STATE OF CALIFORNIA

Energy Resources Conservation and Development Commission

In the Matter of:

APPLICATION FOR CERTIFICATION
FOR THE IVANPAH SOLAR
ELECTRIC
GENERATING SYSTEM

DOCKET NO. 07-AFC-5

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DATE JAN 05 2010
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REBUTTAL TESTIMONY FOR TOPICS TO BE HEARD IN JANUARY, 2010, ADDITIONAL EXHIBITS, AND PROOF OF SERVICE

INTERVENOR CENTER FOR BIOLOGICAL DIVERSITY

January 5, 2010

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REBUTTAL TESTIMONY FOR TOPICS TO BE HEARD IN JANUARY, 2010
ADDITIONAL EXHIBITS, AND PROOF OF SERVICE
INTERVENOR CENTER FOR BIOLOGICAL DIVERSITY

INTRODUCTION

Pursuant to the Revised Notice of Prehearing Conferences and Evidentiary Hearing issued November 23, 2009, Intervenor Center for Biological Diversity (the "Center") provides this Rebuttal Testimony for Topics to be Heard in January, 2010.

All of the testimony presented herein was prepared by Ileene Anderson, a signed declaration is provided for this rebuttal testimony.

Center Attorney Lisa T. Belenky assisted in compiling this testimony and the additional documents submitted. A List of the *Additional* Exhibits and copies of the additional exhibits are also being submitted with this testimony.

The Center for Biological Diversity reserves the right to supplement and/or revise this testimony at any time up to and including the close of the evidentiary hearings. Moreover, many of the factual issues discussed in this Rebuttal Testimony involve both legal and factual questions while others are predominately legal issues. Therefore, the Center respectfully reserves the right to address all disputed issues identified at the hearings through testimony, rebuttal, cross-examination, or at later stages of this process including in briefing following the evidentiary hearing.

Rebuttal Testimony of Ileene Anderson Re: Impacts to Sensitive Wildlife from the Proposed Ivanpah Solar Electric Generating System

Re: Impacts to Sensitive Wildlife from the Proposed Ivanpah Solar Electric Generating System

After my review of the applicant's testimony, I still agree that the project as proposed would have major impacts to the biological resources of the Ivanpah Valley, affecting many sensitive plant and wildlife species and eliminating a broad expanse of relatively undisturbed Mojave Desert habitat (FSA at 6.2-95). Through this rebuttal, I bolster my previous testimony on the biological sections of the FSA and rebut the applicant's testimony on wildlife and habitat issues.

Wildlife

Wildlife Habitat

The project will cause permanent impacts to the on-site plant communities and habitat for wildlife despite "restoration", because the BLM regulations based on the Northern and Eastern Mojave Plan's rehabilitation strategies[1] only requires 40% of the original density of the "dominant" perennials, only 30% of the original cover. Dominant perennials are further defined as "any combination of perennial plants that originally accounted cumulatively for at least 80 percent of relative density".[2] Even though the BLM requirements fail to truly "restore" the plant communities to their former diversity even over the long term and cover, the Closure Rehabiliation and Recovery Plan revegetation criteria are even less robust, requiring after 10 years only 12% cover, 0.40 diversity and 10 species richness[3]. Neither the BLM or project revegetation criteria require native annual species as a component of revegetation, despite the fact that native wildlife rely heavily on spring and fall annuals for survival[4]. For all these reasons it is my opinion that permanent impacts will occur to the site despite revegetation.

At a minimum, all of the issues in Biological Resources Appendix B[5] should be incorporated into the final Closure, Revegetation and Rehabilitation Plan to help insure a more successful revegetation effort.

Birds

Clark Mountain, which is directly adjacent to the site, is noted as an Important Bird Area[6]. In fact, two very rare birds in California, the Whip-poor will (Arizona race)

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[1] BLM 2002

[2] Ibid

[3] Data Response, Set K, TN-52208 at pg. 7-32

[4] Jennings 2002, Shoemaker et al. 1976

[5] FSA at pg. 6.2-150- 6.2-164

and the hepatic tanager are known to successfully nest on Clark Mountain. Birds migrate to Clark Mountain from the Colorado River Basin[7] – a route that goes over the project site. The FSA/DEIS fails to evaluate the impact to this migratory pathway from the project as described in my previous testimony.

It has come to my attention that holding ponds will be present on site[8]. Each of the three power blocks will have a 240 square foot pond associated with it. These concrete lined pools, which will be six feet deep[9], will be an attractive nuisance to birds as they migrate through the area, attracting them onto the project site. No discussion of this infrastructure is identified in the biological section of the FSA, nor are impacts analyzed or minimization measures identified. Examples of minimization could include requiring covered or contained infrastructure, which would not only eliminate bird (and other wildlife) attraction, but would reduce evaporation and therefore water use in this arid environment.

Insects

Based on the plants identified on site[10], I researched and consulted with entomologists about the rare insect species that could occur on site. Over twenty rare butterflies have host plants that occur on site including species of metalmarks, marble butterflies, skippers and small blue butterflies. Additionally the desert swallowtail (*Papilio polyxenes coloro*) and the Pahaska Skipper (*Hesperia pahaska martini*) have been documented in the general site vicinity[11]. No surveys were done to evaluate the insects that occur on site and the no analysis of impact to those species of eliminating over 4,000 acres of habitat is provided. No analysis was done on the operation of the solar plant and its effects on the adjacent and migratory insects, some of which may be essential pollinators for rare and common plants. Forseeable impacts include attraction of the species to the mirrors and focusing beams, and subsequent insect collisions and incineration.

Specific Biological Mitigation Measures for Wildlife and Habitat

The applicant's proposed deletions of Bio-19 and 20 are not based on the best available science. Regarding Bio-19, the project site contains foraging resources for bighorn sheep[12]. In the absence of surveys for the sheep usage in the FSA/DEIS, impacts to bighorn sheep populations must be assumed. Mitigation measures must be put in place to avoid, minimize and mitigate project impacts as suggested by Jorgenson[13] and California Department of Fish and Game[14]. Therefore Bio-19 should be retained.

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[6] Audubon IBA East Mojave Peaks
[7] Audubon IBA East Mojave Springs
[8] FSA at pg. 6.13-5
[9] Ibid
[10] 2008-10-08_SUPPLEMENTAL_DATA_RESPONSES_1D_TN-48188
[11] http://butterfliesofamerica.com
[12] Testimony of M. Jorgenson
[13] Ibid
[14] 2009-10-27_CDFG_PSA_Comments_TN 53837 DFG comments on PSA

Regarding Bio-20, despite the "low impact approach" of the project, the project site will still have impacts to State waters from the heliostat posts, service roads, fencing and other infrastructure. Additional mitigation measures are still required to offset the impacts from the project to waters of the State. It is my opinion that with careful selection of mitigation lands, these impacts would likely be able to be mitigated within the mitigation lands for desert tortoise and other sensitive species. Therefore Bio-20 should be retained.

Conclusions

I would like to summarize my conclusions as follows:

Even with a revegetation effort on the project site after closure, the BLM "success" requirements are so low that the wildlife habitat will still be impacted, therefore off-site mitigation is appropriate and necessary. The applicant's success criteria are less than the BLM's requirements, and therefore inappropriate. At a minimum, the issues in Biological Appendix B of FSA need to be incorporated and additional species need to be included in the revegetation including annual species in order to increase the ability of the site to provide a level of functional, sustainable wildlife habitat after site closure.

The Clark Mountains are in Important Bird Area, migration occurs to this range from the Colorado River drainage, and the proposed project site lies between these two areas. Holding ponds could be an "attractive nuisance" to birds on the site. The two issues were not addressed in the FSA or in the applicant's testimony.

The insect fauna was not surveyed on the proposed project site, despite a potential suite of rare species and pollinators that could occur. Therefore no analysis of impacts was included in the FSA or the applicant's testimony.

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ADDITIONAL EXHIBIT LIST

(Exhibits Numbers 900-933 were provided along with CBD's Opening Testimony; below is a list of the Additional Exhibits submitted with Rebuttal Testimony)

Doc. No.	Author and title
934	Jennings, Bryan W., 2002, Diet Selection by the Desert Tortoise in Relation to the Flowering Phenology of Ephemeral Plants Chelonian Conservation and Biology, 2002, 4(2):353-358
935	Shoemaker, V. H., K. A. Nagy, W. R. Costa, Energy Utilization and Temperature Regulation by Jackrabbits (*Lepus californicus*) in the Mojave Desert, Physiological Zoology, Vol. 49, No. 3 (Jul., 1976), pp. 364-375
936	National Audubon Society 2008, Important Bird Areas in the U.S. Important Bird Areas in California (IBA), East Mojave Peaks. Available at http://www.audubon.org/bird/iba
937	National Audubon Society 2008, Important Bird Areas in the U.S. Important Bird Areas in California (IBA), Audubon IBA Desert Springs, East Mojave Springs. Available at http://www.audubon.org/bird/iba

Dated: January 5, 2010

Respectfully submitted,

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California Energy Resources Conservation and Development Commission

In the Matter of:

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DECLARATION OF SERVICE

I, Lisa T. Belenky, declare that on January 5, 2010, I served and filed copies of the attached *REBUTTAL TESTIMONY FOR TOPICS TO BE HEARD IN JANUARY, 2010, ADDITIONAL EXHIBITS, AND PROOF OF SERVICE,* INTERVENOR CENTER FOR BIOLOGICAL DIVERSITY dated January 5, 2010. The original document, filed with the Docket Unit, is accompanied by a copy of the most recent Proof of Service list, located on the web page for this project at: [www.energy.ca.gov/sitingcases/ivanpah]. The document has been sent to the other parties in this proceeding (as shown on the Proof of Service list) and to the Commission's Docket Unit, in the following manner:

(Check all that Apply)
FOR SERVICE TO ALL OTHER PARTIES:

__X__ sent electronically to all email addresses on the Proof of Service list as listed below;
____ by personal delivery or by depositing in the United States mail at with first-class postage thereon fully prepaid and addressed as provided on the Proof of Service list above to those addresses NOT marked "email preferred."
AND

FOR FILING WITH THE ENERGY COMMISSION:
__X__ sending two paper copies and one electronic copy, mailed and emailed respectively, to the address below (preferred method);
OR
_____ depositing in the mail an original and 12 paper copies, as follows:

CALIFORNIA ENERGY COMMISSION
Attn: Docket No. 07 AFC 5
1516 Ninth Street, MS-4
Sacramento, CA 95814-5512
docket@energy.state.ca.us

I declare under penalty of perjury that the foregoing is true and correct.

Lisa T. Belenky
Lisa T. Belenky

Sent via email to: sdeyoung@brightsourceenergy.com; tstewart@brightsourceenergy.com; jcarrier@ch2m.com; jdh@eslawfirm.com; e-recipient@caiso.com; tom_hurshman@blm.gov; Raymond_Lee@ca.blm.gov; dfgpalm@adelphia.net; tgulesserian@adamsbroadwell.com; mjconnor@westernwatersheds.org; gloria.smith@sierraclub.org; devorah.ancel@sierraclub.org; joanne.spalding@sierraclub.org; gssilliman@csupomona.edu; jbasofin@defenders.org; atomictoadranch@netzero.net; gsuba@cnps.org; thansen@cnps.org; granites@telis.org; bbrizzee@cc.sbcounty.gov; jbyron@energy.state.ca.us; jboyd@energy.state.ca.us; pkramer@energy.state.ca.us; jkessler@energy.state.ca.us; dratliff@energy.state.ca.us; publicadviser@energy.state.ca.us; docket@energy.state.ca.us

Two paper copies of all documents were sent via Fed Ex Overnight to:

CALIFORNIA ENERGY COMMISSION
Attn: Docket No. 07-AFC-5
1516 Ninth Street, MS-4
Sacramento, CA 95814-5512

Chelonian Conservation and Biology, 2002, 4(2):353–358

Diet Selection by the Desert Tortoise in Relation to the Flowering Phenology of Ephemeral Plants

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ABSTRACT. – **During spring 1992 in the western Mojave Desert, California, I measured desert tortoise (*Gopherus agassizii*) diet and monitored the flowering phenology of all study site plants. Rainfall between January and March 1992 was well above average and nearly all plant species from the area flowered. Although tortoises ate at least 44 plant species, only 10 species comprised 81.4% of their diet. These preferred plants flowered at different times, which led to much temporal variability in tortoise diet. Tortoises preferred succulent to dry plants, and selected plants during certain phenological states, suggesting that plant palatability varied with phenological state. Tortoises selectively ate plant parts (e.g., leaves or flowers) suggesting that plant parts differed in palatability and/or nutrition. Although the nutritional importance of these preferred plants has yet to be demonstrated, the loss or diminished abundance of native plants through replacement by exotic species may adversely affect tortoise nutrition and conservation.**

KEY WORDS. – **Reptilia; Testudines; Testudinidae; *Gopherus agassizii*; tortoise; ephemeral plants; flowering phenology; foraging ecology; herbivore; nutritional ecology; rainfall; western Mojave Desert; California; USA**

Desert tortoise (*Gopherus agassizii*) populations in the western Mojave Desert have suffered severe declines over the past few decades (U.S. Fish and Wildlife Service [USFWS], 1994; Berry, 1997). Although tortoise mortality in affected populations has been attributed to myriad factors (USFWS, 1994), the upper respiratory tract disease syndrome is believed to have been a major force driving this decline (Berry, 1997). Because disease susceptibility in desert tortoises may be linked with diet (Jacobson et al., 1991), population recovery will benefit from a better understanding of tortoise nutritional requirements.

In the western Mojave Desert, desert tortoises forage on annual and herbaceous perennial plants (Berry, 1978; Jennings, 1993; Jennings and Fontenot, 1993; Spangenberg, 1994). Because ephemeral plant biomass during spring depends upon the previous autumn and winter rains (Beatley, 1969), little biomass is produced following dry winters while in spectacular contrast the desert is lushly carpeted by wildflowers after wet winters. The longevity of adult tortoises, which is on the order of decades (Woodbury and Hardy, 1948; Germano, 1992), shows that these animals are able to withstand the year to year vagaries in food and water availability. The wet years seem to contribute the most to individual growth (Medica et al., 1975).

Phenology of ephemeral plants adds complexity to within-season forage availability. For example, the flowering of ephemeral plants in the western Mojave Desert appears not to be simultaneous, but rather a chronological sequence spanning the entire spring (Jennings, 2001). This phenological sequence in flowering ephemerals has also been observed at other desert localities (Beatley, 1974; Burk, 1982; Vidiella et al., 1999). Thus food plant availability may be temporally variable within years and possibly predictable from a tortoise's perspective. Another potential consequence of flowering phenology is that the palatability and nutritiousness of plants could vary among the phenological states of plants (Nagy and Medica, 1986; Nagy et al., 1998). Studies of tortoise foraging ecology should therefore span the entire tortoise activity season so that changes in tortoise diet as well as changes in the phenological states of their food plants can be monitored.

Jennings (1993) demonstrated that adult desert tortoises in the western Mojave Desert during spring 1992 did not eat plant species in relation to their availability, and they exhibited marked seasonal variation in diet. The purpose of this paper is to develop the latter result by describing the seasonal variation in tortoise diet in light of the phenology of their preferred food plants, which hopefully will lead to a better understanding of their nutrient requirements.

METHODS

This study was conducted between 1 March and 21 June 1992 at the Desert Tortoise Research Natural Area (DTNA), a 100 km^2 nature preserve located in the western Mojave Desert, Kern County, California. I gathered data on tortoise diet and flowering phenology from the northwest corner of the DTNA, an area with elevations ranging from 800–915 m. The vegetation community was comprised of creosote bush scrub (Vasek and Barbour, 1988), which overlies various landforms including flat sandy areas, sandy washes, and low-rocky hills (Jennings, 1993). Annual precipitation occurs primarily during the winter months (1937–99 data from the nearest climate station, Randsburg; National Climate Data Center [NCDC], 2000).

Tortoise diet was estimated from direct observations of 16 free-ranging adult tortoises (8 males and 8 females), 14 of which were equipped with radiotransmitters for concurrent studies involving the physiological ecology and health of wild desert tortoises (e.g., Peterson, 1996; Henen et al., 1998; Christopher et al., 1999; Wallis et al., 1999). I also observed two additional tortoises encountered opportunistically during spring 1992. Dietary observations were recorded as follows. Each morning, a study animal was located using radiotelemetry before that individual emerged from its cover site (i.e., burrow or shrub) to commence foraging. Individuals usually had two daily foraging bouts (i.e., morning and afternoon), but occasionally foraged once, or not at all, on any given day. Daily foraging data were usually obtained from a single animal with a recording of all food items taken by that animal on that day. Once the tortoise emerged, I then followed the individual at distances of 4 to 8 m to observe all foraging behaviors yet to minimize animal disturbances. When a tortoise was observed feeding, the plant species, plant parts consumed (i.e., stems, leaves, flowers, and seeds), number of bites taken, whether the plant was in a succulent or dried state, and the date and time were recorded on a micro-cassette recorder. Plants were considered "succulent" if they were green and "dry" if they were brown. Nomenclature for plant species follows Hickman (1993).

Data on flowering phenology for annual and perennial species were obtained through daily observations of plants on the study site. Flowering phenology of each species was partitioned into five stages: *emergence* (ephemerals only): plant shoots emerged above the surface; *first flowering*: minority of individuals in flower; *peak flowering*: most individuals in flower; *past-peak flowering*: majority of individuals still succulent but few still in flower; and *dried*: majority of individuals completely dry or, in the case of shrubs, completely in seed with no flowers remaining (see Jennings, 2001).

I evaluated the influence of plant phenology on tortoise diet in two analyses. First, I compared the number of bites, per week, taken by tortoises on their top ten forage species to the species-specific "phenology profiles." These phenology profiles indicate when in the spring 1992 the various phenological stages of each food plant were available to tortoises. The goal of this analysis was to ascertain the degree by which tortoises were focusing their attention on particular phenological states of their preferred food plants. On a finer scale, I determined whether or not tortoises targeted certain parts of plants for consumption. In this analysis, I partitioned the above-ground plant form into four categories (parts): stems, leaves, flowers, and seeds, so that the frequency of use of these plant parts by tortoises could be tabulated. I quantified overall consumption of each plant part during spring 1992 by counting the number of plants in which at least a single bite on a given plant part was taken by a tortoise.

RESULTS

The western Mojave Desert received above average precipitation in early 1992, as the Randsburg weather station recorded 134.5 mm during February and 78.3 mm in March, far exceeding the monthly averages of 32.5 mm and 24.4 mm for these two months (NCDC, 2000). This heavy rainfall resulted in the germination and flowering of at least 71 species of annuals and herbaceous perennials and 7 species of shrubs on the study site. Study animals emerged from their burrows between 24 March and 2 April, then began foraging. Following emergence from hibernation, tortoises continued almost-daily foraging bouts until June 21 by which time all study animals had become inactive inside their respective burrows. The 16 study animals were observed to take 35,388 bites from 2423 individual plants.

Although tortoises sampled at least 44 species of plants, only 10 preferred species (7 annuals and 3 herbaceous perennials) comprised the bulk (81.4%) of their diets (Table 1). This summary, however, obscures within-

Table 1. Top 10 preferred species of plants* in desert tortoise diet during spring 1992 at the DTNA.

Species	Common Name	Family	Life Form	No. Bites	% Bites
Lotus humistratus	Hairy Lotus	Fabaceae	Annual	10512	29.7
Mirabilis bigelovii	Four O' Clock	Nyctaginaceae	Herbaceous Perennial	3820	10.8
Chamaesyce albomarginata	Rattlesnake Weed	Euphorbiaceae	Herbaceous Perennial	3801	10.7
Astragalus layneae	Layne Locoweed	Fabaceae	Herbaceous Perennial	2902	8.2
Prenanthella exigua	Egbertia	Asteraceae	Annual	1977	5.6
Astragalus didymocarpus	Two-seeded Milkvetch	Fabaceae	Annual	1623	4.6
Camissonia boothii	Booth's Evening Primrose	Onagraceae	Annual	1367	3.9
Erodium cicutarium	Stork's Bill	Geraniaceae	Annual	1150	3.3
Chorizanthe brevicornu	Brittle Spineflower	Polygonaceae	Annual	919	2.6
Phacelia tanacetifolia	Lacy Phacelia	Hydrophyllaceae	Annual	710	2.0
Totals				28781	81.4

*Other foods eaten by tortoises by decreasing number of bites included: dead leopard lizard (*Gambelia wislizenii*), 695 bites (2%); *Amsinckia tessellata,* 590 bites (2%); *Cryptantha circumcissa,* 561 bites (2%); *Plantago ovata,* 430 bites (1%); *Mentzelia* spp., 428 bites (1%); *Eriastrum eremicum,* 404 bites (1%); *Gilia minor,* 342 bites (1%); *Stylocline micropoides,* 334 bites (1%); unknown plant material, 322 bites (1%); and *Camissonia palmeri,* 266 bites (1%).

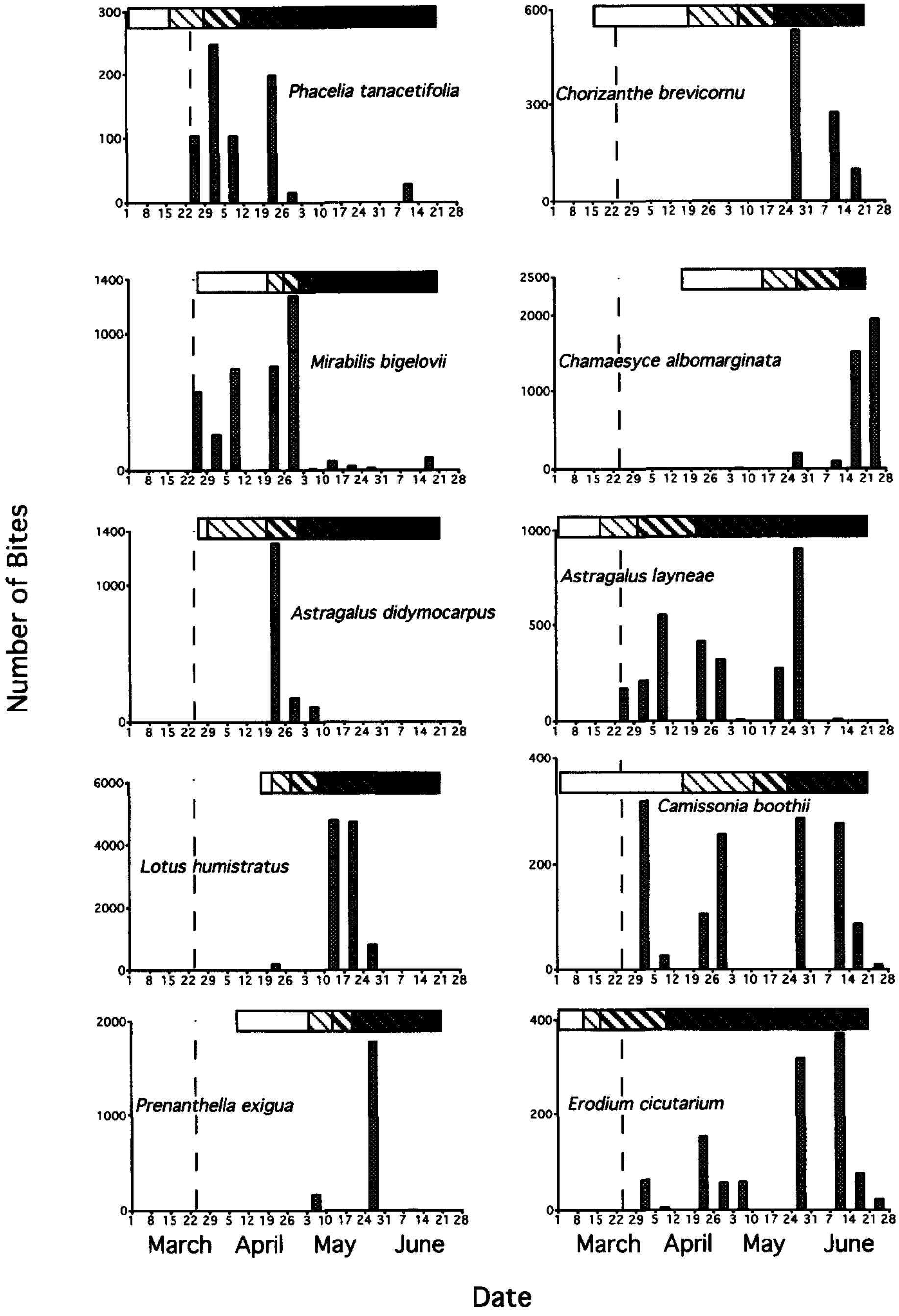

Figure 1. Temporal variation in tortoise diet and flowering phenology of the top 10 preferred forage plants. Vertical bars on each graph represent the numbers of bites per week on a particular plant species. Horizontal bars at the top of each graph show the flowering phenology stages of the same plant (from left to right: plain white bar = *emergence*; white bar with thin diagonal dark lines = *first flowering*; white bar with thick diagonal lines = *peak flowering*; dark bar with white diagonal lines = *past-peak flowering*; and black bar = *dried* (see text for definitions of these phenological stages; after Jennings, 2001).

season variation in tortoise diet. Tortoises primarily fed upon individuals of *Phacelia tanacetifolia* and *Mirabilis bigelovii* during early spring before switching to *Astragalus didymocarpus*, *Lotus humistratus*, and *Prenanthella exigua* in middle spring then later eating *Chorizanthe brevicornu* and *Chamaesyce albomarginata* near the end of spring (Fig. 1). Several other plants, *Camissonia boothii*, *Astragalus layneae*, and *Erodium cicutarium*, were eaten by tortoises throughout spring (Fig. 1).

Tortoises focused their foraging efforts on specific phenological stages of their preferred food plants. For instance, tortoises fed from individuals of *P. tanacetifolia*, *M. bigelovii*, *A. layneae*, *C. boothii*, and *E. cicutarium* at the earliest possible opportunity when these plants were in the emergence or first flowering stages (Fig. 1). Other plant species such as *A. didymocarpus*, *L. humistratus*, *P. exigua*, *C. brevicornu, and C. albomarginata* were not consumed until these plants progressed into peak flowering and even past-peak flowering stages (Fig. 1). Regardless of when

Table 2. Frequency of consumption of plant parts by desert tortoises at the DTNA during spring 1992. Values represent the numbers of plants eaten. Common names for each species are given in Table 1.

Species	Total	Stems	Leaves	Flowers	Seeds
Lotus humistratus	1008	1008	1008	168	999
Mirabilis bigelovii	40	38	40	16	1
Chamaesyce albomarginata	101	101	101	101	1
Astragalus layneae	72	56	69	23	0
Prenanthella exigua	134	134	0	133	114
Astragalus didymocarpus	126	123	123	126	0
Camissonia boothii	161	110	148	34	21
Erodium cicutarium	206	103	104	30	152
Chorizanthe brevicornu	56	56	55	41	0
Phacelia tanacetifolia	35	28	27	29	1

tortoises initiated their consumption of preferred food plants they abruptly ceased to feed on any plants that had advanced to a dried state (Fig. 1). In fact, dried plants only comprised 4.2% of all tortoise diet and tortoises did not begin eating dried plant material until the last few weeks of spring, a time when most plants on the study plot were dry.

The frequency of consumption of different plant parts may provide insights into the timing of tortoise preference of these plants during spring. Tortoises generally consumed the stems, leaves, and flowers of their preferred plants, though some peculiarities in plant part selection were also observed (Table 2). For example, the flowers of *M. bigelovii*, *A. layneae*, *C. boothii*, and *E. cicutarium* seemed to be consumed far less often than stems and leaves on these plants (Table 2). The flowers of *M. bigelovii* and *A. layneae* may have been too difficult to reach by tortoises because the flowers on these herbaceous perennials tended to grow well above ground. This explanation cannot apply to *C. boothii*, as tortoises invariably bit off the flowers of these plants and allowed them to drop to the ground uneaten. Seeds were generally not eaten, exceptions including *L. humistratus*, *P. exigua*, and *E. cicutarium* (Table 2).

DISCUSSION

The western Mojave Desert received higher than average rainfall during winter 1992 (Jennings, 2001). From the perspective of a tortoise, spring 1992 must have been an outstanding year regarding food and water availability because nearly all species of plants known to occur on the study site flowered and became available as potential forage. Emergence and flowering of some ephemeral plants was well underway by the time tortoises emerged from hibernation and were available for forage until the end of June when tortoise aboveground activity ceased (Jennings, 1993). I did not monitor tortoise activity over the summer months, so it is unknown to what extent further foraging occurred. However, because only a trace amount of rain fell in the area during summer 1992 (NCDC, 2000), and since summer tortoise activity is believed to be dependent upon summer rainfall (Nagy and Medica, 1986), as occurs in the eastern Mojave Desert (Turner, 1982), it seems unlikely that much foraging could have taken place at the DTNA during this time. Marlow (1979), who studied tortoise behavior and physiology at the DTNA between 1969–1978, also noticed that peak foraging activity occurred during spring; this was followed by a dramatic slowdown in activity in early summer, which in turn led to a long period of little activity lasting until the following spring.

Despite the tremendous availability of potential food plants throughout spring tortoises concentrated their foraging efforts upon a small fraction of the ephemeral flora. Only 10 species of plants accounted for more than 80% of tortoise diet. The flowering phenologies of these preferred plants were quite variable, with some plants coming into full bloom in early spring, others in mid-spring, and still others in late spring (Jennings, 2001). Tortoises kept pace with this turnover of preferred foods resulting in dramatic seasonal variation in their diet. Data indicate that the flowering of plants during spring occurs as an orderly sequence with each species flowering at a specific time (Jennings, 2001). If the flowering phenologies of ephemeral plants occurred in such a recurrent manner, then tortoises may effectively predict when to locate preferred foods, thereby economizing their daily foraging efforts and behavior in general.

Although tortoises usually ate preferred plants in entirety, they tended to target these plants during particular phenological stages, thereby suggesting that the different phenological states may have varied in palatability (and possibly nutritional value) to tortoises. For example, tortoises ate some plants in their emergence stage, namely *M. bigelovii* and *C. boothii*, thereby primarily consuming the vegetative portions of these plants, not the flowers and seeds. The apparent rejection of certain plant parts by tortoises may be explained by either inaccessibility to high-growing flowers on relatively large forage plants (i.e., *M. bigelovii* and *A. layneae*) or possibly on palatability grounds (i.e., *C. boothii*). Why, for instance, do tortoises bite off and then reject the flowers of *C. boothii* without eating them?

Consuming succulent plants usually enable tortoises to maintain water and nitrogen budgets, whereas eating dry plants may cause water and nitrogen deficits (see Nagy et al., 1998). Thus, it is not surprising that tortoises generally prefer, when available, succulent as opposed to dry forage plants (Nagy and Medica, 1986; Jennings and Fontenot, 1993; Spangenberg, 1994). In the present study, comparisons between the phenologies of the preferred plants with the dates when tortoises consumed them showed that tortoises precisely stopped eating individuals of a particular plant species once the plants became dry. Interestingly, Nagy and Medica (1986) discovered that tortoises in the eastern Mojave Desert actually became osmotically stressed by a spring diet of succulent plants. Notwithstanding, succulent forage plants must somehow be more beneficial than detrimental to tortoises, perhaps in the long-term, despite apparent short-term osmotic imbalances caused by their consumption. Indeed, physiological studies of desert tortoises suggest that individuals can tolerate temporary imbalances in nutrients to withstand the harsh desert environment and maintain nutrient balances to grow and reproduce in the long-term (Nagy and Medica, 1986; Peterson, 1996; Henen, 1997).

The results of this study underscore the importance of observing foraging tortoises throughout their activity season, otherwise perceptions of tortoise dietary habits may be incomplete owing to the variable flowering phenologies of forage plants. Of equal importance may be the documentation of flowering phenologies for primary forage plants as differences in nutritional states of plants may change with age. Tortoises in this study exhibited food preferences at the level of plant species, phenological state of a plant, and plant parts. This selective foraging behavior implies that the palatability, and possibly nutritive value, of plants varies among plants and their parts (Nagy et al., 1998).

Although at least 71 species of ephemeral plants were available for forage, over 80% of tortoise diet was based on only 10 plant species. Tortoise dietary requirements may therefore be quite specialized, at least for populations in the western Mojave Desert. An implication of such apparent selectivity is that habitat degradation leading to the loss or diminished abundance of preferred plants could have deleterious consequences for tortoise health. For example, proliferation of exotic annual plant species such as *Schismus* spp. and *Bromus* spp. in the Mojave Desert (Brooks, 1992; Jennings, 1993; Esque, 1994) may be negatively impacting native ephemeral species either through competition (Brooks, 2000) or aiding fire propagation in an environment where fire was historically absent (Jennings, 1997; Brooks, 1999, 2002). Indeed, the 10 preferred plant species identified in this research occur in extremely low densities and are therefore vulnerable to extirpation (Jennings, 1993). Further evidence that these plants may be extremely important to the welfare of tortoises comes from observations of the truly astounding abilities of tortoises to successfully locate these rare plants (Jennings, 1993). Discovering these subtle but potentially critical details of tortoise foraging ecology is only the first step in comprehending tortoise ecological and nutritional requirements. Nutritional assays (including water content) of desert plants can then address tortoise foraging ecology in finer detail, which may ultimately explain why tortoises are so selective in their diet.

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ENERGY UTILIZATION AND TEMPERATURE REGULATION BY JACKRABBITS (LEPUS CALIFORNICUS) IN THE MOJAVE DESERT[1]

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Energy expenditure for black-tailed jackrabbits in the Mojave Desert is highest in winter (172 kcal kg^{-1} day^{-1}) when ambient temperatures were consistently below the zone of thermoneutrality. During late spring, summer, and early fall energy expenditure is 142 kcal kg^{-1} day^{-1} despite appreciable seasonal and diurnal temperature shifts. The annual energy expenditure for maintenance is estimated to be 55,200 kcal kg^{-1} yr^{-1}. This exceeds standard metabolic rate by a factor of 2.3. Jackrabbits were able to metabolize 65% of the energy contained in the spring diet of succulent annual plants. Metabolic efficiency fell to 45% for the summer diet containing green annuals (mostly *Salsola*) and some shrub browse, and to only 18% in winter when the animals ate shrub browse and dry annuals. Jackrabbits eat most of the plant material they cut, usually wasting no more than 15% of the amount consumed. By increasing body temperature to circa 41 C on hot summer days, jackrabbits save water that would otherwise be spent for evaporative cooling, but this leaves little margin for heat storage during exercise.

INTRODUCTION

Estimates of energy utilization by animals in their natural environment are important to understanding both the physiology of the organism and its role in the ecosystem. Jackrabbits are conspicuous and important components of the southwestern desert biota. They are medium-sized herbivores and differ from their better studied rodent counterparts in a number of important respects. Jackrabbits generally do not burrow and are therefore exposed to extreme temperatures. Herbivorous rodents are primarily seed-eaters, whereas hares and rabbits largely utilize annual plants, including grasses, and shrub browse. They are the primary mammalian consumers of these resources and, despite relatively sparse populations, may contribute a major component to the biomass and energy turnover by mammals in some regions (Chew and Chew 1970). Hares may also compete with domestic animals and have significant impact on crop plants. Thus estimates of their energy utilization are of interest from several viewpoints.

The literature is replete with metabolic rates of animals measured under

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relatively standard laboratory conditions, but extrapolation from these data to the field situation requires assumptions that are difficult to evaluate. A variety of methods have been employed to measure energy metabolism in the field with varying degrees of success (see Gessaman 1973). We used three independent methods for measuring metabolic rates of black-tailed jackrabbits (*Lepus californicus*) in the Mojave Desert. It was impractical to work with completely free-ranging animals, so we captured adult animals and studied them in large (0.4-hectare) enclosures containing natural desert vegetation. These enclosures and the behavior of the animals are described in detail elsewhere (Costa, Nagy, and Shoemaker 1976; Nagy, Shoemaker, and Costa 1976). Our initial approach was to estimate energy utilization from water intake (measured isotopically), and the water content and energy yield of the natural diet. We also made some measurements of CO_2 production using the doubly labeled water method. However, the most fruitful approach proved to be direct measurement of food consumption of jackrabbits in the enclosures.

MATERIAL AND METHODS

Energy expenditure measured from water intake.—This method is theoretically feasible if all water input is associated with the food, either as preformed water or metabolic water, and the water content and energy yield of the diet are known. For a steady state, nondrinking animal, water intake (Wi) is the sum of the preformed water in the food (Wf) and the metabolic water production (Wm):

$$Wi = Wf + Wm \, ; \qquad (1)$$

Wf is related to the dry mass of the food (Mf) by the food's water content (Wf/Mf):

$$Wf = Mf \times (Wf/Mf) \, ; \qquad (2)$$

Wm is related to the dry mass of the food through the mass specific energy content of the food (Ef/Mf), the metabolic efficiency (Em/Ef) and the yield of metabolic water per unit of energy metabolized (Wm/Em):

$$Wm = Mf \times \frac{Ef}{Mf} \times \frac{Em}{Ef} \times \frac{Wm}{Em} \, . \qquad (3)$$

Substitution of equations (2) and (3) into equation (1) and solving for the dry mass of the food intake yields:

$$Mf = Wi \Big/ \left[\frac{Wf}{Mf} + \left(\frac{Ef}{Mf} \times \frac{Em}{Ef} \times \frac{Wm}{Em}\right)\right] \qquad (4)$$

or: g dry food kg^{-1} day^{-1}

$$= \frac{\text{ml } H_2O \text{ intake kg}^{-1}\text{ day}^{-1}}{\dfrac{\text{ml } H_2O \text{ preformed}}{\text{g dry food}} + \left(\dfrac{\text{kcal food}}{\text{g dry food}} \times \dfrac{\text{kcal metab.}}{\text{kcal food}} \times \dfrac{\text{ml } H_2O \text{ prod.}}{\text{kcal metab.}}\right)} \, .$$

Metabolic rate can be calculated from dry food intake:

$$Em = Mf \times \frac{Ef}{Mf} \times \frac{Em}{Ef} \qquad (5)$$

or: kcal metabolized kg^{-1} day^{-1} = g dry food kg^{-1} day^{-1} × (kcal food)/(g dry food) × (kcal metab.)/(kcal food). Water intake was measured with tritiated water, and the dry mass composition of the diet was determined from analysis of stomach contents of animals in the enclosures as previously reported (Nagy et al. 1976). Samples of all plant species in the enclosures were taken at the beginning and end of each determination period and dried to constant weight at 70 C, and this permitted calculation of the water content of the average diet. The metabolizable energy obtained by jackrabbits eating various natural diets was determined using caged animals as described below. Thus all of the parameters required to calculate food intake and energy metabolism were measured except Wm/Em, which we assumed to be 0.12 ml H_2O/kcal (Brody 1945).

Utilization of energy in natural diets.—Young jackrabbits were hand reared and maintained in cages (40 × 60 × 35 cm) outdoors at the Riverside campus of the University of California. They were fed laboratory rabbit chow and provided with water ad lib when they were not being used in a feeding experiment. To investigate the utilization of natural diets by these animals, components of the diet of field animals were collected in large quantities near the field study site. Fresh plant material was mixed in the same proportion by dry mass found by analysis of the stomachs of the animals studied in the field enclosures (see Nagy et al. 1976), and was stored at 4 C prior to use. The spring diet consisted primarily of succulent annual plants, the summer diet was mostly tumbleweed (*Salsola iberica*) with some perennial shrubs and dry annuals, and the winter diet consisted primarily of the dry stems of annual plants and the leaves and stems of creosote bush (*Larrea divaricata*).

The caged animals were shifted to the field diet by gradually reducing the amount of rabbit chow and water provided for about 1 wk. Then, measured amounts of food of known water content were given each night and unconsumed food was collected each morning, dried, and weighed to determine the dry mass of food consumed. Feces were collected on 3.2 mm wire mesh mounted beneath the cage. A large plastic bag was fashioned into a funnel surrounding the cage bottom, and this drained urine into a flask attached to the tip. The animals were weighed daily and the amount of food given was adjusted to that required for maintenance of body mass. (Jackrabbits were unable to maintain mass when eating the winter diet alone, so they were provided with drinking water ad lib.)

Collections of feces and urine were made each morning. Urine volumes were measured and feces were dried to constant mass at 70 C. Gelatin capsules containing carmine powder were force-fed at the beginning and end of each feeding trial so that feces derived from this food could be identified. These feces were pooled by animal and homogenized prior to analysis. Urine samples were pooled by animal and then lyophylized. The energy contents of dried food, feces, and urine were determined by oxygen bomb calorimetry. The fraction of the calories ingested and not recovered in the feces and urine is designated as the metabolic efficiency (E_m/E_f in eq. [3]). We also calculated the fraction of the calories ingested and not recovered in the feces, which we refer to as assimilative efficiency.

Energy expenditure measured from food consumption.—Two fenced enclosures (ca. 300 m^2) at the Mojave Desert site were stripped of annual vegetation and one animal was maintained in each. These animals were provided with dry alfalfa leaves and pans of water. The enclosures contained shrubs which provided natural shelter, and these were not eaten by the jackrabbits when alfalfa was available. The food consumption of these animals was measured throughout the year by determining the dry mass of alfalfa removed from tared plastic feeders. The water content of the alfalfa (ca. 5%) was measured at the time of initial and final weighings. Each measurement period lasted 2–5 days, and several consecutive measurements were frequently made. Animals were weighed at the beginning and end of each measurement period to verify that they were in steady state. The behavior of the jackrabbits in these enclosures corresponded closely to that previously described for animals in larger enclosures (Costa et al. 1976).

Caged animals were also fed measured amounts of alfalfa leaves to determine energy utilization efficiencies as described above for natural diets.

Energy expenditure measured using doubly labeled water.—Rates of CO_2 production in field animals were determined with HTO-18 according to the method of Lifson and McClintock (1966). December measurements were made on five jackrabbits eating natural vegetation: two in 1972 and three in 1973. In July 1974, six determinations were made on five animals given alfalfa and water ad lib. The oxygen-18 content of water distilled from blood samples was measured using the proton activation method of Wood et al. (1975), and tritium activities in blood water were determined by liquid scintillation. The equations we used to calculate metabolic rates from doubly labeled water data are given by Nagy (1975). The relationships 0.81 liter CO_2 (liter $O_2)^{-1}$ and 4.8 kcal (liter $O_2)^{-1}$ were used to convert metabolic rate values from ml CO_2 to kcal.

Wastage.—Jackrabbits sometimes cut considerably more material than they consume, and we assessed the amount of wastage to get a more complete picture of the impact of jackrabbits on the plant community. Prior to determinations of diet and water turnover, all debris likely to be mistaken for material pruned by jackrabbits was removed from the enclosures. At the end of the determination period the enclosures were inspected again and all plant cuttings were collected, sorted by species and their dry masses determined.

Body temperature.—We measured body temperature of jackrabbits in the enclosures during hot summer days. A frequency modulated temperature telemeter (BioCom Minilink) was tuned, potted in beeswax, calibrated, and surgically implanted in the body cavity of a jackrabbit. A grid of antenna wire in the enclosure led to an FM receiver coupled to a frequency counter. The body temperature of the undisturbed animal was monitored for 24 h, as were air temperature and soil temperatures in exposed and shaded areas. Subsequently, the effect of forced daytime activity on body temperature was determined. While one observer monitored body temperature, another entered the enclosure and chased the animal until it retreated under a shrub and did not emerge when the observer approached it. Body temperature was monitored during the chase and for an hour thereafter.

RESULTS

Utilization of diets.—Jackrabbits were most effective at utilizing spring annuals and alfalfa, metabolizing almost two-thirds of the energy intake, whereas they were able to utilize only 18% of the energy contained in the winter diet (table 1). These differences are attributable entirely to assimilation because urinary energy losses were 7%–8% of energy intake on all diets. The rate of intake of dry matter and of total calories varied much less between diets than did the intake of metabolizable calories (table 1). Caged animals maintained on spring annuals and on dry alfalfa obtained 91 and 93 metabolizable kcal kg^{-1} day^{-1} respectively, whereas animals eating the winter diet obtained only 25 kcal kg^{-1} day^{-1}. Thus jackrabbits were apparently not in energy balance during determina-

TABLE 1

UTILIZATION OF NATURAL DIETS AND ALFALFA BY CAGED JACKRABBITS MAINTAINED OUT OF DOORS

	SPRING (MARCH) DIET			SUMMER (JULY) DIET			WINTER (DECEMBER) DIET			ALFALFA (SUMMER		
	Dry Mass Flux	Caloric Coeff.	Energy Flux	Dry Mass Flux	Caloric Coeff.	Energy Flux	Dry Mass Flux	Caloric Coeff.	Energy Flux	Dry Mass Flux	Caloric Coeff.	Energy Flux
	g dry wt ($\text{kg}^{-1}\ \text{day}^{-1}$)	kcal g^{-1}	kcal ($\text{kg}^{-1}\ \text{day}^{-1}$)	g dry wt ($\text{kg}^{-1}\ \text{day}^{-1}$)	kcal g^{-1}	kcal ($\text{kg}^{-1}\ \text{day}^{-1}$)	g dry wt ($\text{kg}^{-1}\ \text{day}^{-1}$)	kcal g^{-1}	kcal ($\text{kg}^{-1}\ \text{day}^{-1}$)	g dry wt ($\text{kg}^{-1}\ \text{day}^{-1}$)	kcal g^{-1}	kcal ($\text{kg}^{-1}\ \text{day}^{-1}$)
Influx:												
Food	38.1	3.64	139	35.9	3.99	143	32.1	4.45	143	33.2	4.47	148
Efflux:												
Feces	10.4	3.58	37.2	16.4	4.19	68.7	24.4	4.41	108	8.7	4.97	43.2
Urine	7.38	1.48	10.9	5.50	1.66	9.13	2.93	3.34	9.78	5.80	2.01	11.7
Total	...	...	48.1	...	...	77.8	...	...	118	...	...	54.9
Assimilative efficiency[a]		0.732			0.520			0.247			0.706	
Metabolic efficiency[b]		0.653			0.459			0.178			0.627	

[a] Assimilative efficiency = $(\text{kcal}_{\text{food}} - \text{kcal}_{\text{feces}})/\text{kcal}_{\text{food}}$.

[b] Metabolic efficiency = $(\text{kcal}_{\text{food}} - \text{kcal}_{\text{feces}} - \text{kcal}_{\text{urine}})/\text{kcal}_{\text{food}}$.

tion of utilization efficiencies for the winter diet, although body mass losses were slight (0.7% day^{-1}) during this period. On the summer diet caged animals obtained 67 metabolizable kcal kg^{-1} day^{-1} and maintained body mass.

Field metabolic rates measured from alfalfa consumption.—Rates of alfalfa consumption of jackrabbits in enclosures in the Mojave Desert varied relatively little over the year (fig. 1) despite marked changes in environmental temperature (table 2). From the caloric content and metabolic efficiency for alfalfa, alfalfa consumption can be converted to metabolizable calories obtained. Between mid-March and late October, alfalfa consumption was essentially constant and averaged 50.6 g kg^{-1} day^{-1}. This corresponds to an energy expenditure of 142 kcal kg^{-1} day^{-1} for this 7.5-month period. During the coldest months (December–February), alfalfa consumption averaged 61.4 g kg^{-1} day^{-1} or 172 metabolizable kcal kg^{-1} day^{-1}. We estimated the metabolic rate for November and early March as the average of the winter and summer values to compute an annual energy expenditure of 55,200 kcal kg^{-1} yr^{-1}.

Measurement of food and energy fluxes from water influx.—We used equations (4) and (5) to calculate food and energy utilization for jackrabbits eating natural vegetation in the spring (late March). The animals maintained body mass and water influx and efflux were equal (Nagy et al. 1976). Using the appropriate values for food energy content and metabolic efficiency (table 1), and water influx rate and dietary water content (from tables 1 and 2 in Nagy et al. [1976]), we calculate that the animals ate an average of 49 g dry food kg^{-1} day^{-1} and thereby ingested 179 kcal kg^{-1} day^{-1}. We also calculate that these animals eliminated 13 g of dry matter and 48 kcal kg^{-1} day^{-1} via the feces, and 9.5 g of dry matter and 14 kcal kg^{-1} day^{-1} via the urine. This leaves 117 kcal kg^{-1} day^{-1} for respiration. The mean rate of alfalfa consumption in the field for late March (fig. 1) was 49.4 g dry alfalfa kg^{-1} day^{-1}. From the caloric con-

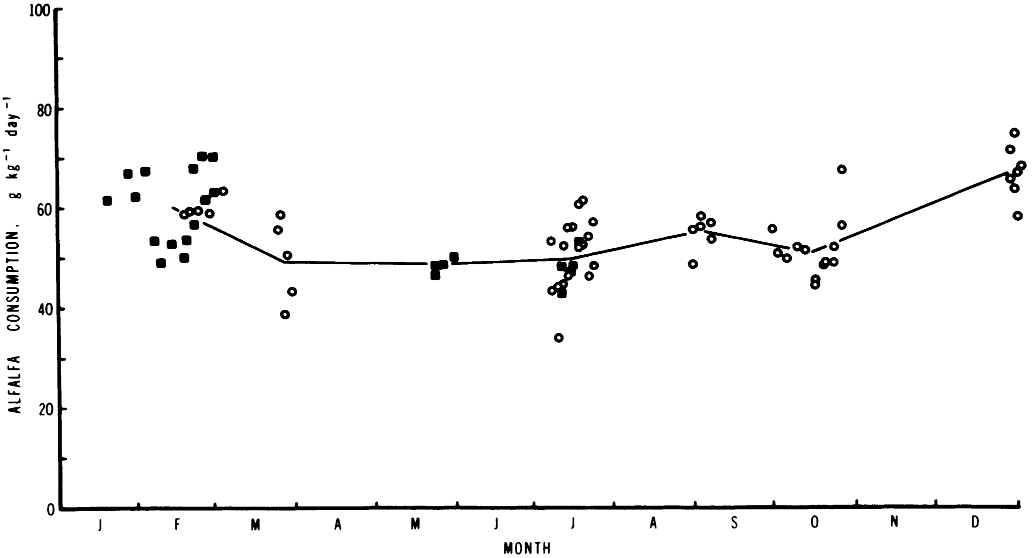

FIG. 1.—Consumption of alfalfa by jackrabbits (*Lepus californicus*) maintaining weight in field enclosures in 1973 (○) and 1974 (■).

tent and metabolic efficiency for alfalfa (table 1), this represents a metabolic expenditure of 139 kcal kg^{-1} day^{-1}. Although this value is higher than the energy expenditure of 117 kcal kg^{-1} day^{-1} measured from water influx, there is reasonable agreement considering the small sample sizes and the opportunities for error in both estimates.

Animals in the field enclosures did not maintain body mass during the summer and winter trials. They lost more water than they gained, and almost certainly utilized energy reserves as well. If energy reserves are metabolized, then equation (4) underestimates metabolic water production and hence overestimates food consumption. Even so, food consumption calculated using this equation falls far short of requirements predicted on the basis of alfalfa consumption during these seasons.

Field metabolic rates measured using doubly labeled water.—In July, rates of CO_2 production measured with HTO-18 averaged 1.32 ml g^{-1} h^{-1} (SE = 0.11, N = 6). This corresponds to an energy expenditure of 188 kcal kg^{-1} day^{-1}, which is somewhat higher than the 140 kcal kg^{-1} day^{-1} predicted from alfalfa consumption. December metabolic rates averaged 1.10 ml CO_2 g^{-1} h^{-1} (SE = 0.09, N = 5) or 156 kcal kg^{-1} day^{-1}. This estimate is lower than the 187 kcal kg^{-1} day^{-1} calculated from alfalfa consumption. The doubly labeled water values are less reliable than those estimated from alfalfa consumption because fewer values were obtained with HTO-18, and because oxygen-18 contents of many blood samples were too low to measure accurately.

Wastage.—There was no detectable wastage in spring when succulent annuals were available, whereas readily measurable quantities were wasted in both summer and winter. In 1973 the dry mass

TABLE 2

MEAN MAXIMUM AND MINIMUM AIR TEMPERATURES (°C) AT THE DESERT RESEARCH STATION, HINKLEY, CALIFORNIA

YEAR	MONTH											
	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
1972:												
Max.	16.6	22.7	28.8	28.3	33.8	41.1	43.3	38.3	36.1	25.5	18.8	13.8
Min.	−6.1	−1.6	2.7	3.8	8.8	15.5	18.8	16.1	11.1	6.6	1.1	−5.5
1973:												
Max.	13.9	18.7	18.5	26.7	35.3	40.4	43.3	41.2	37.5	30.6	20.7	17.9
Min.	−4.9	0.3	1.8	4.8	10.3	14.9	17.7	17.2	10.1	3.8	0.7	−3.8

of wasted material in these seasons was only 3–4 g kg^{-1} day^{-1}. Wastage averaged about 10 g kg^{-1} day^{-1} in winter 1972, not including one animal that cut and left 90 g kg^{-1} day^{-1} in the 2 days immediately prior to his death. Wasted material in winter was primarily woody stems and associated leaves of shrubs (*Larrea divaricata*, *Atriplex canescens*, *A. polycarpa*, *Lycium pallidum*, and *Ambrosia dumosa*). Summer wastage was composed of *Salsola iberica* and *Larrea divaricata*.

Body temperature.—In summer, the body temperature of an undisturbed jackrabbit was 37–38 C at night, rose during the morning, and remained at circa 41 C throughout the afternoon. Body temperature is shown along with ambient temperatures for a 24-h period in mid-August in figure 2*A*. Disturbances of the animal at any time during a summer day caused a rapid rise in body temperature, followed by a decline when the animal was allowed to rest in its form (fig. 2*B*). The highest heating rate (ca. 0.28 C min^{-1}) was observed in the early morning when the initial body temperature was low and the animal maintained a high level of activity until body temperature approached 42 C after about 12 min. When forced to be active at midday, the animal had been disturbed by activity in an adjacent enclosure, and its body temperature was already 42 C. It sustained activity for only 3 min, heating at a rate of 0.22 C min^{-1}. In the evening, the animal maintained vigorous activity for about 8 min, heating again at a rate of 0.22 C min^{-1} and retreating to shade when body temperature was about 42 C. Rates of cooling after forced activity were 0.08 C min^{-1} in the morning and at midday, and 0.06 C min^{-1} in the evening.

DISCUSSION

Comparison of methods for measurement of energy expenditure in the field.—Theoretically, the doubly labeled water method is the best of the methods we used because it imposes the fewest restrictions. No knowledge of the animal's diet, water sources, or energy balance is required. However, special facilities and expertise are needed in the analysis of samples (Wood et al. 1975) and for an animal as large as a jackrabbit the cost of H_2O-18 to provide adequate enrichment of the body water is high. This method is better suited to measurements in small animals.

The water influx method is applicable only when food and metabolism are the sole sources of water. The water content and utilization of the diet must be accurately known and the animal must be in energy balance over the measurement period. When these conditions are met, as in our spring measurements, the method works well. This method was particularly useful in this study because it allows evaluation of the relationship between water and energy balance (Nagy et al. 1976), and the component measurements (water fluxes, composition of the natural diet, and utilization efficiencies) are of interest in their own right. If measurement of energy expenditure is the only goal, the time and effort involved in this method make it unattractive.

Direct measurement of food consumption to estimate energy expenditure in the field requires that the environment be modified to eliminate preferred natural foods within an enclosure. These factors could modify energy expenditure, but with jackrabbits this did not appear to be a serious problem. Energy expenditure measured from alfalfa consumption was considerably greater for animals in field enclosures (ca. 140 vs. 90 kcal kg^{-1} day^{-1}) than in caged animals under a similar temperature regime during summer. This presumably reflects restriction of activity in caged animals. The simplicity of direct food consumption measurements made this the method of choice for determining seasonal and annual energy requirements of jackrabbits in this study.

Seasonal energy expenditure by jackrabbits.—Despite large seasonal variations in ambient temperature (table 2), energy expenditure was fairly constant. The highest rates occurred during the coldest months (fig. 1), but these were

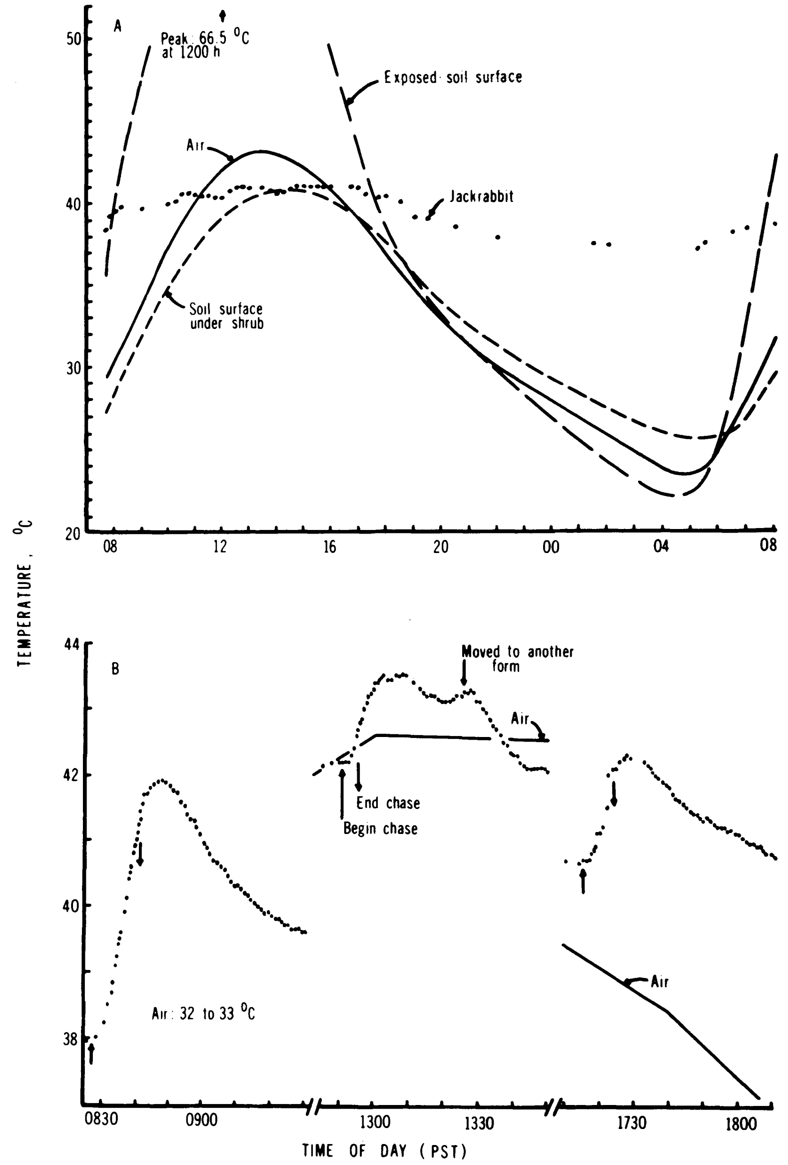

FIG. 2.—*A*, Telemetered body temperature (dots) of an undisturbed jackrabbit during August 15 and 16, 1973, along with corresponding environmental temperatures. *B*, Body temperature responses to forced running during morning, midday, and afternoon hours (Pacific Standard Time) of August 16, 1973. The chase period (delimited by vertical arrows) ended when the hare entered a form under a shrub and was very reluctant to flush. Air movement was slight until afternoon, when a moderate wind arose with gusts up to about 40 km h^{-1}.

only 21% greater than rates measured during late spring, summer, and early fall despite longer activity periods in the winter. Schmidt-Nielsen et al. (1965) estimated the lower critical temperature of *L. californicus* to be 12 C for animals obtained in early spring. Similar measurements of *L. alleni* obtained in late summer (Dawson and Schmidt-Nielsen 1966) indicated a lower critical temperature of 20 C. Dawson and Schmidt-Nielsen reasonably suggest that this difference reflects seasonal changes in pelage. Such changes have been demonstrated in arctic hares (Wang et al. 1973) and cottontail rabbits (Hinds 1973). Ambient temperatures in our study area (table 2) remain consistently below the zone of thermal neutrality only during the winter months when food consumption was highest. During the rest of the year ambient temperatures show drastic diurnal variation and are either above or below the thermoneutral zone for some part of of the average day. Night temperatures are low in spring and fall, and daytime temperatures are very high in summer. Costs of temperature regulation in free-ranging animals cannot be readily predicted on the basis of standard laboratory measurements of metabolism. Effects of wind, solar radiation, and the possibility that some of the heat produced by activity serves also for thermoregulation all complicate the picture. Strong winds are common on cold winter nights in deserts, and jackrabbits were observed to bask in the sun on winter mornings (Costa et al. 1976). All things considered, the relatively modest seasonal fluctuations in energy expenditure are not surprising, but would have been difficult to predict a priori. Nor do we regard the increased energy expenditure in winter to be inconsequential, because it occurs when available forage is poorest (table 1) and could therefore be a critical factor.

Annual energy expenditure by jackrabbits.—A number of investigators have multiplied standard metabolic rate (SMR) by some factor to estimate energy expenditure in the field (see Gessaman 1973). The SMR of *L. californicus* was measured by Schmidt-Nielsen et al. (1965) at 0.57 ml O_2 g^{-1} h^{-1} or, assuming a caloric equivalent of 4.8 kcal (liter $O_2)^{-1}$, 24,000 kcal kg^{-1} yr^{-1}. Our estimate of actual energy expenditure (55,200 kcal kg^{-1} yr^{-1}) exceeds SMR by a factor of 2.3. The SMRs of lagomorphs studied are generally greater than those predicted from accepted metabolism–body size relationships (Wang et al. 1973). Comparing our estimate of annual energy expenditure with SMR predicted from Kleiber's (1961) equation gives a ratio of 2.5.

Chew and Chew (1970) used an indirect method to estimate energy expenditure of mammals (including *L. californicus*) in a desert community. Their method relies heavily on the effect of ambient temperature on resting metabolism and incorporates an estimate of activity costs, and it agrees well with the doubly labeled water method when applied to a free-living rodent, *Perognathus formosus* (Mullen and Chew 1973). Chew and Chew estimate the annual energy expenditure for maintenance of *L. californicus* at 48,400 kcal kg^{-1} yr^{-1} (22,000 kcal $hectare^{-1}$ / 0.455 kg $hectare^{-1}$), and this is 88% of our estimate. Arnold (1942) maintained *L. californicus* in small outdoor enclosures near Tucson, Arizona, and measured their consumption of an air dried mixture of 1.7 parts alfalfa and 1 part barley. Average consumption, which did not vary markedly with season, was 56 g kg^{-1} day^{-1}. Assuming the air-dried food contained about 10% water (Forbes et al. 1941), their measurements of food consumption are nearly identical to ours (fig. 1).

Utilization of diet by jackrabbits.—We doubt that assimilative and metabolic efficiencies of free-living jackrabbits ever exceed 0.73 and 0.65, respectively—the values we obtained for a diet of annual plants in spring (table 1). Thus their minimum gross energy intake can be estimated at 84,500 kcal kg^{-1} yr^{-1}, and minimum fecal and urinary energy outputs are 22,600 and 6,700 kcal kg^{-1} yr^{-1}, respectively. The amount by which these figures underestimate average values will depend on the quality of food available, and this will vary from year to year, with season and with locality. Holter, Tyler, and Walski (1974) fed snowshoe hares on a diet containing about 44% maple browse, 23% commercial rabbit chow, and 33% grain. Their results indicate an assimilative efficiency of about 50% and a metabolic efficiency of 45%, values similar to those we obtained for the summer diet and to that reported by Arnold and Reynolds (1943) for *L. californicus* fed range type forage. Digestibility of browse is apparently quite low in lagomorphs. Forbes et al. (1941) found an assimilative efficiency of only 12% in domestic rabbits fed dogwood (*Cornus paniculata*) browse, whereas deer were able to obtain twice as much energy from this source. We also found very low efficiencies for the winter diet which contained a large proportion of shrub browse. Jackrabbits did not maintain energy balance on this diet even in the laboratory with water provided. This suggests that they are unable to process the large quantities of food that would be required despite their rapid passage time (about half the feces produced in one night represents food consumed that same night). To meet energy requirements on the winter diet, jackrabbits in the field would have to eat 217 g dry food kg^{-1} day^{-1} and produce 165 g dry feces kg^{-1} day^{-1}.

Wastage.—Our observations indicate that jackrabbits usually eat most of the plant material that they cut, and we agree with Arnold (1942) that wastage is highest for "plants which are least relished." Extensive accumulation of cut and uneaten material thus appears to indicate that jackrabbits are experiencing nutritional stress. Currie and Goodwin (1966) suggest that wastage of shrub browse by *L. californicus* in the Great Basin is approximately equal to consumption.

Body temperature.—The diurnal shifts we found in body temperature (fig. 2*A*) are consistent with observations on jackrabbits by Schmidt-Nielsen et al. (1965) and on cottontail rabbits by Hinds (1973). In all cases, undisturbed animals allowed body temperatures to rise to about 41 C during the day in hot weather. Increasing body temperature during the day stores heat that would otherwise have to be dissipated by evaporation. More importantly, for an animal the size of a jackrabbit, it also establishes a more favorable thermal gradient between the animal and its environment, thus reducing water expenditure for thermoregulation.

During forced activity body temperature rose rapidly (fig. 2*B*), and the rate of heat storage this represents can be taken to approximate the difference between metabolic heat production and evaporative heat loss when ambient temperatures are high. Even at modest levels of activity and an ambient temperature of 30 C, domestic rabbits store almost 70% of their heat production and dissipate 20% by evaporation (Kluger et al. 1972). The highest heating rate we observed (0.28 C min^{-1} during the early morning [fig. 2*B*]) represents storage of 14 kcal kg^{-1} h^{-1}which is five times SMR. If the active animal were also losing heat by evaporation at the same rate observed for the exercising domestic rabbit (Kluger et al. 1972) then heat production would exceed storage by 2.8

kcal kg^{-1} h^{-1} and would be about six times SMR.

Following exercise, the animal was resting in the shade and body temperature was close to air temperature, and thus dissipation of stored heat and metabolic heat must have occurred primarily by evaporation. Stored heat was dissipated at a rate of 4.2 kcal kg^{-1} h^{-1} (0.08 C $min^{-1} \times 60$ min $h^{-1} \times 0.85$ kcal °C^{-} kg^{-1}). Metabolic heat production at a body temperature of 42 C can be estimated from data of Schmidt-Nielsen et al. (1965) as 3.8 kcal kg^{-1} h^{-1} (0.8 liter O_2 kg^{-1} $h^{-1} \times 4.8$ kcal liter O_2^{-1}). Thus the total heat loss rate following exercise is about 8.0 kcal kg^{-1} h^{-1} which would require evaporation of 14 ml H_2O kg^{-1} h^{-1} (assuming 0.58 kcal lost per ml H_2O evaporated). This agrees with the maximal rate of 13 ml kg^{-1} h^{-1} measured by Schmidt-Nielsen et al. (1965).

Our data on the thermal relations of jackrabbits in summer indicate a voluntary diurnal hyperthermia (ca. 41 C) which is very useful in water conservation but leaves little margin for heat storage during activity. Following exercise, jackrabbits can cool rapidly by evaporation.

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IMPORTANT BIRD AREAS IN CALIFORNIA

East Mojave Peaks

State:	US-CA	**Area (Ha):**	78,773
Status:	Recognized	**Elevation-Min (m):**	716
Priority	Global	**Elevation-Max (m):**	2,037

County: Inyo
San Bernardino

Site Summary

The extreme eastern Mojave Desert features three large mountain ranges whose unique natural habitats warrant their recognition as an IBA: the Kingston, Clark and New York ranges. Visible from I-15 just inside the border of Nevada, each supports large tracts of Joshua Tree woodland on lower slopes, grading into Pinyon-Juniper woodland and a floristically diverse desert chaparral, and finally into tiny groves of White Fir above 7000' on their peaks. Unique in California, these sky islands of forest separated by vast deserts are miniature versions of their larger counterparts in southern Nevada (e.g. Spring Mtns.) and Arizona, with which they share several species. The habitat within the Kingstons is entirely protected as a BLM wilderness area, and the New Yorks are located within the Mojave National Preserve. About of Clark Mountain is protected by the Mojave National Preserve, with the exception of the southeast corner just north of Mountain Pass, which was left outside the preserve boundary for a mining operation. These mountains have been the subject of long-term studies in biogeography since the early 1900s, and continue to captivate ornithologists (see Cardiff and Remsen 1981).

Ornithological Significance

The relatively lush Joshua Tree woodland on the lower slopes of these peaks support strong populations of desert birds, notably Bendire's Thrasher, Juniper Titmouse, Scott's Oriole, and, in the New Yorks, Gilded Flicker. Broad-tailed Hummingbird, Plumbeous Vireo and Virginia's Warbler are common in pinyon-rich chaparral on Clark Mountain, and wherever this habitat occurs on steep-sloped canyons, Gray Vireo breed in what is likely their largest population away from eastern San Diego County. The most unusual bird communities, however, are restricted to the tops of these peaks, occurring most consistently in the fir grove on Clark Mountain. Hepatic Tanager and Whip-poor-will (arizonae race) virtually unknown elsewhere in California, are regular nesters on Clark (and at least the former in the New Yorks as well), and joined by occasional strays from Arizona, including Painted Redstart, Red-faced Warbler, and Grace's Warbler.

Help us learn more about the birds at this IBA! Enter your birding data online at California eBird! (http://ebird.org/california/)

Conservation Issues

Owing to its remoteness, much of the habitat within this IBA is secure. However, massive new mining operations at Clark Mountain should be closely watched.

IMPORTANT BIRD AREAS IN CALIFORNIA

National Audubon Society 2008. Important Bird Areas in the U.S.
Available at http://www.audubon.org/bird/iba 12/2008

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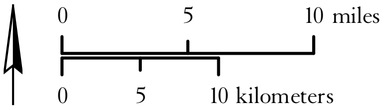
For up to date information about California Important Bird Areas, visit www.ca.audubon.org/iba.

East Mojave Peaks Important Bird Area



Audubon CALIFORNIA

Legend

□ Neighboring Important Bird Areas

□ East Mojave Peaks

Projection and Datum: California Teale Albers NAD83
Date: December 2008

IMPORTANT BIRD AREAS IN CALIFORNIA

East Mojave Springs

State: US-CA

Status: Recognized

Priority State

County: San Bernardino

Area (Ha): 681

Elevation-Min (m): 1,034

Elevation-Max (m): 1,719

Site Summary

This IBA draws attention to three major springs in the east Mojave Desert with similar avifauna. All are oases of riparian habitat associated with desert ranges surrounded by arid scrub. Horsetheif Spring, in the north, lies at the eastern edge of the Kingston Range (see East Mojave Peaks IBA above), and is reached by taking Excelsior Mine Rd. north 30 miles from I-15. It features a small grove of Fremont Cottonwoods. Piute Spring, adjacent to Ft. Piute about 20 miles due west of Bullhead City, AZ, flows above ground for several hundred meters through volcanic rock, supporting a thin strip of willow forest. Cornfield Spring emerges from the western flank of the Providence Mountains just east of Kelso. Horsetheif is located on BLM land, and the latter two sites are within the Mojave National Preserve. There are several other springs with vital riparian scattered across the east Mojave, mostly associated with desert ranges (e.g. Sunflower and Panamint Springs, Old Woman Mtns.; Cove Spring, Granite Mtns.). All should be considered important for birds in this harsh environment.

Ornithological Significance

These springs are most heavily-used by birds during spring migration (April-May), when songbirds are moving up into the state from the Colorado River. The nesting avifauna, including Least Bell's Vireo and Yellow-breasted Chat, is highly dependent on the condition of the riparian vegetation at each, which is at times overgrazed (by cattle and by feral horses and burros) or burned (due to arson).

Help us learn more about the birds at this IBA! Enter your birding data online at California eBird! (http://ebird.org/california/)

Conservation Issues

Efforts to fence cattle and vandals from these springs have met with limited success. As long as the desert is seen by a subset of its users as a place to "raise hell", these fragile habitats will need to be protected and closely monitored. Recent (court-ordered) actions by BLM to close particularly sensitive areas have caused a serious backlash among the OHV community, exacerbating an already tenuous truce between desert preservationists and others (R. Kobaly, pers. comm.).

National Audubon Society 2008. Important Bird Areas in the U.S.
Available at http://www.audubon.org/bird/iba 12/2008

Remember, you can help us learn more about the birds at our IBAs! Enter your birding data online at California eBird! (http://ebird.org/california/)

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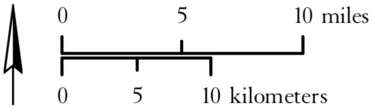
East Mojave Springs Important Bird Area



Audubon CALIFORNIA

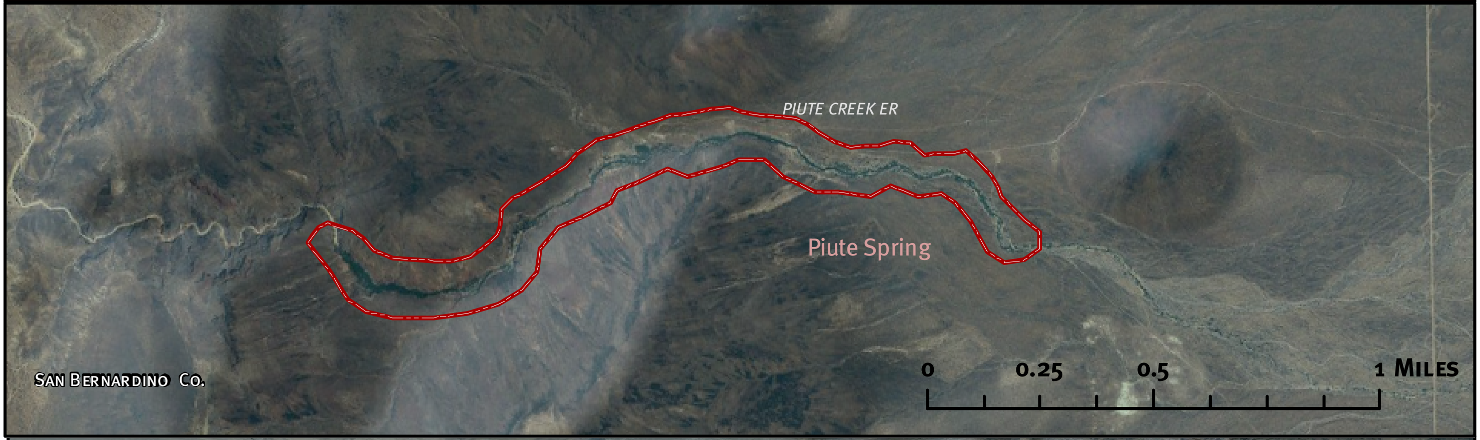
Legend

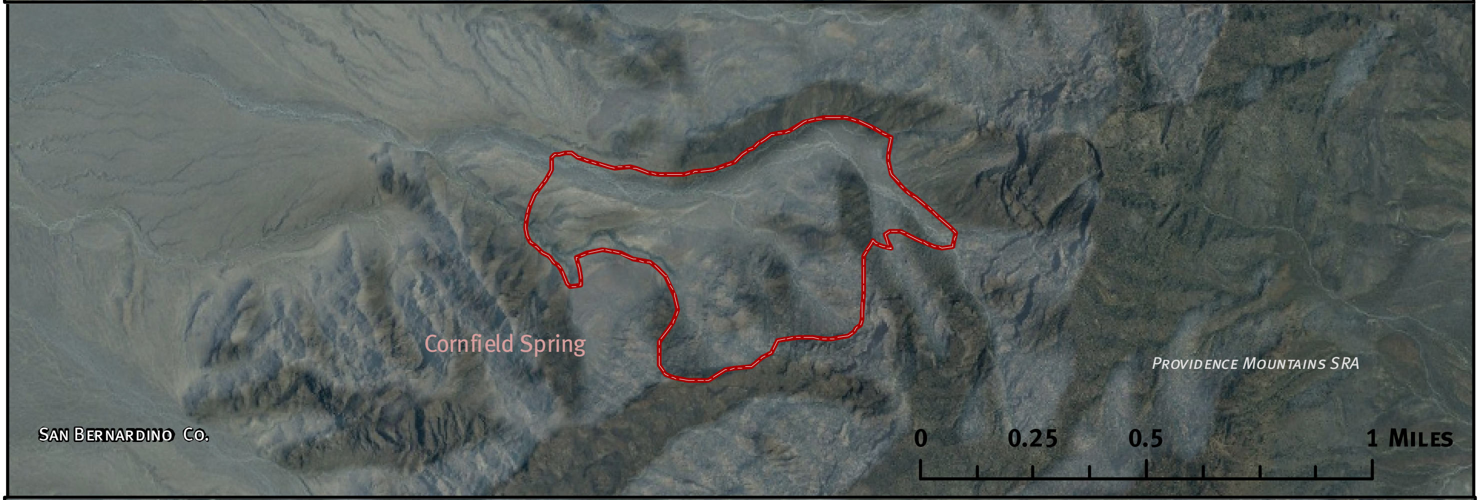
☐ Neighboring Important Bird Areas

☐ East Mojave Springs

Projection and Datum: California Teale Albers NAD83
Date: December 2008

East Mojave Springs Important Bird Area





Audubon CALIFORNIA

Legend

- ☐ Neighboring Important Bird Areas
- 🟥 East Mojave Springs

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Date: December 2008