brooks, V. Cullinan, J. Downs, and R. McKinley. 2016. Precipitation regime classification for the Mojave Desert: Implications for fire occurrence. Journal of Arid Environments 124:388–397.

Tracy, C. R., R. Averill-Murray, W. I. Boarman, D. Delehanty, J. Heaton, E. McCoy, D. Morafka, N. Nussear, B. Hagerty, and P. Medica. 2004. Desert tortoise recovery plan assessment. Desert Tortoise Recovery Plan Assessment Committee for the U.S. Fish and Wildlife Service.

Tuberville, T. D. 2022. Progress Update, Desert Tortoise Management Oversight Group.

Tuberville, T. D., K. A. Buhlmann, R. Sollmann, M. G. Nafus, J. M. Peaden, J. A. Daly, and B. D. Todd. 2019. Effects of short-term, outdoor head-starting on growth and survival in the Mojave desert tortoise (*Gopherus agassizii*). Herpetological Conservation and Biology 14:171–184.

Tuma, M. W., C. Millington, N. Schumaker, and P. Burnett. 2016. Modeling Agassiz's desert tortoise population response to anthropogenic stressors. Journal of Wildlife Management 80:414–429.

Turner, F. B., P. Hayden, B. L. Burge, and J. B. Roberson. 1986. Egg production by the desert tortoise (*Gopherus agassizii*) in California. Herpetologica 42:93–104.

U. S. Fish and Wildlife Service. 1994. Desert Tortoise (Mojave population) Recovery Plan. Portland, Oregon.

U. S. Fish and Wildlife Service. 2010. Mojave population of the desert tortoise (*Gopherus agassizii*): 5-year review: summary and evaluation. Reno, Nevada.

U. S. Fish and Wildlife Service. 2022. ESA Section 7 Consultation.

Underwood, E. C., R. C. Klinger, and M. L. Brooks. 2019. Effects of invasive plants on fire regimes and postfire vegetation diversity in an arid ecosystem. Ecology and Evolution 9. <www.ecolevol.org>.

U.S. Department of Defense. 2021. Department of Defense Climate Risk Analysis.

U.S. Fish and Wildlife Service. 1990. Endangered and threatened wildlife and plants; determination of threatened status for the Mojave population of the desert tortoise. Federal Register 55:12178-12191. Volume 55.

U.S. Fish and Wildlife Service. 2011. Revised Recovery Plan for the Mojave Population of the Desert Tortoise (*Gopherus agassizii*).

U.S. Fish and Wildlife Service. 2015. Range-Wide Monitoring of the Mojave Desert Tortoise (*Gopherus agassizii*): 2013 and 2014 Annual Reporting.

U.S. Fish and Wildlife Service. 2016. Range-wide Monitoring of the Mojave Desert tortoise (*Gopherus agassizii*): 2015 and 2016 Annual Reporting. Volume 10.

U.S. Fish and Wildlife Service. 2018. Range-Wide Monitoring of the Mojave Desert Tortoise (*Gopherus agassizii*): 2017 Annual Reporting.

U.S. Fish and Wildlife Service. 2019a. Status of the Desert Tortoise.

U.S. Fish and Wildlife Service. 2019b. Range-Wide Monitoring of the Mojave Desert Tortoise (*Gopherus agassizii*): 2018 Annual Reporting.

U.S. Fish and Wildlife Service. 2020a. Range-Wide Monitoring of the Mojave Desert Tortoise (*Gopherus agassizii*): 2019 Annual Reporting DRAFT.

U.S. Fish and Wildlife Service. 2020b. Translocation of Mojave Desert Tortoises from Project Sites: Plan Development Guidance.

U.S. Fish and Wildlife Service. 2022a. Mojave Desert Tortoise (*Gopherus agassizii*) 5-Year Review: Summary and Evaluation.

U.S. Fish and Wildlife Service. 2022b. Range-Wide Monitoring of the Mojave Desert Tortoise (*Gopherus agassizii*): 2021 Annual Reporting DRAFT.

U.S. Fish and Wildlife Service. 2022c. Range-Wide Monitoring of the Mojave Desert Tortoise (*Gopherus agassizii*): 2020 Annual Reporting.

VanDerWal, J., H. T. Murphy, A. S. Kutt, G. C. Perkins, B. L. Bateman, J. J. Perry, and A. E. Reside. 2013. Focus on poleward shifts in species' distribution underestimates the fingerprint of climate change. Nature Climate Change 3:239–243.

Vaske, J. J., and M. P. Donnelly. 2007. Public Knowledge and Perceptions of the Desert Tortoise. (HDNRU Report No. 81). Report for the National Park Service.

Webb, R. H., and S. S. Stielstra. 1979. Sheep grazing effects on Mojave Desert vegetation and soils. Environmental Management 3:517–529.

Weeks, A. R., C. M. Sgro, A. G. Young, R. Frankham, N. J. Mitchell, K. A. Miller, M. Byrne, D. J. Coates, M. D. B. Eldridge, P. Sunnucks, M. F. Breed, E. A. James, and A. A. Hoffmann. 2011. Assessing the benefits and risks of translocations in changing environments: a genetic perspective. Evolutionary Applications 4:709–725.

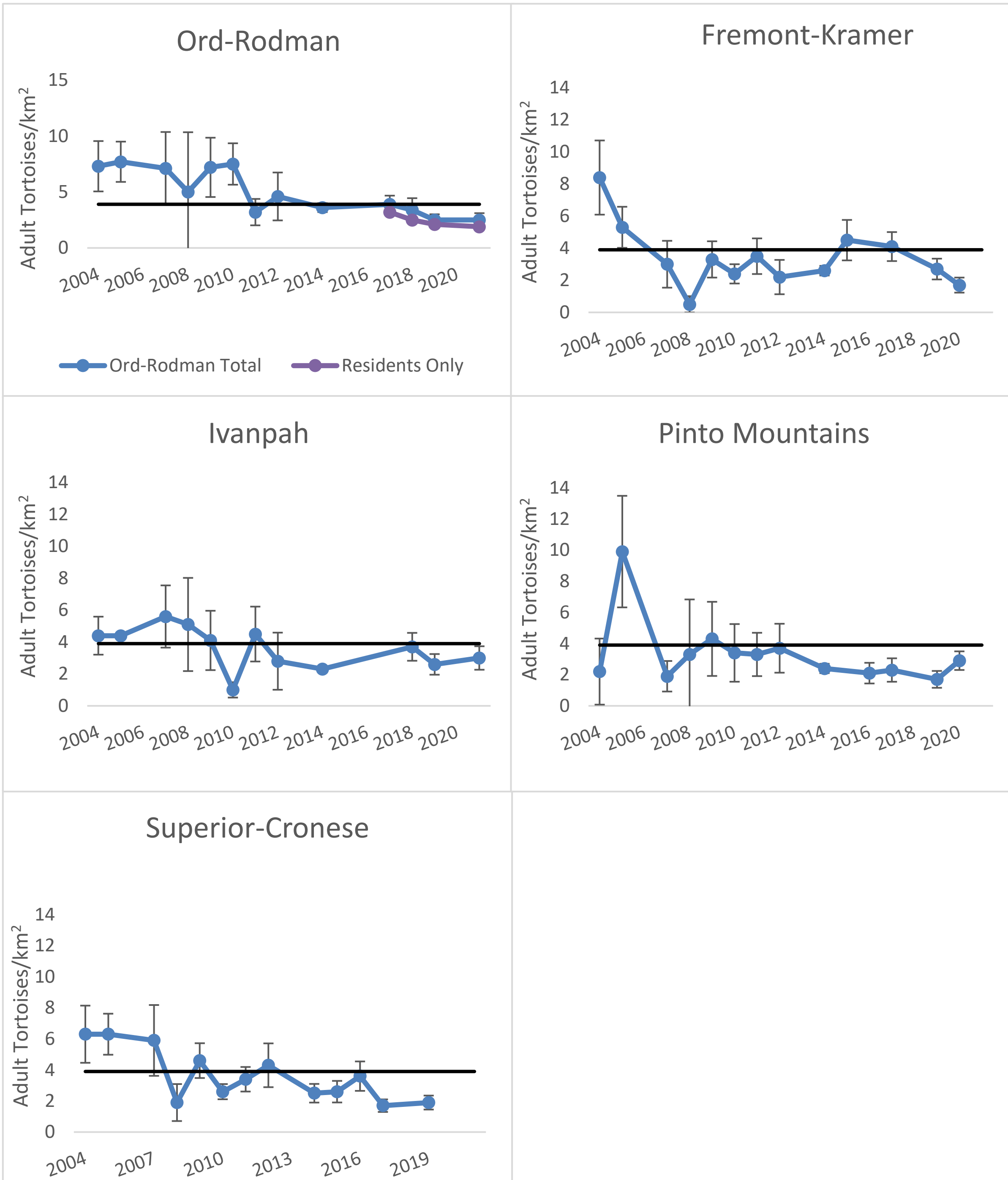
Wikipedia. 2023. Military budget of the United States. <https://en.wikipedia.org/wiki/Military_budget_of_the_United_States>.

Williams, A. P., B. I. Cook, and J. E. Smerdon. 2022. Rapid intensification of the emerging southwestern North American megadrought in 2020–2021. Nature Climate Change 12:232–234.

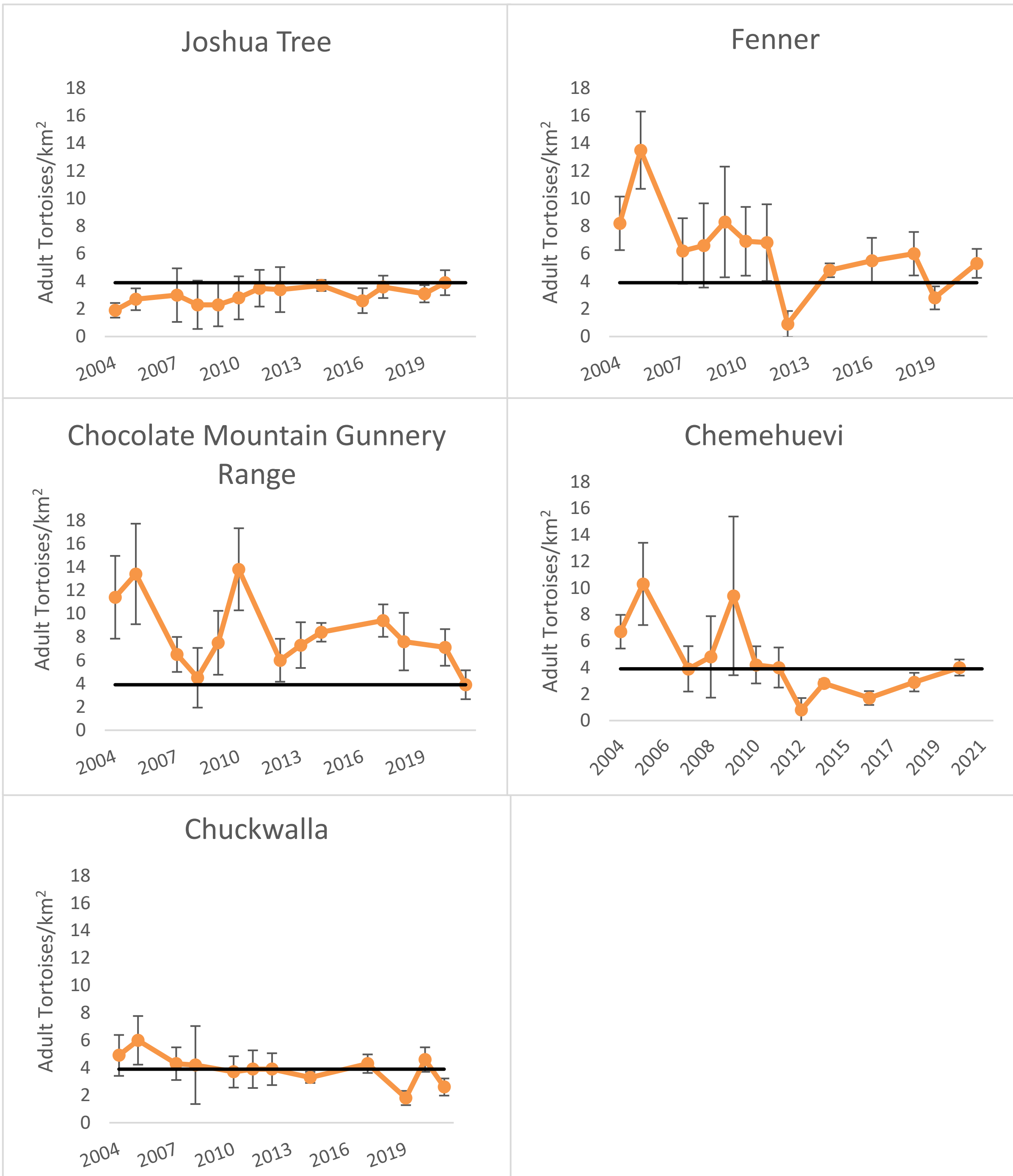
Wolf, A., N. B. Zimmerman, W. R. L. Anderegg, P. E. Busby, and J. Christensen. 2016. Altitudinal shifts of the native and introduced flora of California in the context of 20th-century warming. Global Ecology and Biogeography 25:418–429.

Woodbury, A. M., and R. Hardy. 1948. Studies of the Desert Tortoise, *Gopherus agassizii*. Ecological Monographs 18:145–200.

APPENDIX A FIGURES



Appendix Figure 1. Estimated densities of adult tortoises (≥ 180 mm carapace length) in Tortoise Conservation Areas in the Eastern and Western Mojave Recovery Units in California 2004–2021. Black horizontal line represents 3.9 adults/km^2, the estimated minimum density needed for population viability. 2004–2014 have standard errors (SE), 2015–2021 have coefficients of variation that have been converted to standard errors.



Appendix A Figure 2. Estimated densities of adult tortoises (≥ 180 mm carapace length) in Tortoise Conservation Areas in the Colorado Desert Recovery Units in California 2004–2021.

Black horizontal line represents 3.9 adults/km^2, the estimated minimum density needed for population viability. 2004–2014 have standard errors (SE), 2015–2021 have coefficients of variation that have been converted to standard errors.

Pursuant to Fish and Game Code section 2074.6, the review process included independent and competent peer review of the draft status review by persons in the scientific/academic community acknowledged to be experts on Mojave Desert Tortoise and related topics, and possessing the knowledge and expertise to critique the scientific validity of the status review contents. Appendix B contains the specific comments provided to the Department by the individual peer reviewers, the Department's written response to the comments, and any amendments made to the status review (Fish & G. Code, § 2074.6; Cal. Code Regs., tit. 14, § 670.1, subd. (f)(2)). Independent experts that reviewed the status review are listed in Table 1, below.

Table 1. Status Review Peer Reviewers

Name	Affiliation
Reviewer 1 name	
Reviewer 2 name	
Reviewer 3 name	