Lower Colorado River Multi-Species Conservation Program

Balancing Resource Use and Conservation

2019 Updates to Colorado River Cotton Rat (*Sigmodon arizonae plenus*) (CRCR) Basic Conceptual Ecological Model for the Lower Colorado River

Photo courtesy of Nick Rice

January 2021

Work conducted under LCR MSCP Work Task G6

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2019 Updates to Colorado River Cotton Rat (*Sigmodon arizonae plenus*) (CRCR) Basic Conceptual Ecological Model for the Lower Colorado River

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ACRONYMS AND ABBREVIATIONS

CAP	critical activity or process
CEM	conceptual ecological model
CF	controlling factor
CRCR	Colorado River Cotton Rat (*Sigmodon arizonae plenus*)
HE	habitat element
LCR	lower Colorado River
LCR MSCP	Lower Colorado River Multi-Species Conservation Program
LSO	life-stage outcome
m	meter(s)
Reclamation	Bureau of Reclamation
USFWS	U.S. Fish and Wildlife Service

Symbols

≈	approximately equal to
<	less than

Definitions

For the purposes of this document, vegetation layers are defined as follows:

Canopy – The canopy is the uppermost strata within a plant community. The canopy is exposed to the sun and captures the majority of its radiant energy.

Understory – The understory comprises plant life growing beneath the canopy without penetrating it to any extent. The understory exists in the shade of the canopy and usually has lower light and higher humidity levels. The understory includes subcanopy trees and the shrub and herbaceous layers.

Shrub layer – The shrub layer is comprised of woody plants between 0.5 and 2.0 meters in height.

Herbaceous layer – The herbaceous layer is most commonly defined as the forest stratum composed of all vascular species that are 0.5 meter or less in height.

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Attachment

1 Colorado River Cotton Rat (*Sigmodon arizonae plenus*) (CRCR) Habitat Data

Foreword

This report provides an update to the original conceptual ecological model (CEM) prepared for the Lower Colorado River Multi-Species Conservation Program (LCR MSCP) for the Colorado River cotton rat (*Sigmodon arizonae plenus*) (CRCR) (Johnson and Unnasch 2015). (This animal is a subspecies of the Arizona cotton rat [*Sigmodon arizonae*]). This update incorporates information reported in publications and presentations at professional meetings since the completion of the original CRCR conceptual ecological model and also incorporates information from the professional experiences of LCR MSCP staff and other experts. An updated version of the CEM workbook incorporates the new information. This report constitutes an appendix to the original CEM. The full CEM report, including its life-stage diagrams, has not been updated.

The structure of this report follows the structure of the original CEM report. Specifically, it presents and documents updates to chapters 1–6. It does not include updates to the original Executive Summary or chapters 7–8, because these were not updated.

The updates presented in this report change the CRCR conceptual ecological model in several respects. We have added three new components: a new habitat element (Habitat Connectivity) to better describe dispersal needs and related gene flow impediments for the species and two new controlling factors (Irrigation and On-Site Water Management) to better describe management actions for CRCR habitats. Some link interaction strengths have been modified, and reasons clarified based on updated information, most importantly, Grazing.

This report also provides a list of all literature cited in the updates to chapters 1–6. In addition, it provides a list of all changes made to the name of the CEM components to standardize terminology across all CEMs.

This report both explicitly and implicitly identifies possible new research and monitoring questions concerning gaps in knowledge that may bear on adaptive management of CRCR. These questions may or may not reflect the current or future goals of LCR MCSP decision making and are in no way meant as a call for the Bureau of Reclamation to undertake research to fill the identified knowledge gaps.

Updates to Chapter 1 – Introduction

The information in paragraph 3 in the initial section of chapter 1 is updated as follows:

The most widely used sources of information for the Colorado River cotton rat (*Sigmodon arizonae plenus*) (CRCR) conceptual ecological model (CEM) are BIO-WEST, Inc. (2005), California Department of Fish and Game (2005), Lower Colorado River Multi-Species Conservation Program (2008, 2016), and Neiswenter (2010, 2011, 2014, 2016). These publications summarize and cite large bodies of earlier studies. Where appropriate and accessible, those earlier studies are directly cited. The CEM also integrates numerous additional sources, particularly reports and articles completed since the aforementioned publications, information on current research projects, and the expert knowledge of LCR MSCP biologists (Calvert 2007, 2009; Hill 2011, 2017a, 2017b, 2018a; Hill and Calvert 2016; Hill and Lyon 2019, 2020; Smith 2017). In addition, pertinent references were used from throughout the range of cotton rats generally, to supplement the basic information from the lower Colorado River (LCR) region. The purpose of a conceptual ecological model is not to provide an updated literature review but to integrate the available information and knowledge into a CEM so it can be used for adaptive management.

Update to Colorado River Cotton Rat Reproductive Ecology

This description is updated as follows:

There is little detailed information about the reproductive ecology of CRCR, but it is likely similar to the related hispid cotton rat (*Sigmodon hispidus*), which has a short but fecund life. Hispid cotton rats typically reach maturity around 40 days, live an average of 6 months (Cameron and Spencer 1981), and can reproduce throughout the year. A critical component of their ecology is their ability to disperse to new habitats. Most cotton rat populations exist in isolated patches of suitable habitat, but they can rapidly recolonize old patches or reach new habitats quite readily, especially if not too distant (on the scale of hectares/kilometers). Dispersal in hispid cotton rats seems to be density dependent and correlated with changes in environmental conditions (Joule and Cameron 1975); however, more research is needed to determine if this is always the case for related cotton rats such as CRCR.

CONCEPTUAL ECOLOGICAL MODEL PURPOSES

This update does not propose any changes to this section of chapter 1; however, when the CEMs are fully updated, chapter 1 should be revised to indicate that the CEM methodology followed here is a crucial foundation for carrying out effects analyses as described by Murphy and Weiland (2011, 2014) and illustrated by Jacobson et al. (2016).

CONCEPTUAL ECOLOGICAL MODEL STRUCTURE FOR THE CRCR

No change. This will not be updated for the existing CEMs.

Updates to Chapter 2 – CRCR Life-Stage Model

This update standardizes the names of the CRCR life stages by changing from Nest and Adult to Pups and Adults, respectively, using the plural noun form for each, and to maintain consistency with the other LCR MSCP conceptual ecological model updates. The names of the original life-stage outcomes are standardized as follows: Reproduction changes to Fertility. There is no change to Survival. This update drops the word "rate" from the names of life-stage outcomes because all life-stage outcomes are rate variables by definition. Table 1 and figure 1 (at the end of this chapter) are updated accordingly.

UPDATE TO INTRODUCTION TO THE CRCR LIFE CYCLE

The introduction is updated as follows:

The CRCR life cycle is likely similar to the related hispid cotton rat, which is one of high fecundity during a short lifespan. Hispid cotton rats become sexually mature at around 40 days and can breed throughout the year, although they usually live 6 months on average. This life history strategy likely enabled cotton rats to adapt to and recolonize riparian habitats periodically disturbed by flooding events (Neiswenter 2011, 2016).

UPDATE TO CRCR LIFE STAGE 1 – PUPS

This life stage description is updated as follows:

Little is known about the nests and nesting behavior of CRCR; however, it is likely similar to the related hispid cotton rat. In that species, the females build a grass nest in shallow depressions or underground in burrows (Baar et al. 1974 and references therein). There are usually 5–6 pups per litter (Burt and Grossenheider 1976), though sometimes up to 15 pups are born (Cameron and Spencer 1981). The young develop rapidly during this stage—blind at birth, they are completely dependent on the parent for care. The mother nurses them until weaning, which occurs between 4–7 days (Burt and Grossenheider 1976), up to 10–15 days (Cameron and Spencer 1981).

UPDATE TO CRCR LIFE STAGE 2 – ADULTS

This life stage description is updated as follows:

The adults life stage includes both subadults and breeding adults. It begins when the young are weaned and are no longer dependent on maternal care. Hispid cotton rats typically become sexually mature at about 40 days of age (Burt and Grossenheider 1976); however, there is no discernable difference in critical life processes between these subadults (age ≈7–40 days) and sexually mature adults. For this reason, these time periods are considered together to be the adults life stage. Non-migratory, they are active day and night (California Department of Fish and Game 2005; Zimmerman 1970 *in* Gwinn et al. 2011). The life expectancy for hispid cotton rats can be short, usually averaging 6 months (Cameron and Spencer 1981; Goertz 1964).

UPDATE TO LIFE-STAGE MODEL SUMMARY

Table 1.—(Revision of original table 1) CRCR life stages and life-stage outcomes in the LCR ecosystem

Life stage	Life-stage outcome(s)
1. Pups	• Pup survival
2. Adults	• Adult survival • Adult fertility

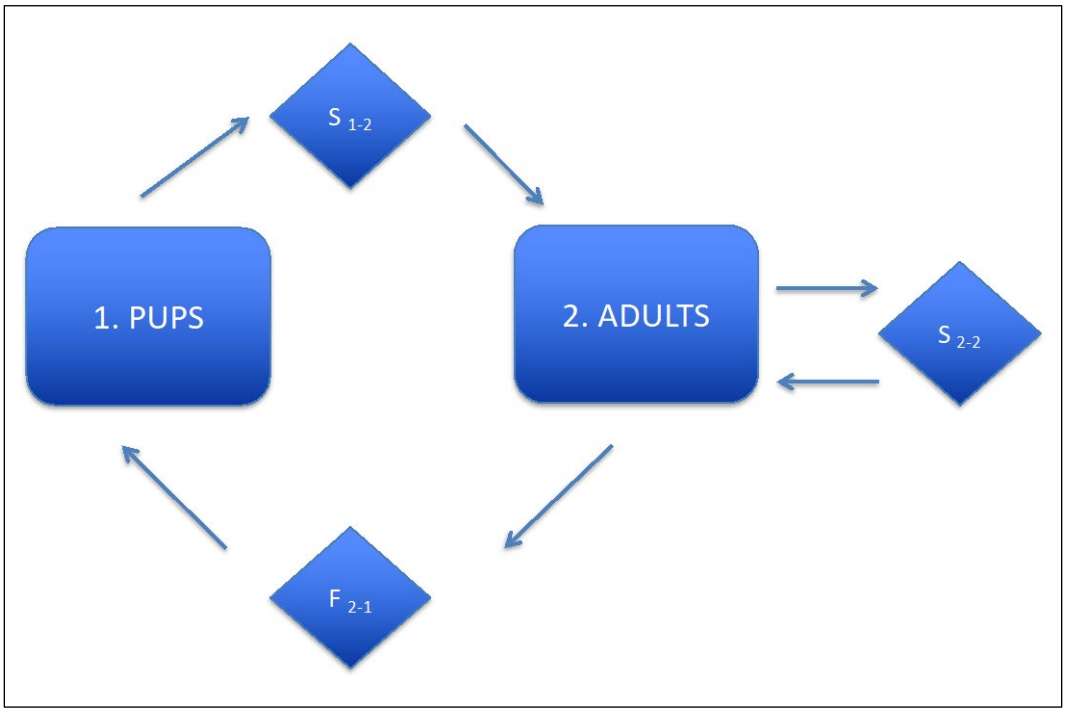

Figure 1.—(Revision of original figure 1) Proposed CRCR life history model. Squares indicate the life stages, and diamonds indicate the life-stage outcomes. S_{1-2} = survival of pups, s_{2-2} = survival of weaned juveniles until breeding and of adults between breeding events, and F_{2-1} = adult cotton rat fertility.

Updates to Chapter 3 – Critical Biological Activities and Processes

This update revises or adds additional information to all eight critical biological activities and processes. The following paragraphs describe these changes. Table 2 is also updated to reflect life stage name changes as follows:

Table 2.—(Revision of original table 2) Distribution of CRCR critical biological activities and processes among life stages
(Xs indicate that the critical biological activity or process is applicable to that life stage.)

Life stage ➔ **Critical biological activity or process 🡻**	Pups	Adults
Disease	**X**	**X**
Dispersal		**X**
Foraging		**X**
Gene flow		**X**
Nest attendance		**X**
Nursing	**X**	
Predation	**X**	**X**
Predator avoidance behavior		**X**

DISEASE

The discussion of this critical biological activity or process is updated as follows:

This process refers to diseases caused by infectious agents. Hispid cotton rats are parasitized by trematodes, cestodes, nematodes, and fleas (Mollhagan 1978), each of which can be disease carriers. In addition, cotton rats are often used in studies of infectious diseases in humans, as they are susceptible to many human pathogens (Niewiesk 2015). Although CRCR populations may, in part, be regulated by disease (LCR MSCP 2019), there is little or no information available about diseases in CRCR specifically, although CRCR in all life stages are conceivably susceptible to disease.

The rat lungworm disease caused by the roundworm (*Angiostrongylus cantonensis*) has spread into the Southeastern United States and was recently found in Oklahoma in a hispid cotton rat (York et al. 2015). Depending in part on the suitability of hispid cotton rats as a viable host species, and the direction of spread, this disease could potentially threaten other cotton rat populations, including CRCR, in the future.

DISPERSAL

The discussion of this critical biological activity or process is updated as follows:

Hispid cotton rats will disperse into new habitat patches as conditions become favorable. They may follow corridors of dense vegetation (e.g., moving along unlined canals or mown roadsides and roadside ditches) but also appear capable of dispersing to new habitats across "atypical" habitat (Diffendorfer and Slade 2002). Hispid cotton rats are also capable swimmers (Hawthorne 1994). Not only have CRCR have been observed swimming, some individuals have been captured on islands of habitat within the Colorado River (J. Hill and C. Dodge 2018, personal communications).

Research on cotton rats provides differing results on cotton rat dispersal. A paper on the long-distance dispersal of hispid cotton rats that looked at the characteristics of dispersing animals found that most dispersers were subadult males, with a trend toward greater movement during the autumn months (Diffendorfer and Slade 2002). Other researchers found no sex bias in dispersing cotton rats (Joule and Cameron 1975; Stafford and Stout 1983), while work by Diffendorfer et al. (1995) on habitat fragmentation and small mammals showed that it was adult male cotton rats that moved most often among habitat patches. They report that most dispersing females were non-reproductive.

These differing results may be due to location (northern versus southern populations), variation in experimental design, or other factors such as distances studied. Although there are no specific data on dispersal of CRCR, dispersal is an important mechanism structuring small mammal populations and allowing for colonization of the ephemeral riparian habitats along the LCR. In fact, mammal biologists have observed the related Yuma hispid cotton rat (*Sigmodon hispidus eremicus*) colonization of restored LCR habitat 3 years after planting at Hunters Hole (Hill 2017a).

FORAGING

The discussion of this critical biological activity or process is updated as follows:

Related hispid cotton rats generally are herbivores, feeding on stems, leaves, and seeds of a variety of grasses, and occasionally consuming insects and small invertebrates (Martin et al. 1961); the CRCR likely does the same. Newborn pups are nursed by the female (see below, "Nest Attendance"), and foraging is done only by subadults and breeding adults as part of the adults life stage.

GENE FLOW

The discussion of this critical biological activity or process is updated as follows:

This refers to the process of transferring genes from one population of cotton rats to another, usually through dispersal of CRCR. This, in turn, affects genetic diversity (i.e., the genetic homogeneity versus heterogeneity of a population during each life stage). The greater the heterogeneity, the greater the possibility that individuals of a given life stage will have genetically encoded abilities to survive their encounters with the diverse stresses presented by their environment and/or take advantage of the opportunities presented (Allendorf and Leary 1986). Cotton rat populations along the LCR experience boom and bust cycles, with population numbers occasionally being reduced to a small number of individuals (Neiswenter 2011; Smith 2017). This may lead to a lack of genetic diversity (genetic bottlenecks) that could make individuals in isolated populations more susceptible to environmental stresses. It has been noted that there are genetic concerns for CRCR populations due to their isolated and spotty distribution along the LCR (Neiswenter 2011, 2016; LCR MSCP 2016). This is in part due to the construction of dams and reservoirs along the river that fragments riparian habitat and impedes dispersal among cotton rat populations (J. Hill 2018b, personal communication).

NEST ATTENDANCE

The discussion of this critical biological activity or process is updated as follows:

Female CRCR build the nest and care for and nurse their young until weaning. The presence of the mother is critical to the survival of the young, depends in part on her survivorship, and affects the pups life stage.

NURSING

The discussion of this critical biological activity or process is updated as follows:

This process only applies to the pups life stage because cotton rat pups nurse from mothers to eat and stay alive. A pup's ability to eat is determined by the provisioning rate of its mother.

PREDATION

The discussion of this critical biological activity or process is updated as follows:

Predation is a threat to CRCR at all life stages, and it obviously affects subpopulation persistence to varying degrees. Although the most common predators of cotton rats are well known (see chapter 4, "Predators"), the depredation rates at any CRCR life stage are not known.

PREDATOR AVOIDANCE BEHAVIOR

The discussion of this critical biological activity or process is updated as follows:

Avoiding predation is a major activity of herbivores such as cotton rats. Apart from the outright mortality associated with predation, there are non-lethal costs to the presence of predators in the landscape. For example, research on related hispid cotton rats showed that the detection of predators in a habitat by the rats, whether detected visually, by scent, or by listening to alarm call cues from other species such as blue jays (*Cyanocitta cristata*), reduced the time spent foraging for food and the ability of cotton rats to quickly detect optimal foraging patches (Felts and Schmidt 2010). Hispid cotton rats have also been shown to modify their foraging behavior in the presence of the imported red fire ant (*Solenopsis invicta*), most likely to avoid envenomation by the ants (Darracq et al. 2016). In addition, the perceived presence of predators reduced the home range size for cotton rats (Wiegert 1972). Since CRCR prefer dense vegetation (Neiswenter 2014, 2016), the absence of such vegetation also may affect antipredator behaviors.

Updates to Chapter 4 – Habitat Elements

This update adds one new habitat element, Habitat Connectivity, and standardizes the names of two habitat elements, with Maternal Care becoming Parental Care and Predator Density becoming Predators. Five of six original habitat elements are updated. The following paragraphs describe these changes. Table 3 is also updated:

Table 3.—(Revision of original table 3) Distribution of CRCR habitat elements and the critical biological activities and processes that they directly affect across all life stages

(Xs indicate that the habitat element is applicable to that critical biological activity or process.)

Critical biological activity or process ➔ / **Habitat element ⬇**	Disease	Dispersal	Foraging	Gene flow	Nest attendance	Nursing	Predation	Predator avoidance behavior
Food availability			**X**					
Habitat connectivity (*new*)		**X**						
Herbaceous vegetation assemblage		**X**			**X**		**X**	**X**
Infectious agents	**X**							
Local hydrology		**X**			**X**			
Parental care *(renamed)*						**X**		
Predators (*renamed*)							**X**	**X**

Note: Gene flow is affected indirectly by several habitat elements, including the herbaceous vegetation assemblage, habitat connectivity, and local hydrology, as they impact dispersal.

FOOD AVAILABILITY

The definition of this habitat element is updated as follows:

Full name: **The diversity, sizes, abundance, and spatial and temporal distributions of the species on which CRCR feed**. This element refers to the availability of food resources, whether stems, leaves, seeds of grasses and other

forbs, or invertebrates that individual CRCR will encounter during each life stage and the density and spatial and temporal distributions of the food supply in proximity to the nest. Although not many details are available about the CRCR diet, related hispid cotton rats feed mainly on grasses, and may consume other plant materials, and even insects from time to time (California Department of Fish and Game 2005). For example, at a coastal Texas prairie, reproductive hispid cotton rat females selected for habitat patches that included both monocots and dicots, as the combination provides a nutritionally balanced diet. [1] Cotton rats in these locations also foraged by shifting their home range daily in a clockwise pattern, increasing the likelihood of encountering sufficient nutritional food items (Cameron 1995). Importantly, research on hispid cotton rats has shown that the food supply for breeding females during pregnancy and during lactation directly influences litter size and survivorship of nursing young (Mattingly and McClure 1982, 1985).

HABITAT CONNECTIVITY

This is a new habitat element.

Full name: **The capacity of a suitable habitat network to support or inhibit movement of organisms as determined by the spatial distribution of natural and artificial barriers that may prevent or inhibit such movement**. Although little information is available for CRCR, related hispid cotton rats disperse along corridors of dense vegetation, often moving through streamside riparian habitat or along unlined canals and roadside ditches. They may also be able to move through "atypical" habitat (Diffendorfer and Slade 2002). CRCR have been observed swimming, with some captured on islands of habitat within the Colorado River (J. Hill and C. Dodge 2018, personal communications).

Habitat connectivity affects the taxonomic and genetic composition of cotton rat populations in different reaches of the Colorado River. The severity of fragmentation (loss of connectivity) depends on the number and spatial extent of barriers, their relative placement, and their permeability (ability to allow some passage of the subject fauna). It has been noted that there are genetic concerns for CRCR populations due to their isolated and spotty distribution along the LCR (Neiswenter 2011, 2016; LCR MSCP 2016), in part due to the construction of dams and reservoirs along the river that fragments riparian habitat and impedes dispersal among cotton rat populations (J. Hill 2018b, personal communication).

[1] Monocots provide carbohydrates and fiber. Dicots provide proteins, lipids, and minerals (Cameron and Spencer 2008; Kincaid and Cameron 1985).

HERBACEOUS VEGETATION ASSEMBLAGE

The definition and discussion of this habitat element is updated as follows:

Full name: **The species diversity, abundance/density, spatial and temporal distributions, and vertical structure of herbaceous vegetation**. Cotton rats require grasses and other low herbaceous vegetation to provide habitat structure and protection from predators, for nesting material, and for food. CRCR have been found in a variety of mesic habitats (e.g., sloughs, backwater marshes with emergent vegetation, Fremont cottonwood-Goodding's willow (*Populus fremontii-Salix gooddingii*) (hereafter cottonwood-willow) riparian areas, and agricultural fields along canals) with wetland vegetation that includes tule (*Scirpus acutus*), wiregrass (*Cynodon dactylon*) in cottonwood-willows (Grinnell 1914 *in* BIO-WEST, Inc. 2005), mule-fat (*Baccharis salicifolia*), and cattails (*Typha* sp.) as well as other emergent vegetation, including common reed (*Phragmites australis*) (Calvert 2009; Hill 2017a, 2017b, 2018a; Zimmerman 1970 *in* BIO-WEST, Inc. 2005), bulrush (*Scirpus* sp.) and arrowweed (*Pluchea sericea*) (BIO-WEST, Inc. 2005; Calvert 2007; Hill 2011, 2017b, 2018a; Hill and Lyon 2020). Hoffmeister 1986 (*in* BIO-WEST, Inc. 2005) also reports them in drier grassy areas. CRCR will use habitats with either native or non-native grasses or other vegetation. In fact, much of the habitat used by CRCR along the LCR is currently comprised of mostly non-native vegetation such as Johnsongrass (*Sorghum halepense*) (Calvert 2009; Hill 2017a; Hill and Calvert 2016; Neiswenter 2014, 2016). [*Note*: Yuma hispid cotton rats are now using native grasses such as alkali sacaton (*Sporobolus airoides*) and blue grama (*Bouteloua gracilis*) at Yuma East Wetlands and Hunters Hole (Hill 2017a, 2017b, 2018a). It is likely that CRCR are able to use similar plant species (C. Dodge 2018, personal communication)].

The development of an herbaceous understory is an important factor in determining the presence of Arizona cotton rats (*Sigmodon arizonae*) (Andersen and Nelson 1999 *in* LCR MSCP 2016). In particular, it is the density of vegetation < 1 meter (m) in height, rather than the species composition, that appears to be the most important habitat parameter for cotton rats (Neiswenter 2014, 2016). Neiswenter (2011, 2014) found greater vertical vegetation density between 10–12 and 90–100 centimeters at CRCR capture sites along with higher ground cover of forbs. Hispid cotton rats also appear to select for shrubs at least 1 m high (Bowne et al. 1999) or with greater stem density at that height above the ground (Stokes 1995). Neiswenter (2016) observed CRCR frequently using dense *Chlorocantha* shrub patches, which are about 1 m tall. While CRCR rely on different vegetation types to provide optimal vegetation density, hispid cotton rats generally avoid areas with dense tree canopy cover (Goertz 1964).

Another factor in habitat selection is related to the reproductive status of the animals in questions. While cotton rats generally prefer monocots, Kincaid and Cameron (1985) and Cameron and Spencer (2008) observed at their coastal Texas prairie sites that reproductive female hispid cotton rats selected habitat patches with mixed monocots and dicots. This diversity of vegetation provided a more nutritionally balanced diet.

INFECTIOUS AGENTS

The definition of this habitat element is updated as follows:

Full name: **The types, abundance, and distribution of infectious agents of CRCR individuals and their vectors**. Infectious agents refer to the spectrum of viruses, bacteria, fungi, and parasites capable of infecting CRCR that individuals are likely to encounter during each life stage. Hispid cotton rats are parasitized by trematodes, cestodes, nematodes, and fleas (Mollhagan 1978), each of which can be disease carriers. A new potential infectious agent is the roundworm, which causes rat lungworm disease, recently found in a hispid cotton rat in Oklahoma (York et al. 2015). In addition, cotton rats are often used in studies of infectious diseases in humans, as they are susceptible to many human pathogens (Niewiesk 2015). However, the effects of disease and other infectious agents are poorly understood.

LOCAL HYDROLOGY

The definition of this habitat element is updated as follows:

Full name: **Aspects such as the distance to standing water or the presence of adjacent water bodies, timing and volume of floods, depth to the water table, and soil moisture levels**. Each depends on a hydrologic regime that maintains sufficient water and flow to support native riparian or wetland vegetation. CRCR are often found near water, whether natural streams (e.g., alluvial bottoms along the LCR [Goldman 1928]) or manmade irrigation canals, ponds, and agricultural fields (Hoffmeister 1986) (see Gwinn et al. 2011). In Nevada, they were found nesting just above the water line in a cattail marsh (Hall 1946 *in* BIO-WEST, Inc. 2005). However, when Bradley (1966) returned to the location in 1965, he found the habitat had almost dried up, cattails being replaced by Bermudagrass (*Cynodon dactylon*) and thistles, most likely due to changes to hydrology from river channeling during the filling of Lake Powell. In a Louisiana study, most hispid cotton rats were captured in dense grassy vegetation near pond edges (Goertz and Long 1973). Recently, CRCR have been found in grassy areas in restored cottonwood-willow and honey mesquite (*Prosopis glandulosa*) riparian habitats along the LCR (LCR MSCP 2016).

habitats along the LCR (LCR MSCP 2016). CRCR are able to tolerate some stream or irrigation flooding, moving to higher ground until water subsides (A. Calvert and J. Hill 2015, personal communications).

PARENTAL CARE

This habitat element replaces the original, Maternal Care. The discussion remains unchanged.

PREDATORS

This habitat element replaces the original, Predator Density, with a slightly updated definition as follows:

Full name: **The taxonomic and functional composition, abundance, and spatial and temporal distributions of species that may prey on CRCR during each life stage**. This element refers to a set of closely related variables that affect the likelihood that different kinds of predators will encounter and successfully prey on CRCR during any life stage. The variables of this element include the species and sizes of the fauna that prey on CRCR during different life stages and the density and spatial distribution of these fauna in the habitats used by cotton rats. Nesting on the ground exposes related hispid cotton rats and their young to many predators, including raptors (e.g., northern harriers [*Circus cyaneus*], sharp shinned hawks [*Accipiter striatus*], great horned owls [*Bubo virginianus*]), snakes, and mammals (e.g., coyotes [*Canis latrans*], bobcats [*Lynx rufus*], foxes, and mustelids) (A. Calvert and J. Hill 2015, personal communications; Schnell 1968). Little is known about depredation rates of CRCR at any life stage. For hispid cotton rats generally, avian predators have been found to be the most important predators regulating population density (Neiswenter 2011; Schnell 1968; Wiegert 1972), and this may partially explain their avoidance of habitat patches with a high percentage of bare ground (Cameron and Spencer 2008).

Other potential predators may include imported red fire ants. Although not currently documented from Arizona, an infestation of these exotic fire ants was discovered in Yuma in 1999 and extirpated (Pest Control Technology 1999). They are known to attack newborn rodents in the nest and could become a threat to cotton rats should the ants become established in the LCR region. Additionally, the presence of non-native red fire ants has been shown to alter foraging behavior of hispid cotton rats in experimental plots in Georgia, presumably through interference competition (Darracq et al. 2016).

Competition among rodent species does occur (e.g., hispid cotton rats compete with other cricetid rodents, especially microtines and *Mus musculus*) (California Department of Fish and Game 2005). In the LCR, Yuma hispid cotton rats could potentially outcompete CRCR, as Yuma hispid cotton rats are larger animals, but these two species have not been found to co-occur in the LCR (Blood 1990; Hill and Calvert 2016; J. Hill and C. Dodge 2018, personal communications; Neiswenter 2010). Because there are no data as to whether competition with other rodent species is a significant issue for CRCR, it has not been included as a component of this habitat element.

Updates to Chapter 5 – Controlling Factors

This update adds two new controlling factors, Irrigation and On-Site Water Management, and updates the discussion of all controlling factors. Table 4 is also updated as follows:

Table 4.—(Revision of original table 4) Habitat elements directly affected by controlling factors

(Xs indicate that the controlling factor is applicable to that habitat element.)

Controlling factor ➔ / **Habitat element ↓**	Fire management	Grazing	Habitat management & restoration	Irrigation (*new*)	Nuisance species introduction & management	On-site water management (*new*)	Water storage-delivery system design & operation
Food availability							
Habitat connectivity (*new*)							**X**
Herbaceous vegetation assemblage	**X**	**X**	**X**		**X**	**X**	
Infectious agents					**X**		
Local hydrology				**X**			**X**
Parental care (*renamed*)							
Predators (*renamed*)			**X**		**X**		

Note: Food availability is affected indirectly by fire management, grazing, habitat management & restoration, irrigation, and nuisance species introduction & management through their effects on the herbaceous vegetation assemblage. Parental care is affected indirectly by controlling factors that affect the herbaceous vegetation assemblage, local hydrology, and predators.

FIRE MANAGEMENT

The discussion of this controlling factor is updated as follows:

This factor addresses any fire management, whether prescribed fire or fire suppression, which may occur along the LCR and could affect CRCR or their habitat. Effects may include creation of habitat that supports or excludes cotton

rats (e.g., roadside disking of vegetation used by CRCR), reduction in the food supply, or support of species that pose threats to cotton rats such as predators, competitors, or carriers of infectious agents. Although typically not a major threat in most riparian habitats, severe wildfires have affected cottonwood-willow riparian habitat in the past decade (Graber et al. 2007) and could pose a threat to any cotton rat populations in similar habitats in part by removing the dense cover on which they depend. A recent fire at the Havasu National Wildlife Refuge burned habitat previously occupied by CRCR (Hill 2017a; J. Hill and C. Dodge 2018, personal communications).

In addition, the presence of flammable native or exotic grasses may increase fire frequency and/or intensity in desert systems and associated riparian habitats. Climate change is also projected to affect fire frequency along the LCR (U.S. Fish and Wildlife Service [USFWS] 2013).

Following a fire, studies have documented decreases in local abundances of several rodent species, including *Sigmodon* sp. that require dense vegetation (Bock and Bock 1978; Colbert, III 2016; Conner et al. 2011; Kirchner et al. 2011; Litt 2007; Morris et al. 2011; Simons 1991). In some studies, initial declines in hispid cotton rat abundance were attributed mainly to increased avian predation due to lack of cover, with some emigration also likely (Colbert, III 2016; Morris et al. 2011). Although Litt (2007) observed that differences in *Sigmodon arizonae* and other *Sigmodon* species abundances pre- and post-fire persisted at least 2 years in semi-desert grasslands in Arizona, with vegetation regrowth, cotton rat abundances did recover. In a South Carolina coastal system, Colbert, III (2016) observed population recovery 3 months after a burn. Hispid cotton rats returned to a Texas prairie site 8 months after a prescribed burn (Kirchner et al. 2011).

In the LCR, small fires are a regular occurrence in the Yuma region and have not affected the continued presence of the related Yuma hispid cotton rats in the area (Hill 2017a, 2017b; J. Hill and C. Dodge 2018, personal communications). After a fire at Hunters Hole, for example, Yuma hispid cotton rats returned to the site once the site revegetated. Conner et al. (2011) suggest that the benefits of applying fire for long-term habitat maintenance may outweigh the short-term negative effects of prescribed fire on hispid cotton rat abundance in longleaf pine (*Pinus palustris*) habitats in the Southeastern United States, and the same may be true in LCR habitats. Similarly, the use of prescribed fire in certain LCR locations to clear senesced grasses and woody vegetation from ditches and other ruderal areas may benefit cotton rats.

GRAZING

The discussion of this controlling factor is updated as follows:

This factor addresses the grazing activity on riparian habitats along the LCR and in surrounding areas that could affect cotton rats or their habitat. Overgrazing by cattle (Bovidae), burros (*Equus asinus*), or mule deer (*Odocoileus hemionus*) across the arid Southwestern United States has substantially degraded riparian habitat in many areas (see Appendix G *in* USFWS 2002) (*Note:* Bureau of Reclamation [Reclamation] staff and researchers have observed mule deer browsing on some LCR sites, which may affect vegetation communities if populations increase to the point that overgrazing occurs.) Overgrazing may thin the understory, prevent the establishment of cottonwood and willow seedlings, and remove the herbaceous cover (Kauffman et al. 1997), possibly affecting foraging and nesting habitats for cotton rats. Although not discussed in background papers for CRCR, grazing is a factor that affects riparian habitat generally, and high-density grazing in particular may affect animals that rely on a dense herbaceous layer. McCulloch (1959) reported that high-density grazing by cattle reduced the number of hispid cotton rats in Oklahoma. However, mule deer (see note above) or burros (reported at Planet Ranch and may occur elsewhere [C. Ronning 2019, personal communication]) would be the more common grazers potentially using CRCR habitat, not cattle. While there are sheep in nearby agricultural areas, they have not been found at any LCR MSCP sites. For these reasons, grazing impacts are not considered a major concern at this time (J. Hill and C. Dodge 2018, personal communications).

HABITAT MANAGEMENT & RESTORATION

The discussion of this controlling factor is updated as follows:

This factor addresses the active management and restoration activities to restore grasslands in riparian habitats, as well as marshes and backwater areas within the LCR, and includes not only mechanical or chemical clearing of existing vegetation but also the vegetation community planted and the pattern in which it is planted within restoration areas.

Cotton rats are known to use marsh vegetation, including cattails and tule (*Scirpus* sp.), and they use grassy habitats that occur in cottonwood and willow riparian areas. CRCR also have been found frequenting habitats with the native shrub *Chlorocantha* (A. Calvert 2015, personal communication; Neiswenter 2011, 2014, 2016).

Habitat restoration plantings have supported CRCR at a number of LCR locations, but habitats can change as a function of natural succession and habitat age. For example, at both the Palo Verde Ecological Reserve and Cibola Valley Conservation Area, restored cottonwood and willow trees in riparian areas have shaded out the understory typically used by CRCR (Hill 2011), and mule-fat is now shading out Johnsongrass at the Cibola NWR Unit #1 Conservation Area Nature Trail (Hill and Calvert 2016). The vegetation in the riparian habitat at the Beal Lake Conservation Area, where CRCR were captured in 2006 and 2012, has shifted from Johnsongrass to arrowweed and may indicate that they don't use this vegetation mosaic or use it in densities that make it difficult to detect species presence with only 1–3 nights of rodent trapping (Hill 2017a; Hill and Calvert 2016).

IRRIGATION

This is a new controlling factor.

This factor addresses the human activities of artificially introducing water to the landscape to influence habitat. In many cases, this may be implemented to simulate more natural riparian processes or to manage soil salinity levels. The LCR MSCP and USFWS irrigate portions of several conservation areas along the Lower Colorado River Valley to create and manage habitat for general wildlife, LCR MSCP covered species, and associated wetland habitat. In particular, CRCR have been found at a number of restoration sites, including the Beal Lake Conservation Area, Palo Verde Ecological Preserve, Cibola Valley Conservation Area, Cibola National Wildlife Refuge, and Pintail Slough at the Havasu National Wildlife Refuge.

The amount of water provided through irrigation affects the species composition and density of the moist herbaceous plant community required by cotton rats for food, shelter, and nesting. The amount of water available is also affected by management actions to reduce or terminate water applications at a site (e.g., to reallocate water to other sites within the limits of Reclamation water rights). Changes in irrigation that alter the local hydrology to affect herbaceous cover and mid-story and over-story structure can result in habitat that is less structurally suitable for CRCR (see chapter 4, "Herbaceous Vegetation Assemblage"). For example, a change in the watering schedule at Pintail Slough and resulting habitat senescence may be a contributing factor to the decline in CRCR at the site in recent years (Hill and Calvert 2016).

NUISANCE SPECIES INTRODUCTION & MANAGEMENT

The discussion of this controlling factor is updated as follows:

This factor addresses the intentional or unintentional introduction of nuisance species (animals and plants as well as microbes) and/or their control that affect cotton rat survival and reproduction. The nuisance species may poison, infect, prey on, compete with, or present alternative food resources for CRCR during one or more life stages; cause other alterations to the riparian food web that affect CRCR; or affect physical habitat features such as vegetation cover.

For example, the presence of dense stands of invasive saltcedar (*Tamarix* sp.) in riparian areas where the hydrology has been severely altered may affect the germination and establishment of cottonwood and willow and growth of the dense grass cover required by cotton rats. Saltcedar also alter soil chemical properties (Merritt and Shafroth 2012), such that even after its control and removal, re-establishment of the dense grassy vegetation on which CRCR depend may be difficult, especially in the LCR where natural hydrologic processes also have been altered.

While some non-native species can provide suitable habitat (e.g., CRCR readily use Johnsongrass [Calvert 2009; Hill 2017a]), other invasive species, such as Bermudagrass, reduce habitat quality for cotton rats in part by preventing the establishment of native grasses preferred by CRCR (Hill 2018a; Hill and Dodge 2018, personal communications). CRCR has been found to respond positively to the presence of another non-native grass, Lehman's love grass (*Eragrostis lehmanniana*), with greater abundance and survival in experimental plots; however, rates of CRCR reproduction were reduced overall (Litt and Steidl 2016).

Other nuisance exotic grasses have increased wildfire frequency and intensity (see above, "Fire Management"). The use of herbicides to control invasive plants such as saltcedar or common reed may alter riparian and marsh vegetation structure, especially if non-target herbicides are broadly applied.

ON-SITE WATER MANAGEMENT

This is a new controlling factor.

This factor addresses the types, frequencies, and durations of official activities that affect the delivery and distribution of regulated water within sites managed to

support CRCR habitat. In particular, this addresses water management for ponds and marshes maintained by the LCR, such as Hart Mine Marsh at the Cibola National Wildlife Refuge, where CRCR have been found (Hill and Lyon 2019, 2020).

The amount and stability of water provided through pond and marsh water level management affects the vegetation community fringing the wetlands, with implications for cotton rat habitat use and survival. On-site water management may also include actions to reduce or terminate water applications at a site (e.g., to reallocate water to other sites within the limits of Reclamation water rights).

WATER STORAGE-DELIVERY SYSTEM DESIGN & OPERATION

The discussion of this controlling factor is updated as follows:

Much of the habitat used by CRCR is along regulated waterways. The water moving through these systems is highly managed to allow for storage and delivery (diversion) to numerous international, Federal, State, Tribal, and municipal users and for hydropower generation. This factor includes river and off-channel water management, including pumping of groundwater and diversion of river water to manage water levels in refuge ponds, as well as dewatering and flushing of marsh habitats. A number of important CRCR habitats are found adjacent to the river, for example, the Big Bend Conservation Area and the accretion bench at the Palo Verde Ecological Reserve. The amount of water, flooding frequency, water depth, and stability of adjacent water bodies, each affect the species composition and density of the moist herbaceous plant community required by cotton rats for food, shelter, and nesting. Construction of reservoirs and associated dams along the main stem of the river also impedes gene flow by preventing dispersal of cotton rats among sites.

Updates to Chapter 6 – Conceptual Ecological Model by Life Stage

The following sections identify all changes made to the CRCR conceptual ecological model workbook other than changes that involve only updates to names. These latter changes are listed separately in table 5 (see "Summary of Standardization of Terms" at the end of this chapter). The items in each section of this chapter are arranged alphabetically. The abbreviations, CF for controlling factor, HE for habitat element, CAP for critical activity or process, and LSO for life-stage outcome are provided to identify component types where needed. Each item also identifies the life stage(s) to which the item applies.

New Links with Controlling Factors as Causal Agents

Irrigation effect on Local Hydrology (HE): Irrigation is a new controlling factor added to the CEM to better address water management at individual restoration sites at which CRCR occur. The link is hypothesized to be complex and unidirectional, with proposed high intensity (as water directly affects the local hydrology; medium spatial scale (in this case, it depends upon the amount of acreage irrigated by Reclamation [acreage numbers are within the medium category]); and low temporal scale (although sites managed with irrigation are under longer term management, if irrigation ceases, changes will be rapid). Overall, the link interaction strength is medium. Link predictability is medium (water flow affects local hydrology and is affected by drought), and link understanding is high. *Applies to both life stages.*

On-Site Water Management effect on Herbaceous Vegetation Assemblage (HE): On-Site Water Management is a new controlling factor added to the CEM to address water management more finely at the site level. It specifically refers to management of water levels of ponds and marshes. The link is hypothesized to be complex and unidirectional, with proposed high intensity (water availability affects vegetation growth, density, and diversity); medium spatial scale, and medium temporal scale (impoundments hold water for a longer time period). Overall, the link interaction strength is medium. Link predictability is medium (on-site water management is not the only factor affecting the vegetation community), and link understanding is high. *Applies to both life stages.*

Water Storage-Delivery Design & Operation effect on On-Site Water Management (CF): The link is hypothesized to be complex and unidirectional, with high link intensity (available water supply directly affect amount of water

available for on-site water management); medium spatial scale (related to the size of wetlands or ponds under management); and medium temporal scale (ponds or pools created by marsh bottom excavating and contouring will retain water for longer time periods, especially if supplemented on a regular basis under management plan). Overall, the link interaction strength is medium. Link predictability is medium (adding or removing water affects the water management regime, but the exact regime is difficult to predict ahead of time), and link understanding is high. *Applies to both life stages.*

Water Storage-Delivery Design & Operation effect on Irrigation (CF): The link is hypothesized to be complex and unidirectional, with proposed medium intensity (available water supply directly affects the amount of water available for irrigation); medium spatial scale (related to the amount of acreage irrigated by Reclamation [acreage numbers are within the medium category]); and medium temporal scale (sites managed with irrigation are under longer term management). Overall, the link interaction strength is medium. Link predictability is medium (adding or removing water changes the irrigation regime, but the exact regime is difficult to predict ahead of time), and link understanding is high. *Applies to both life stages.*

Water Storage-Delivery Design & Operation effect on Habitat Connectivity (HE): Construction of reservoirs and associated dams along the main stem of the Colorado River reduces shoreline habitat connectivity and impedes gene flow by preventing dispersal of cotton rats among sites. The link is hypothesized to be negative and unidirectional, with medium link intensity, high spatial scale (the LCR has been altered by major dam and reservoir construction), and high temporal scale (these structures are there for the long term). Overall, the link interaction strength is high. Link predictability is high (small mammals cannot disperse around dams and reservoirs), and link understanding is high. *Applies to both life stages.*

DELETED LINKS WITH CONTROLLING FACTORS AS CAUSAL AGENTS

No change.

UPDATED LINKS WITH CONTROLLING FACTORS AS CAUSAL AGENTS

Grazing effect on Herbaceous Vegetation Assemblage (HE): The original CEM characterized this link as medium overall, with high link intensity, high spatial scale, and low temporal scale (due to the potential impact that high densities of grazers, particularly cattle, can have on vegetation over large areas, although the time frame for recovery is relatively short). However, given the fact that there are no cattle in or near cotton rat habitats, that grazers like mule deer or burros are not overly abundant, and sheep from adjacent agricultural areas have not been found to wander onto LCR lands, we have reduced the strength of this interaction. The model now considers the link intensity to be low; spatial scale is low (we are mainly considering this on a site-by-site basis, not across a larger landscape); and temporal scale remains the same at low (once grazers are removed, vegetation should rebound within a 10-year timeframe). Link predictability and link understanding remain the same. *Applies to both life stages.*

Water Storage-Delivery Design & Operation effect on Local Hydrology (HE): The original link character was considered to be positive. The model now proposes the link character type to be complex, with low temporal scale. All other link values remain the same. All link understanding reasons have been updated. *Applies to both life stages.*

NEW LINKS WITH HABITAT ELEMENTS AS CAUSAL AGENTS

Habitat Connectivity effect on Dispersal (CAP): Habitat Connectivity is a new habitat element, added to better address issues of movement and potential gene flow. The link is hypothesized to be positive and unidirectional (greater connectivity, the more likely dispersal can occur), with high link intensity (without suitable habitat, it is unlikely that cotton rats will disperse even if they can use "atypical" habitat on occasion); low spatial scale (cotton rats do not disperse great distances); and low temporal scale (cotton rats have a short life span). Overall, the link interaction strength is medium. Link predictability is low (even with suitable habitat connectivity, it is difficult to predict what animals will do, other factors involved), and link understanding is medium (importance of habitat connectivity to dispersal fairly well understood). *Applies to the adults life stage.*

Herbaceous Vegetation Assemblage effect on Habitat Connectivity (HE): The type of vegetation community and its configuration on the landscape affects habitat connectivity. The link is hypothesized to be complex and unidirectional, with high link intensity (dense herbaceous vegetation is important to cotton rats but they also use "atypical" habitat on occasion); low spatial scale; and low temporal scale (suitability of vegetation corridor to cotton rats can change over short spatial and time scales). Overall, the link interaction strength is medium. Link predictability and understanding are medium (other factors will affect connectivity of vegetation community [e.g., flood or drought, fire etc.]) *Applies to the adults life stage.*

Deleted Links with Habitat Elements as Causal Agents

No change.

Updated Links with Habitat Elements as Causal Agents

Predators effect on Predation (CAP): The link reason was updated for clarification. *Applies to the pups life stage.*

Infectious Agents effect on Disease (CAP): The link intensity, spatial scale, and temporal scale have been changed from high, unknown, and unknown to low, low, and low, respectively. Infectious agents do cause disease and are a potential concern that would act at small temporal and spatial scales; however, no pathogens have been identified as a current concern. *Applies to both life stages.*

New Links with Critical Activities/ Processes as Causal Agents

No change.

Deleted Links with Critical Activities/ Processes as Causal Agents

No change.

Updated Links with Critical Activities/ Processes as Causal Agents

Disease effect on Foraging (CAP): The original link understanding was considered to be unknown. The model now proposes the link understanding to be low for consistency among models. The link understanding reason has been updated. All other link values remain the same. *Applies to the adults life stage.*

Disease effect on Nest Attendance (CAP): The original link understanding was considered to be unknown. The model now proposes the link understanding to be low for consistency among models. The link understanding reason has been updated. All other link values remain the same. *Applies to the adults life stage.*

Disease effect on Dispersal (CAP): The original link understanding was considered to be unknown. The model now proposes the link understanding to be low for consistency among models. The link understanding reason has been updated. All other link values remain the same. *Applies to the adults life stage.*

Disease effect on Survival (LSO): The original link understanding was considered to be unknown. The model now proposes the link understanding to be low for consistency among models. The link understanding reason has been updated. All other link values remain the same. *Applies to both life stages.*

Disease effect on Fertility (LSO): The original link understanding was considered to be unknown. The model now proposes the link understanding to be low for consistency among models. The link understanding reason has been updated. All other link values remain the same. *Applies to the adults life stage.*

Disease effect on Nursing (CAP): The original link understanding was considered to be unknown. The model now proposes the link understanding to be low for consistency among models. The link understanding reason has been updated. All other link values remain the same. *Applies to the pups life stage.*

Predation effect on Pups Survival (LSO): The link reason was updated to remove competition from the discussion. *Applies to the pups life stage.*

New Links with Life-Stage Outcomes as Causal Agents

No change.

SUMMARY OF STANDARDIZATION OF TERMS

Table 5.—(New table for this update) Updated CRCR conceptual ecological model component names (Blue indicates new or revised items; italicized entries are explanatory comments.)

CRCR conceptual ecological model, updated terms, 2019	CRCR conceptual ecological model, original terms, 2015–16
Life stages	
Pups (*renamed)*	Nest
Adults (*renamed)*	Adult
Life-stage outcomes	
Adult Fertility (*renamed*)	Reproduction
Adult Survival (*renamed*)	Survival
Pup Survival (*renamed*)	
Critical biological activities and processes	
Disease	Disease
Dispersal	Dispersal
Foraging	Foraging
Gene Flow	Gene Flow
Nest Attendance	Nest Attendance
Nursing	Nursing
Predation	Predation
Predator Avoidance Behavior	Predator Avoidance Behavior
Habitat elements	
Food Availability	Food Availability
Habitat Connectivity (*new*)	
Herbaceous Vegetation Assemblage	Herbaceous Vegetation Assemblage
Infectious Agents	Infectious Agents
Local Hydrology	Local Hydrology
Parental Care (*renamed*)	Maternal Care
Predators (*renamed*)	Predator Density
Controlling factors	
Fire Management	Fire Management
Grazing	Grazing
Habitat Management & Restoration	Habitat Management & Restoration
Irrigation *(new*)	
Nuisance Species Introduction & Management	Nuisance Species Introduction & Management
On-Site Water Management (*new*)	
Water Storage-Delivery System Design & Operation	Water Storage-Delivery Design & Operation

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ATTACHMENT 1

Colorado River Cotton Rat (*Sigmodon arizonae plenus*) (CRCR) Habitat Data

Table 1-1.—Colorado River cotton rat (*Sigmodon arizonae plenus*) (CRCR) habitat data
(*Note*: This is an update of table 2.1 found in attachment 2 of the original CRCR model document.)

Habitat element	Value or range	Location	Reference
Food availability	No values or ranges in the literature, just species lists.		
Habitat connectivity	Cotton rats move through streamside riparian habitats and along canals and roadside ditches; CRCR are good swimmers.	Lower Colorado River	J. Hill and C. Dodge 2018, pers. communications
	Hispid cotton rats (*Sigmodon hispidus*) can move through "atypical" habitat.	Kansas	DIffendorfer and Slade 2002
Herbaceous vegetation assemblage	Structure most important. Species composition variable, native or non-native. Johnsongrass (*Sorghum halepense*) commonly used.	Lower Colorado River	Neiswenter 2016
	Density of grassy vegetation within 1 meter (m) of ground most important.	Lower Colorado River	Neiswenter 2014, 2016
	Greatest density between 10–12 and 90–100 centimeters above ground.	Lower Colorado River	Neiswenter 2011, 2014
	Hispid cotton rats prefer sites with shrubs at least 1 m high and dense ground cover.	South Carolina	Bowne et al. 1999
	CRCR frequent *Chlorocantha* shrub patches ≈1 m tall.	Lower Colorado River	Neiswenter 2016
	Cotton rats avoid areas with dense tree canopy cover.	Oklahoma	Goertz 1964
	Hispid cotton rats select refuge sites with a greater number of stems at 1 m above the ground (forbs or woody perennials), with lightly vegetated surface.	Kansas	Stokes 1995
Infectious agents	No values or ranges in the literature.		
Local hydrology	Hispid cotton rats found near water, natural streams, or human-made irrigation canals, ponds, or agricultural fields.	Lower Colorado River	Allen 1895; Burt 1933; Goldman 1928; and Hoffmeister 1986 *in* Gwinn et al. 2011
	CRCR found in restored Fremont cottonwood-Goodding's willow (*Populus fremontii-Salix gooddingii*) and honey mesquite (*Prosopis glandulosa*) riparian habitat.	Lower Colorado River	Lower Colorado River Multi-Species Conservation Program 2008, 2016
	Found in tall grasses at the edges of ponds.	Louisiana	Goertz and Long 1973
	CRCR nested just above water line in cattail (*Typha* sp.) marsh.	Nevada	Hall 1946 *in* BIO-WEST, Inc. 2005
Predators	No values or ranges in the literature, just species lists.		

Note: The data presented in this table reflect those available in the literature at the time this model was developed. These data have not been validated.

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