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The world at your feet: desert biological soil crusts

Jayne Belnap

Desert soil surfaces are generally covered with biological soil crusts, composed of a group of organisms dominated by cyanobacteria, lichens, and mosses. Despite their unassuming appearance, these tiny organisms are surprisingly important to many processes in past and present desert ecosystems. Cyanobacteria similar to those seen today have been found as 1.2 billion-year-old terrestrial fossils, and they probably stabilized soils then as they do now. Biological crusts are vital in creating and maintaining fertility in otherwise infertile desert soils. They fix both carbon and nitrogen, much of which is leaked to the surrounding soils. They also capture nutrient-rich dust, and can stimulate plant growth. These organisms are able to tolerate extreme temperatures, drought, and solar radiation, despite having relatively little wet time for metabolic activity. Under most circumstances, they are extremely vulnerable to climate change and disturbances such as offroad vehicles and grazing livestock. Recovery times are generally measured in decades or centuries.

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Most people imagine the desert as a lifeless place, covered with rocks and sand, but this is not true. Deserts are exploding with life, although much of it is barely visible to the untrained eye. Despite their barren appearance, rocks and sand are often covered with a thin film of cyanobacteria, microfungi, lichens, and/or mosses that can occur on the surface or within the rock (endolithic) and on or just below the sand. The organisms living on and just beneath the soil surface are collectively known as biological soil crusts (Figure 1).

This incredibly diverse group has been called many things since it was first named in the 1950s, including cryptogamic, cryptobiotic, microphytic, microfloral, organogenic, and microbiotic soil crusts (Harper and Marble 1988). These communities often dominate the living ground cover in hot, cool, and cold arid and semi-arid regions. They also occur in temperate regions where plant cover is reduced, either temporarily (eg tree falls) or permanently (eg pine barrens). Despite their widespread occurrence, the major influence biological crusts have on

In a nutshell:

- Biological soil crusts are composed of soil cyanobacteria, lichens, and mosses, and are found in environments with sparse plant cover
- These crusts are essential in providing stability and fertility to desert soils
- The component organisms are easily damaged by soil surface disturbance, and are very slow to recover
- Protecting biological soil crusts should be a top management priority in desert regions, or we will lose the important ecosystem services they provide

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terrestrial ecosystems has only been recognized in the past two decades (Belnap and Lange 2001).

Cyanobacteria form the matrix of biological soil crusts. They first appear in the fossil record as marine stromatolites over 3 billion years ago (Walter *et al.* 1976). These large floating mats have been credited with oxygenating the atmosphere and forming the basis of the marine food web. The earliest terrestrial cyanobacteria are found in 1.2 billion-year-old rocks (Horodyski and Knauth 1994). Just as soil crusts do today, cyanobacteria probably accelerated the weathering of exposed bedrock and conferred stability on the newly formed soils as they spread across the land, thus aiding the evolution and spread of vascular plants and other terrestrial life forms (Schwartzman and Volk 1989).

Ins and outs of soil crusts

The term "biological soil crust" refers to the cohesiveness of the soil surface created by soil crust organisms. Most of this cohesion is due to large filamentous cyanobacteria, most notably the ubiquitous genus Microcoleus (Figure 2a), which is common around the world. When moistened, Microcoleus filaments extend towards the soil surface, and retract as the soil dries. This frequent movement results in copious sheath material being left in the uppermost soil layers, linking otherwise loose particles together to form larger soil aggregates (Figure 2b). It is easy to see this aggregation: hold a piece of desert soil aloft and look for small dangling soil clumps attached to cyanobacterial sheaths (Figure 3). Physical soil crusts, which result from raindrop or trampling impacts, often coexist with biological crusts, and also contribute to soil cohesion. Unlike biological crusts, physical crusts reduce water infiltration, often inhibit plant establishment, and

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Figure 1. (a-c) Soil crusts cover the large interspaces between vascular plants. (d) Close-up showing crust mounds that greatly roughen soil surfaces, enhancing retention of water, organic matter, dust, and seeds.

do not always protect the soil surface from erosion, because they dissolve when wet.

Hundreds of species of cyanobacteria and eucaryotic green algae are associated with biological soil crusts (Evans and Johansen 1999). Since these photosynthetic organisms require light, most biomass is concentrated in the upper soil layers (Figure 4, top). At the soil levels where they occur, they alter pH as well as oxygen, ammonium, and nitrate concentrations. Most of the cyanobacteria and green algae in biological crusts are small in size relative to Microcoleus, and are of secondary importance in forming the crust matrix. These smaller species (eg Nostoc, Scytonema, Chroococcidiopsis) have limited mobility, and therefore manufacture large amounts of pigments to protect themselves from excess radiation on the surface. Microcoleus has almost no protective pigmentation, and lives tucked beneath the pigmented species, at a depth where ultraviolet radiation is reduced, but photosynthetically active radiation is still adequate (Figure 4, bottom). Without the radiation "umbrella" offered by the pigmented species, Microcoleus experiences high summer mortality (Bowker et al. 2002). This type of microbial stratification is common in both terrestrial and aquatic habitats (Bowker et al. 2002).

The external morphology of biological soil crusts is determined by climate and species composition, and this

morphology influences how materials such as dust, water, and seeds move across the surface (Figure 5). Smooth crusts, dominated by cyanobacteria, are found in hyperarid regions without frost heaving, and where potential evapotranspiration (PET) is too high (due to excessively low rainfall and/or high air temperatures) to support lichens or mosses. As PET decreases, moss and lichen cover increases. Rugose crusts, with a microtopography of up to 3 cm, are found in hot deserts (high PET) where there is no frost heaving and very low lichen-moss cover. Pinnacled crusts, with a microtopography of up to 15 cm, occur in cool deserts (moderate PET) where lichen cover is <40% and soils freeze in winter. Rolling crusts are found in cool and cold deserts (low PET) where soils freeze, but the cohesion of the high lichen-moss cover restricts pinnacling to about 5 cm.

The taxa of soil crusts are similar around the world, despite their occurrence in areas with a wide range of climates and vegetation types. Many genera and species occur on almost all continents, including *Microcoleus vaginatus*, *Psora decipiens*, *Collema tenax*, *Collema coccophorum*, and *Catapyrenium squamulosum*. Non-related taxa exhibit comparable structures and functions, implying that soil surface conditions have produced convergent evolutionary trends within these taxa (Belnap *et al.* 2001a).



Figure 2. Scanning electron micrographs of biological soil crusts: (left) Microcoleus vaginatus in desert soils, x 700. (right) Microcoleus vaginatus sheaths, winding through sand grains, x 90.

In the frying pan

The desert soil surface is one of the most extreme environments on earth. The combination of incoming solar rays and those reflected from the soil surface creates a zone of high radiation. Soil surface temperatures can range from -20° C to over 70° C. Rainfall is infrequent and sparse. The ability of crust organisms to tolerate extreme dehydration is a key to survival. Dry-weight water content can drop to 5% or less, terminating all metabolic processes (Bewley and Krochko 1982). This allows these organisms to withstand extended periods of high heat, strong light, and no water.

Other adaptations also help soil crust organisms to survive on the soil surface. Many species have ways to prolong their activity periods. For instance, many lichens can photosynthesize at high and low temperatures, have large water-holding capacities, and require little moisture to begin metabolism (Lange 2001). Mosses have special structures to store and conduct water, light hairs, and revolute (curled-under) leaf margins to reduce water loss through transpiration (Frey and Kürschner 1991). Pigments are used by many crust species to reflect and/or absorb excessive radiation. Pigmented tissue can keep 50-93% of incoming radiation from reaching the interior of these organisms. If excessive radiation enters the cell, intracellular carotenoids and xanthophylls are there to absorb it (Castenholz and Garcia-Pichel 2000). Unpigmented species can use pigmented species as protection, as discussed above. In addition, mosses, lichens, and liverworts can "roll up" while drying, thereby protecting their sensitive photosynthetic tissue from radiation (Büdel and Wessels 1986; Frey and Kürschner 1991).

Multiple roles

Biological crusts have many roles in the formation, stability, and fertility of soils. Relatively undisturbed crusts have more biomass and are better able to perform the functions discussed below, than crusts kept at an early successional stage by disturbance. Despite current levels of information on biological crusts, there is much we don't know, and there are many possible ecosystem services that have never been investigated.

Dust trapping

The increased surface roughness and sticky polysaccharide sheaths associated with biological soil crusts increase the capture of nutrient-rich dust. This dust can augment the levels of most plant-essential nutrients, including nitrogen, phosphorus, and potassium, up to fourfold (Reynolds *et al.* 2001). This increases both the fertility and water-holding capacity of soils (Verrecchia *et al.* 1995). The greater surface roughness found in welldeveloped crusts captures more dust than disturbed (flattened) surfaces.



Figure 3. Close-up view of a soil surface, sliced vertically. The soil aggregates are formed by web-like cyanobacterial fibers, which also hold the aggregates in place.

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Figure 4. (top) Micro-profiles of cyanobacterial biomass (indicated by chlorophyll a), oxygen production, and pH. Solid lines indicate samples in darkness, dotted lines indicate light (500 $umol/m^2/s$). (bottom) Spectral attenuation of visible radiation as it passes through soil. Notice how the quantity of shorter (UV) wavelengths drops off much more quickly than do longer, photosynthetically active wavelengths, and how light trapping at the surface increases radiation above incident radiation levels.

Weathering

Soil crust organisms in the US, Venezuela, and South Africa increase substrate alkalinity from about pH 8 to about pH10.5 (Garcia-Pichel and Belnap 2001). Crusts also hold water longer, enhancing mineral dissolution and freeze-thaw action. Combined, these factors can accelerate bedrock weathering rates up to 100 times (Schwartzman and Volk 1989). The greater biomass associated with well-developed crusts would be expected to have higher rates than the reduced biomass of disturbed crusts.

Soil physical structure

Polysaccharides extruded by crust organisms bind soil particles together into aggregates critical to soil functioning (Figure 2). Aggregate surfaces are where most soil biota and nutrient transformations occur, and aggregates increase soil aeration, infiltration (Herrick and Wander 1998), and resistance to soil erosion (McKenna-Neuman *et al.* 1996). Because all crust organisms secrete polysaccharides, crusts with greater biomass (relatively undisturbed crusts) foster more soil aggregation than those with lower biomass (disturbed crusts).

Soil stabilization

Soils in arid regions are slow to form and are highly erodable (Dregne 1983). Biological soil crusts protect desert surfaces from wind and water erosion. Whereas welldeveloped biological crusts containing lichens and mosses protect these surfaces almost completely from wind and water erosion, disturbed (cyanobacterial) crusts allow up to 35 times more sediment loss in high winds or overland flow (Belnap and Eldridge 2001).

Soil-water relations

The effect of biological soil crusts on water infiltration and soil moisture depends on climate, soil texture, soil structure, and the flora and morphology of the crusts. Because organisms in smooth and rugose crusts reduce the size and number of pores where water can enter the soil, and there is little soil surface roughness to increase water residence time, water infiltration is generally decreased. This can be offset somewhat by water stored by the crust organisms, depending on the amount of rainfall. The resultant runoff in these high PET regions is critical in supporting the often heterogeneously distributed or banded downslope plants. Experimental disruption of the biological crust in these regions, allowing greater localized infiltration, can lead to the death of downslope plants (Eldridge et al. 2000). In contrast, pinnacled and rolling crusts found in regions with lower PET have greatly roughened surfaces that slow water enough to increase infiltration. (Again, the crust organisms themselves absorb and store water.) Highly localized infiltration supports a higher cover of the more homogeneously distributed vegetation found in cooler deserts.

Carbon and nitrogen inputs

Biological soil crusts are an important source of fixed nitrogen and carbon in deserts where vascular plant cover is limited (Beymer and Klopatek 1991; Belnap 2001a). Most inputs occur during the cooler fall, winter, and spring. Carbon inputs range from 0.4-2.3 $g/m^2/year$ for cyanobacterial crusts to $12-37 g/m^2/year$ year for lichen crusts (Evans and Lange 2001). Both free-living and lichenized cyanobacteria also contribute fixed nitrogen. Many deserts have only a few nitrogen-fixing plants and atmospheric inputs are low (Peterjohn and Schlesinger 1990; Wullstein 1989). As lichen crusts can fix up to 10 kg/ha/year (cyanobacterial crust can fix up to1 kg/ha/year) (Belnap 2002), their input can be the dominant source of new nitrogen for desert soils (Evans and Ehleringer 1993). Much of the carbon and nitrogen fixed by crusts is released upon wetting, so rainfall events contribute both water and nutrient pulses to desert soils. The carbon and nitrogen released by the soil crusts is used by nearby vascular plants, fungi, actinomycetes, and bacteria (Belnap 2001b).



Figure 5. External morphologies of biological crusts, as determined by climate and species composition.

Albedo (reflective power)

Lichen-moss crusts reflect only half the light of uncrusted or cyanobacterially crusted surfaces, decreasing surface energy flux by approximately 40 Joules/sec/m² and increasing surface temperatures by 10-14°C (Belnap 1995). Surface temperatures regulate many ecosystem functions, including rates of nitrogen and carbon fixation, microbial activity, plant nutrient uptake and growth, soil water evaporation, and seed germination (Belnap 2003). Timing of these events is often critical for desert plants, and relatively small alterations can reduce species fitness and seedling establishment, eventually affecting community structure (Bush and Van Auken 1991). Many ants, arthropods, and small mammals partition their environment on the basis of foraging times and burrowing depths, both controlled by surface temperature (Crawford 1991).

Vascular plants and soil fertility

In deserts, vascular plant cover increases crust cover at lower elevations, probably because of the shade found under the plant canopy. At higher elevations, vascular plants and plant litter occupy most of the soil surface, reducing colonization opportunities for crust organisms.

Crust morphology can influence plant establishment patterns. Smooth and rugose crusts increase the tendency of seeds and organic matter to skid from the space between plants on to the next obstacle, be it rock or plant, whereas pinnacled and rolling crusts increase the retention of seeds and organic materials (Belnap *et al.* 2001b). Although a few laboratory studies have shown that soil crusts in hot deserts may reduce native plant germination, this has not been corroborated under field conditions. In contrast, multiple field studies show that germination and survival of native plants is either higher or unaffected in biologically crusted, as compared with uncrusted, areas. Several studies in both Australia and the US indicate that soil crusts can slow the germination of exotic annual grasses (Belnap *et al.* 2001b).

Once established, vascular plants growing in crusted soils generally have greater biomass and higher nutrient concentrations than plants growing in uncrusted soils. There are many ways in which biological crusts can influence soil fertility and plant nutrient concentrations: (1) contributing carbon and nitrogen to the soils; (2) exuding sticky, negatively charged polysaccharides which bind and prevent leaching loss of positively charged nutrients essential to plants; (3) secreting ringshaped chemical compounds called chelators that keep nutrients available for plants, despite high soil pH; (4) increasing soil temperatures and nutrient uptake rates; (5) increasing dust capture and soil stabilization, thereby improving soil fertility and water-holding capacity; and (6) increasing soil aggregation. In addition, soil food webs under biological crusts are more diverse and food web groups are more abundant than under cyanobacterial crusts, so decomposition rates and nutrient availability are generally higher (Belnap 2001b). Because lichen-moss crusts have greater diversity, biomass, and soil surface roughness than cyanobacterial crusts, the influence of the factors listed above are greater when soils support a lichen-moss cover rather than a cyanobacterial cover.

Resistance and resilience to disturbance

Many types of disturbances threaten the integrity of biological soil crusts, including climate change, increasing human use, and invasion by exotic annual grasses and the subsequent increase in fire risk. Most of these disturbances produce a similar result: the total crust cover is reduced, disturbance-intolerant lichens and mosses are replaced with more disturbance-tolerant cyanobacteria, soil surface temperatures are reduced, and soil surfaces are flattened. The reduction of crust cover and loss of lichens and mosses lead to a loss of soil stability and reduced soil fertility as less polysaccharide material is extruded, less carbon and nitrogen is fixed, less dust and other surface materials are captured, fewer chelators and growth factors are secreted, nutrient uptake rates are lowered, and soil food web organisms decrease in number and diversity. Flattened soil surfaces change the way crusts affect local hydrologic regimes and vascular plant establishment. In other words, the contribution of biological soil crusts to the surrounding ecosystem is greatly compromised.

Land use

As tough as soil crust organisms are in the face of natural stresses (heat, radiation, drought), they are no match for animal hooves, human feet, tank treads, or off-road vehicle tires. The compressional and shear forces these activities generate essentially pulverize soil crusts, especially when they are dry (as they most often are). This leaves pieces of crust free to blow or wash away. If buried, they die, since they need light to photosynthesize. Relative to other disturbance types, direct human impact has probably been most responsible for the simplification and/or destruction of biological soil crusts, and human activities remain the dominant cause of crust loss. Human use of deserts, in terms of recreation, energy development, livestock grazing, habitation, and military exercises, is expanding rapidly (Brooks and Pokshishevsky 1986). Although no firm quantitative estimates are available, the fragility of soil crusts, combined with the extensive expansion of human activities over the past century, has undoubtedly led to a historically unprecedented loss of lichen-moss cover, and associated ecosystem services, over vast swaths of the western US. Given the inability of soil crusts to withstand the forces generated by such activities, and in view of their slow recovery rates in most deserts, the decreases we currently observe in crust cover and diversity are likely to be relatively permanent. Although the situation is less well known in other countries, the increase in human use of "marginal" lands has become apparent, as the size and frequency of global dust storms have increased dramatically over time (Pimm 2001).

Exotic annual grasses and fire

Invasion by annual grasses also results in the loss of crust cover and biodiversity, as annuals occupy plant interspaces once dominated by soil crusts, and the rich perennial diversity of the crusts is replaced by a few cyanobacterial and annual moss species. In the absence of fire, the increase in rodent numbers and their burrows is probably responsible for this compositional shift. However, the presence of annual grasses also increases the size and frequency of wildfires. Crust organisms will die if burned. In the past, fires generally skipped from shrub to shrub, bypassing the soil crusts between them. However, the presence of annuals in the interspaces means that fires now often scorch large areas, including the soil crusts between plants. Short fire cycles prevent colonization by perennial lichens and mosses, leaving soils dominated by cyanobacteria and annual mosses. Given the millions of hectares of western rangelands that are now dominated by exotic annual grasses (mostly in areas with lower PET), and the hundreds of thousands of hectares that are annually being converted, irreversibly, to annual grass, we stand to lose large amounts of well-developed lichen-moss crusts throughout much of the cooler western US deserts.

Atmospheric changes

Soil crusts are metabolically active only when wet, and their rates of physiological functioning are highly responsive to temperature. Because climate models predict higher temperatures, greater summer precipitation, and drier-than-normal winters for the western US (Cayan 1996), soil crust structure and function will undoubtedly be affected. Soils will dry faster at higher temperatures. In moderate and high PET deserts, soil crusts often already experience carbon deficits in the summer (Jeffries *et al.* 1993). Increased rates of soil drying will mean greater summertime carbon deficits, as crust organisms will be even more likely to dry before respiratory losses are compensated for by photosynthetic gain. Less winter rain will also mean less carbon gain, which translates into less nitrogen fixation, as this process requires photosynthetic products. With reduced access to adequate carbon and nitrogen, crusts will be less able to avoid or repair radiation damage (Belnap et al. unpublished). This will probably result in increased mortality or even alteration of distribution patterns. Current lichen and moss distribution patterns support this scenario: in the US, Australia, and central Asia, lichen diversity decreases sharply as air temperature and summer rainfall increase (Belnap et al. 2001a). Increased ultraviolet (UV) radiation as a result of ozone thinning is expected to be reversed by 2050, due to reductions in chlorofluorocarbon (CFC) production. However, volcanic eruptions, airplane exhaust, and/or the renewed manufacture of CFCs may slow this recovery (UNEP/WMO 2002). All crust species are sensitive to UV, because it increases mortality and disrupts photosynthesis, growth, motility, photomovements (movements induced by light), nitrogen fixation and uptake, and cell differentiation (Castenholz and Garcia-Pichel 2000). The limited activity time of organisms that require rehydration can heighten their susceptibility to UV damage. For example, while soil crusts experience some level of UV radiation for approximately 4400 hours per year near Moab, UT, soils can experience less than 100 daylight hours of wetness per year, greatly limiting their ability to acquire the carbon necessary to repair and produce new tissue (Belnap et al. unpublished). Predicted temperature increases are likely to exacerbate this situation, as activity times will be limited even further.

Elevated atmospheric CO₂ levels may increase crust primary production. Soil lichen photosynthesis is CO₂-limited, as rates at ambient CO_2 levels are 70-80% of maximum (Lange et al. 1999). In contrast, higher plants show substantial down-regulation after long-term exposure to elevated CO_2 (Moore *et al.* 1999). We have no comparable data on soil crusts. Cyanobacteria already possess intracellular CO₂ concentration mechanisms, however, and are therefore less likely to experience altered photosynthetic rates than are free-living and lichenized green algae. As a result, more CO₂ may differentially favor green algae and green algal lichens over cyanobacteria and cyanolichens. On the other hand, the greatest impact of elevated CO_2 on soil crusts will probably be an increase in the cover and altered species composition of higher plant communities. Large increases in net primary productivity are predicted to occur in arid ecosystems as a result of enhanced water availability (Melillo et al. 1993). Elevated CO₂ may also shift the competitive balance among higher plants, favoring invasive annual grasses such as cheatgrass (Bromus tectorum) (Smith et al. 1987), resulting in reduced crust cover and diversity, as is seen today in Bromus-dominated communities.

Recovery rates

Total recovery of soil crusts from disturbance can be fairly quick (20 years) in regions with low PET, but extremely

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Figure 6. A simplified model depicting large-scale factors that influence recovery rates in biological soil crusts. Many other factors, such as microhabitat, the size and shape of disturbance, and the condition of adjoining crusts, also influence recovery rates.

slow (\geq 1000 years) in deserts with high PET. Recovery rates depend on the characteristics of the soil, site, climate, and disturbance (Figure 6), the availability of inoculant, and how recovery is defined (Belnap and Eldridge 2001; Figure 7). Coarse soils with low stability, fertility, and water-holding capacity recover more slowly than fine-textured soils. Stable areas, with low slopes, low wind deposition of sand, and/or embedded rocks, are quicker to recover than less stable sites with steep slopes, high sand deposition, and/or unstable rocks. Because crust organisms are only metabolically active when wet, microhabitats such as shrub canopies and regions with lower PET, including higher elevations and cool deserts, recover more quickly than places with higher PET, such as plant interspaces, low elevations, and/or hot deserts. When disturbance is severe or frequent enough to remove crust material, recovery is slower than if organisms are crushed but left in place.

In all deserts, cyanobacteria are often blown in after disturbance. The large, highly mobile filamentous cyanobacteria such as *Microcoleus* can tolerate some burial, and so are generally the first colonizers of unstable soils (Figure 7). Once soils are stabilized by the larger cyanobacteria, the less mobile, smaller cyanobacteria appear. In regions where PET is low enough to support lichens and mosses, the non-mobile, early successional lichen and moss species appear next, often led by the cyanolichen genera *Collema*. This species appears able to reproduce through spores, as colonization often occurs far from intact lichens. As PET decreases further, mid- and late-successional desert lichens, most with green algal phycobionts (the photosynthetic partner), colonize next. These species 188



Figure 7. The successional sequence of biological crust organisms when colonizing a severely disturbed area. Depending on the potential evapotranspiration at a site, the successional sequence may stop at cyanobacteria or a few early successional lichen-moss species (low elevation hyper-arid deserts) or early successional lichens and mosses with a few mid-successional species (low elevation hot deserts). Estimated years to recovery in the different deserts are based on flat sites with coarse soils and disturbance severe enough to remove all material. They are based on linear recovery rates, which probably overestimate recovery times.

seem to rely less on spores for dispersal and more on pieces of nearby lichens washing or rolling in from the disturbance edge. This may be because the high pH of most desert soils greatly limits green algal abundance, making it difficult for germinating fungal spores to find a green algal partner. Recolonization of these later-successional species can therefore be very slow, especially if the disturbed areas are large. Visual recovery (generally based on surface roughness) is much quicker to recover than species composition, biomass, soil stability, or full physiological functioning (Belnap and Eldridge 2001; Figure 7). Because most reported estimates of recovery time have been based on visual assessments, many underestimate the time to full recovery.

Intact crust material salvaged from one area and reapplied to another has long been used to speed up recovery at the small (<10 acres) plot scale (Belnap 1993). Although commercial production of cyanobacterial inoculants has been attempted (Buttars *et al.* 1994), field applications have not yet been successful. Using inoculants for even moderately large disturbances is not feasible now, or in the near future. Even with such cyanobacterial inoculants, only a few lichen species have been successfully grown in the laboratory, and the feasibility of ever producing lichen inoculant is very low. Recovery will therefore still take decades or centuries, and many desert areas will lack fully functioning biological soil crusts for many years after disturbance.

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The outlook for soil crusts

Biological soil crusts provide many of the basic needs for plants and animals found in the desert environment. Unfortunately, human activities are often incompatible with the presence of soil crusts. The cyanobacteria fibers that confer such tensile strength to these crusts are no match for the many stresses placed on them by human activity. Exotic annual grasses and increased fire often follow surface disturbance, further simplifying species composition and flattening the crusts. Increased air temperatures and summer precipitation are likely to further reduce the activity times critical for maintaining and repairing damaged tissue. Compromised crusts contribute less to soil fertility and are less able to offer protection from wind or water erosion. Unlike vascular plant cover, biological crust cover is not reduced during droughts, and unlike physical soil crusts, they are present under all soil moisture conditions. Consequently, biological crusts offer many ecosys-

tem services over time and under adverse conditions. The condition of biological soil crusts should be considered a top management priority in desert regions, because once this resource is gone, it is often gone for more than a human lifetime. It may seem odd to curtail our activities for something so inconspicuous, but it is the only way to protect this microworld that does so much for us.

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Soil Fertility in Deserts: A Review on the Influence of Biological Soil Crusts and the Effect of Soil Surface Disturbance on Nutrient Inputs and Losses

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ABSTRACT: Sources of desert soil fertility include parent material weathering, aeolian deposition, and on-site C and N biotic fixation. While parent materials provide many soil nutrients, aeolian deposition can provide up to 75% of plant-essential nutrients including N, P, K, Mg, Na, Mn, Cu, and Fe. Soil surface biota are often sticky, and help retain wind-deposited nutrients, as well as providing much of the N inputs. Carbon inputs are from both plants and soil surface biota. Most desert soils are protected by cyanobacterial-lichen-moss soil crusts, chemical crusts and/or desert pavement. Experimental disturbances applied in US deserts show disruption of soil surfaces result in decreased N and C inputs from soil biota by up to 100%. The ability to glue aeolian deposits in place is compromised, and underlying soils are exposed to erosion. The ability to withstand wind increases with biological and physical soil crust development. While most undisturbed sites show little sediment production, disturbance by vehicles or livestock produce up to 36 times more sediment production, with soil movement initiated at wind velocities well below commonly-occurring wind speeds. Soil fines and flora are often concentrated in the top 3 mm of the soil surface. Winds across disturbed areas can quickly remove this material from the soil surface, thereby potentially removing much of current and future soil fertility. Thus, disturbance of desert soil surfaces can both reduce fertility inputs and accelerate fertility losses.

INTRODUCTION

In arid and semi-arid environments, vegetation cover is generally sparse. The open spaces between higher plants are usually covered by biological soil crusts (also referred to as cryptogamic, cryptobiotic, microbiotic or microphytic soil crusts), an interwoven community of cyanobacteria, green algae, microfungi, bacteria, lichens, and/or mosses. Cyanobacterial and microfungal filaments weave throughout the top few millimeters of soil, gluing loose soil particles together, forming a coherent crust that stabilizes and protects soil surfaces from erosive forces, as will be discussed below. These crusts occur in all hot, cool, and cold arid and semi-arid regions of the world, but have only recently been recognized as having a major influence on terrestrial ecosystems (Harper and Marble, 1988).

SPECIES COMPOSITION AND GROWTH FORMS

Globally, biological soil crusts have many similarities in species composition, in spite of occurring in unconnected and seemingly dissimilar environments. Many of the dominant cyanobacteria, lichens, and moss species and genera found in soil crusts have a cosmopolitan distribution. The relative dominance of the different species, however, varies with climate. The cyanobacterial flora in deserts where most rain falls during cool seasons are dominated by filamentous species such as *Microcoleus*. Hot deserts, especially those with summer rainfall, are often dominated by smaller genera such as *Scytonema*, *Nostoc* and *Schizothrix*. Common lichens found include *Fulgensia*, *Diploschistes*, *Psora*, *Placidium*, and *Collema*. Common mosses include *Tortula*, *Bryum*, and *Grimmia*.

Four general growth forms are found in different deserts. Hot deserts that lack frost heaving are generally characterized by smooth cyanobacterial crusts or rugose lichen-moss crusts. In cool deserts where frost-heaving is present, soil crusts with low lichen cover are often pinnacled, due to frost-heaving upwards and differential erosion downwards. Crusts in cool deserts with a heavy lichen-moss cover are generally rolling, as frostheaving and erosion are mitigated by the extensive lichen-moss cover.

Because the dominant components of biological soils crusts are photosynthetic organisms, they require sunlight. When soils are dry, the bulk of the crustal biomass is up to 0.5 mm below the soil surface, with some individuals found down to 4 mm (Garcia-Pichel and Belnap, 1996). While mosses and lichens have UV pigments or heavy coloration to protect them from UV, only some cyanobacteria have such protection. Large filamentous species, such as *Microcoleus*, *Lyngbya*,

Desertification in the Third Millennium. Edited by A.S. Alsharhan, W.W. Wood, A.S. Goudie, A. Fowler and E.M. Abdellatif. © 2003 Swets & Zeitlinger Publishers, Lisse, The Netherlands, ISBN 9058095711, p. 245–252. *Phoridium*, and *Oscillatoria* do not have UV-protective pigments, and so are seldom found on the soil surface except on cloudy days when soils are moistened. Cyanobacteria such as *Scytonema* and *Nostoc* do manufacture UV-screening pigments, and can be found on the soil surface.

ECOLOGICAL ROLES

Carbon fixation: Biological soil crusts are an important source of fixed carbon on sparsely vegetated areas common throughout the West (Beymer and Klopatek, 1991). While vascular plants provide organic matter to soils directly underneath them, large interspaces between plants have little opportunity to receive such input. Where biological soil crusts are present, carbon contributed by these organisms help keep plant interspaces fertile, and aid in supporting other microbial populations. This is probably less important in areas with high productivity, and more important as soils get shallower and/or less fertile.

Nitrogen fixation: Nitrogen levels are low in desert ecosystems relative to other ecosystems. Surveys in cold deserts have revealed only a few nitrogen-fixing plants (Wullstein, 1989). Since nitrogen can limit plant productivity (Ettershank et al., 1978; Nobel et al., 1988), maintaining normal nitrogen cycles is critical to maintaining the fertility of semi-arid soils. Most soil crusts in deserts are dominated by complexes of organisms capable of fixing nitrogen, including Microcoleus, Scytonema, Nostoc and the soil lichen Collema. Rainfall events in desert areas too small to promote plant growth often do stimulate crustal activity; thus, time of soil crust activity can be high. As with carbon, crusts contribute nitrogen to soils both underneath plants, and in plant interspaces, counteracting the tendency of nutrients to concentrate around plants. Five to 88% of N fixed by crusts has been shown to leak into the surrounding soils. N leaked from these organisms is available to nearby vascular plants and microbial communities. Vascular plants growing in crusted areas show higher leaf concentrations of N when compared to plants in uncrusted soils. Leaked N has also been found in associated fungi, actinomycetes, and bacteria.

Soil crusts can be the dominant source of nitrogen for desert shrub and grassland communities (Evans and Ehleringer, 1993; Evans and Belnap, 1999), where nitrogen-fixing plants are generally locally scarce. Input estimates range from 1 to 365 kg ha-1 annually (reviewed in Harper and Marble, 1988). Nitrogen inputs are highly dependent on temperature, moisture, and crustal species composition, thus timing, extent and type of climatic regimes and past disturbance is critical in determining fixation rates (Belnap, 1995, 1996). **Dust trapping:** Dust can be an essential component of desert soil fertility, and soil crusts are effective in capturing eolian dust deposits (Fig. 1). Recent work in SE Utah shows dust input significantly increase levels of all major and minor soil nutrients in the tested soils. The bioessential macronutrients N, P, K, and Mg, and micronutrients Cu, Fe, Mn were enriched up to 3 times that of surrounding bedrock (Table 1; Reynolds et al., unpubl. data).

Effects on vascular plants: Germination and Establishment: Soil crusts can influence the location of safe sites for seeds, and the germination and establishment of vascular plants. In hot deserts with smooth cyanobacterial crusts, seeds can skid off the smoothed surfaces. Rugose crusts in these areas can provide limited safe sites. In contrast, seeds in cool and cold deserts find many safe sites where frost-heaved crusts occur.

Crusts can influence the germination of seeds. While soil cracks can provide favorable conditions for small seeds to germinate, most large-seeded plants need soil or litter cover (or an increase in humidity similar to that litter and soil cover can provide) to germinate. Native seeds often have self-burial mechanisms (such as hygroscopic awns) or are cached by rodents. However, germination of seeds that lack such adaptations can be inhibited by crusts. Once seeds germinate, crusts have never been shown to constitute a barrier to root penetration. However, it should be kept in mind that seedling germination per se has not been shown to limit species density in desert plant communities. Rather, studies suggest vascular plant cover in arid lands world-wide is controlled by water and nutrient availability rather than other site factors.

Survival of vascular plants is generally much higher, or unaffected, when crusted areas are compared with uncrusted areas (Lesica and Shelley, 1992; Harper and Marble, 1988). No studies have shown crusts to decrease vascular plant survival.

Many studies have correlated crust cover with vascular plant cover, and results have been variable, with negative, positive, and no relationship found between crust and vascular plant cover (Harper and Marble, 1988; Ladyman and Muldavin, 1996). At more arid sites, correlations between vascular plant cover and cover of crustal components is generally positive, suggesting plants aid survival of crustal components, especially mosses and lichens, perhaps due to microclimate conditions associated with perennial vegetation (such as decreased soil surface temperatures and increased surface moisture). At higher elevations and/or plant cover, it appears that plants inhibit crust cover by restricting the amount of light reaching the soil surface. No study has demonstrated a negative influence of crusts on overall plant cover.

Nutrient levels in vascular plants: Plants growing on crusted soil generally show higher concentrations



Figure 1 Grain size distribution curves for three dune samples. The biological soil crust contains a much higher percentage of silt and clay particles. Adapted from Verrecchia et al., 1995.

 Table 1 Nutrient enrichments of soils above parent materials by Aeolian dust (Reynolds et al., unpubl.).

Bioessential elements	Р	K	Mg	Na	Ca	Mn	Zn	Cu	Fe
Soil	271	1.49	0.37	0.17	2.7	196	21.4	13.8	1.04
Parent material	104	1.27	0.08	0.04	2.1	94	7.8	10.2	0.66
Enrichment (x)	2.6	1.2	4.6	4.3	1.3	2.1	2.7	1.4	1.6

and/or greater total accumulation of various bioessential nutrients when compared to plants growing in adjacent, uncrusted soils, including N, K, Na, Ca, Fe and Mg. Dry weight of plants in pots with cyanobacteria are up to four times greater than in pots without cyanobacteria (Harper and Pendleton, 1993). Dry weight of plants in untrampled areas can be two times greater than in trampled areas (Belnap, 1995; Brotherson and Rushforth, 1983; Shields and Durrell, 1964; Belnap and Harper, 1995).

Several mechanisms have been postulated to explain this effect. Cyanobacterial sheath material is negatively charged, binding positively-charged macro-nutrients and thus preventing their leaching (Belnap and Gardner, 1993; Black, 1968). Cyanobacteria secrete chelators that keep iron, copper, molybdenum, zinc, cobalt, and manganese more available in high pH soils (Lange, 1974). Nutrient differences may also result from a thermal effect. Dark-colored crusts warm soils, thus increasing nutrient uptake rates.

SOIL HYDROLOGY AND STABILIZATION

The effect of biological soil crusts on soil water relations is heavily influenced by soil texture, soil structure, and the growth form of the crusts. In hot deserts, the presence of the mucilaginous cyanobacteria and surface smoothness can decrease water infiltration. In cold deserts where frost-heaving is common, increased surface roughness can increase water pooling and residence time. As a result, here the presence of soil crusts generally increases the amount and depth of rainfall infiltration (Brotherson and Rushforth, 1983; Harper and Marble, 1988; Johansen, 1993; Loope and Gifford, 1972).

Crusts have been shown to reduce soil loss by wind and water erosion in all types of deserts (Williams et al., 1995a, b). Polysaccharides extruaded by the cyanobacteria and green algae, in combination with lichen and moss rhizines entrap and bind soil particles together. As soil aggregates get larger, they are heavier, have a greater surface area, and are more difficult for wind or water to move, thus reducing both wind and water erosion. When wetted, cyanobacterial sheath material swells and covers the soil surface even more extensively than when dry, protecting soils from both raindrop erosion and overland water flow during rainstorms.

Resistance to wind erosion parallels biological crust development (Belnap and Gardner, 1993; McKenna-Neuman et al., 1996). Soils in arid regions are often highly erodible, and soil formation extremely slow, taking 5,000 to 10,000 years or more (Dregne, 1983b). Consequently, reducing soil loss is very important in these regions. Soil aggregates are also important for increasing infiltration and as microenvironments for soil biota.

EFFECTS OF DISTURBANCE

Species composition: Trampling of crusted surfaces generally results in a decrease in crustal species present. Untrampled areas often have 2–10 species of soil lichens and/or 4–6 species of cyanobacteria, while adjacent, trampled areas will have no lichens and only one species of cyanobacteria (Belnap, 1995).

Water erosion: As crustal components are brittle when dry and easily crushed (Belnap and Gardner, 1993; Campbell et al., 1989; Harper and Marble, 1988) the soil aggregates formed by the presence of soil crusts are disrupted when trampled (Dregne, 1983a; Stolzy and Norman, 1961). When the roughened microtopography of undisturbed cool desert crusts are flattened, velocity of surface water flows is increased. Thus, suspended sediments do not settle out and surfaces are subjected to sheet erosion (Harper and Marble, 1988). Surface disturbance also reduces the depth to which abandoned cyanobacterial sheath can accumulate, thereby reducing resistance to water erosion at depth. At many disturbed sites, sheath material is often not observed below 1 mm depth, in contrast to up to 10 cm thick crusts in untrampled areas (Belnap, 1995). Buried sheath material is still capable of binding soil particles together and still increases nutrient and moisture retention of associated soil. However, damage to such abandoned sheath material is non-repairable, since living cyanobacteria are no longer present at these depths to regenerate filament and sheath materials. Consequently, trampling can greatly accelerate desertification processes through increased soil loss and water runoff (Alexander and Calvo, 1990; Beymer and Klopatek, 1992; Eldridge, 1993a, b; Eldridge and Greene, 1994; Foth 1978; Harper and Marble, 1988; Ladyman and Muldavin, 1996).

Wind erosion: Wind is a major erosive force in deserts, where there is little soil surface protection by organic matter or vegetative cover (Goudie, 1978).

Experiments have demonstrated that while welldeveloped, undisturbed crusts protect soil surfaces from wind erosion, any compressional disturbance to these crusts leave surfaces vulnerable to wind erosion (Fig. 2; Belnap and Gillette, 1997 and 1998; Leys, 1990; Williams et al., 1995a).

Decrease in soil wind resistance is directly associated with increased sediment movement (Leys, 1990; Williams et al., 1995a). Since soil formation is slow, soil loss can have long-term consequences. In addition, nearby biological soil crusts can be buried by blowing sediment, resulting in the death of the photosynthetic organisms. Because over 75% of the photosynthetic biomass, and almost all photosynthetic productivity, is from organisms in the top 3 mm of these soils, very small soil losses can dramatically reduce site fertility and further reduce soil surface stability (Garcia-Pichel and Belnap, 1996). In addition, many plants have relatively inflexible rooting depths, and often cannot adapt to rapidly changing soil depths (Belnap, 1995, 1996).

Nutrient cycles: Nitrogenase activity in crusts show short and long-term reductions in response to all types of experimentally-applied disturbance, including human feet, mountain bikes, four-wheel drive trucks, tracked vehicles (tanks), and shallow and deep raking. Consequently, crust disturbance can result in large decreases in soil nitrogen through a combination of reduced biological nitrogen input and elevated gaseous loss of nitrogen and soil loss. Short-term reduction (2 years) in nitrogen inputs range up to 100% (Belnap, 1996), while long-term studies in SE Utah have demonstrated a 42% decrease in soil nitrogen in the 25 years following disturbance. The greatest long-term impact of disturbance may be on the soil microbial pool: production of plant-available nitrogen by soil microbes has been found to decrease almost 80% following disturbance (Evans and Ehleringer, 1993; Evans and Belnap, 1999).

Albedo: Trampled surfaces show up to a 50% increase in reflectance of wavelengths from 0.25 to 2.5 um (Belnap, 1995) when compared to untrampled crusted surfaces. This represents a change in the surface energy flux of approximately 40 watts/m2. Large acreages of trampled areas, combined with lack of urban areas to offset this energy loss, may lead to changes in regional climate patterns in many semi-arid regions (Sagan et al., 1979).

Because of albedo changes, trampled surfaces have significantly lower surface temperatures than untrampled surfaces. Mid-day temperatures in SE Utah in June and July show air temperatures averaged 39°C and bare sand 52°C, while dark crusted surfaces averaged 62°C. In the winter, surface temperatures of welldeveloped crusts are up to 14°C higher than ambient air temperatures (Belnap, 1995).



Figure 2 Threshold friction velocity (TFV) and sediment production measured on undisturbed and disturbed surfaces in Joshua Tree National Park, California, USA. Seven of the eight control sites have TFV above the highest recorded wind speeds; seven of the eight disturbed sites have TFV below recorded wind speeds. Sediment production is increased $35 \times$ with disturbance (Belnap et al., unpublished).

Surface temperatures can regulate many ecosystem functions. Nitrogen and carbon fixation are heavily temperature dependent, with lower temperatures resulting in lowered activity levels. Altered soil temperatures affect microbial activity, plant nutrient uptake rates and soil water evaporation rates. Soil temperatures affect seed germination time and seedling growth rates for vascular plants. Timing of these events is often critical in deserts, and relatively small delays can reduce species fitness and seedling establishment which may eventually affect community structure (Bush and Van Auken, 1991). Food and other resources are often partitioned among ants, arthropods and small mammals on the basis of surface temperature-controlled foraging times (Doyen and Tschinkel, 1974; Crawford, 1991; Wallwork, 1982). Many small desert animals are weak burrowers, and soil surface microclimates are of great importance to their survival (Larmuth, 1978). Consequently, altering surface temperatures can affect nutrient availability and community structure for many desert organisms, thus increasing susceptibility to desertification.



Figure 3 Vulnerability and recoverability of biological soil crusts depend on gradients of site stability, disturbance regimes, and effective precipitation. Crusts at sites with greater stability, lower disturbance frequency and/or intensity, and greater effective precipitation, will be less impacted (dark shading) than sites with lower stability, higher disturbance frequency and/or intensity, and less effective precipitation (light shading). Similarly, recovery time is faster (dark shading) in areas of low vulnerability, and slower (light shading) where vulnerability is higher.

RECOVERY FROM DISTURBANCE

Natural recovery rates: Recovery rates are related to the type, timing, and intensity of disturbances present in the evolutionary history of a given microflora. For instance, crusts in regions that evolved with large ungulate herds (e.g., the US Great Plains, eastern Africa) have a different flora than crusts in areas that evolved with low levels of disturbance from hooved animals (e.g., most hot deserts, US Colorado Plateau), and have a different response to disturbance (Mack and Thompson, 1982). Recovery from disturbance appears to parallel levels of evolutionary soil disturbance. For instance, experimentally-applied disturbances in US deserts show the Sonoran and Chihuahuan deserts have much faster recovery than disturbance in the Mojave and Colorado Plateau deserts (Belnap, unpubl. data). It may be that surfaces that did not evolve with disturbance may depend more heavily on soil surface integrity for natural ecosystem functioning than other regions. As a result, these deserts may be more

negatively affected by soil surface disturbances than regions that evolved with higher levels of surface disturbance, though much research remains to be done.

Recovery rates of cyanobacterial-lichen soil crusts depend on the type and extent of disturbance, the availability of nearby inoculation material, as well as on the temperature and moisture regimes that follow disturbance events (Fig. 3). Estimates of time for visuallyassessed recovery have varied from 5 to 100 years (Harper and Marble, 1988; Johansen 1993; Ladyman and Muldavin, 1996). However, it has been shown that many components of recovery can not be assessed visually (Belnap, 1993). Assuming linear recovery rates, recovery in SE Utah is estimated at 15 years for cyanobacterial biomass, 45-85 years for lichen cover, and 200 years for moss cover in scalped 0.25 m² plots surrounded by well-developed crusts. Lichen recovery in some plots in the Mojave Desert, assessed after 50 years, show recovery times of over 1000 years. Since recovery time is dependent on presence of nearby inoculant, larger disturbed areas will take longer to recover.

Nitrogenase activity recovery appears to be quite slow. In scalped areas on the Colorado Plateau, no nitrogenase activity was detectable after 9 years and N content of soils was still much lower when compared to adjacent control plots. In areas disturbed with 4-wheel drive vehicles, no recovery could be documented after 2 years (Belnap, 1996). Using isotopic ratios of N, soil and plant N and nitrogenase activity levels were found to be significantly lower in an area that had been released from livestock grazing for 30 years when compared to an area that was never grazed (Evans and Belnap, 1999). These data suggest that negative effects on nitrogen dynamics may persist in systems for extended, but variable, periods of time after disturbance cease.

Restoration of normal surface albedos and temperatures will depend on the restoration of cyanobacteria, lichens and mosses. While cyanobacteria form a dark matrix in which other components are embedded, dark mosses and lichens contribute up to 40% of the cover in an undisturbed crust in SE Utah (Belnap, 1993). Consequently, recovery of surface albedo characteristics in severely disturbed areas could take up to 250 years for even very small areas.

Assisted recovery: The use of inoculants to speed up recovery of these crusts has been reported by several authors (St. Clair et al., 1986; Tiedmann et al., 1980; Ashley and Rushforth, 1984; Belnap, 1993). Inoculation has been shown to significantly hasten crustal recovery.

CONCLUSION

Unfortunately, the increasing activities of man in desert areas are often incompatible with the wellbeing of biological soil crusts. The cyanobacterial fibers that confer such tensile strength to these crusts are no match for the compressional stresses placed on them by vehicles or trampling. Crushed crusts contribute less nitrogen and organic matter to the ecosystem. Impacted soils are left highly susceptible to both wind and water erosion. Raindrop erosion is increased, and overland water flows carry detached material away.

Relatively undisturbed biological soil crusts can contribute a great deal of stability to otherwise highly erodible soils. Unlike vascular plant cover, crustal cover is not reduced in drought, and unlike rain crusts, these organic crusts are present year-round. Consequently, they offer stability over time and in adverse conditions that is often lacking in other soil surface protectors. Unfortunately, disturbed crusts now cover vast areas as a result of ever-increasing recreational and commercial uses of these semi-arid and arid areas.

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Wind erodibility of soils at Fort Irwin, California (Mojave Desert), USA, before and after trampling disturbance: implications for land management

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Abstract

Recently disturbed and 'control' (i.e. less recently disturbed) soils in the Mojave Desert were compared for their vulnerability to wind erosion, using a wind tunnel, before and after being experimentally trampled. Before trampling, control sites had greater cyanobacterial biomass, soil surface stability, threshold friction velocities (TFV; i.e. the wind speed required to move soil particles), and sediment yield than sites that had been more recently disturbed by military manoeuvres. After trampling, all sites showed a large drop in TFVs and a concomitant increase in sediment yield. Simple correlation analyses showed that the decline in TFVs and the rise in sediment yield were significantly related to cyanobacterial biomass (as indicated by soil chlorophyll a). However, chlorophyll a amounts were very low compared to chlorophyll a amounts found at cooler desert sites, where chlorophyll a is often the most important factor in determining TFV and sediment yield. Multiple regression analyses showed that other factors at Fort Irwin were more important than cyanobacterial biomass in determining the overall site susceptibility to wind erosion. These factors included soil texture (especially the fine, medium and coarse sand fractions), rock cover, and the inherent stability of the soil (as indicated by subsurface soil stability tests). Thus, our results indicate that there is a threshold of biomass below which cyanobacterial crusts are not the dominant factor in soil vulnerability to wind erosion. Most undisturbed soil surfaces in the Mojave Desert region produce very little sediment, but even moderate disturbance increases soil loss from these sites. Because current weathering rates and dust inputs are very low, soil formation rates are low as well. Therefore, soil loss in this region is likely to have long-term effects. Published in 2006 by John Wiley & Sons, Ltd.

Keywords: biological soil crusts; cyanobacteria; desert; soil aggregate; wind erosion; soil erosion

Introduction

Wind movement of soil particles occurs when wind forces overcome the ability of stabilizing factors to hold the soil surface in place. Factors that stabilize soil surfaces include vascular plant materials (both living and dead), rocks, soil characteristics (e.g. high salt or calcium carbonate content, high clay/silt content, soil aggregates), physical crusts, and the cyanobacteria, lichens and mosses found in biological soil crusts. In deserts, spaces between vascular plant cover are large, the cover of plant litter is low, and most plant roots avoid the dry conditions found at the soil surface. Thus, vegetative matter plays a lesser role in soil protection in deserts relative to other ecosystems. Rocks also protect underlying soils, but in dryland areas where rock cover is low, soils depend on physical factors and biological soil crusts for protection and thus stability (Gillette *et al.*, 1980; Musick, 1998).

Physical crusts, mostly formed in soils with high salt content and fine materials, can protect soils from wind erosion. Biological soil crusts occur on almost all soil types and can cover up to 70 per cent of the soil surface in

desert regions, and often occur on top of physical crusts (Belnap *et al.*, 2003). Polysaccharides secreted by crust organisms bind soil particles together, forming a cohesive crust on the soil surface that resists both wind and water erosion (Belnap, 2003; Belnap *et al.*, 2003). These polysaccharides also contribute to soil aggregate structure, another component critical in reducing soil erosion. Sandy soils are inherently more erodible than fine-textured soils, as they have less salt, clay and silt to enhance physical crusting and soil aggregation. Therefore, sandy soils in deserts are more dependent on rocks and biological soil crusts for surface protection than other soil types (Williams *et al.*, 1995; Leys and Eldridge, 1998).

All these soil surface protectors are highly vulnerable to the compressional and shear forces generated by off-road vehicles (e.g. four-wheel drive trucks, all-terrain vehicles, military vehicles) and to trampling by livestock and humans (reviewed in Belnap and Eldridge, 2003). Physical and biological soil crusts are crushed, rocks are pushed beneath the surface, and soil aggregate structure is lost. Once soils are destabilized, loss of soil fines can reduce site productivity, as plant-essential nutrients are often bound to fine particles, and reduce the often already low soil water-holding capacity. Worldwide, windborne sediments are rapidly increasing as human utilization of arid and semiarid lands increases (Goudie, 1978; Kovda, 1980; Tsoar and Pye, 1987).

Replacement of lost soil fines via newly weathered material is slow in deserts, due to low rainfall and infrequent freeze-thaw events (Dregne, 1983). Dust deposition, a main source of soil fines in deserts, is also quite low in most regions not immediately adjacent to large dust sources (Danin and Yaalon, 1982; Reynolds *et al.*, 2001). When soils are disturbed, loss rates may often far exceed deposition (Gillette *et al.*, 1980; Offer *et al.*, 1992; Belnap and Gillette, 1997, 1998; Reynolds *et al.*, 1998). Therefore, land managers in semiarid and arid regions have long been interested in ways to reduce soil loss. To aid in this effort, we used a wind tunnel and experimental human trampling to examine factors influencing wind erosion at Fort Irwin, California, a military tank training facility located in the centre of the Mojave Desert.

Methods

Site description

This experimental study was located on lands contained within and adjacent to Fort Irwin, near Barstow, California, USA. Average annual precipitation at the sites is 101 mm. Total precipitation during the May 1999–April 2000 experimental period was 46 mm, with 23 mm occurring during the four months immediately preceding the experiment. The dominant vegetation at all the sites was *Larrea tridentata* and *Ambrosia dumosa*.

We chose three 'control' sites (C1–3) that were in areas currently protected from recent military training, but that had been disturbed in the historic past (>20 years) by military manoeuvres (tanks, ground troops, wheeled vehicles). We also chose three other sites (D1–3) that had been recently disturbed (<3 years) by military manoeuvres. (However, high winds prevented measurements from being conducted at D3, one of the selected disturbed sites, and thus no data are presented for this site.) Sites were carefully matched for similar topographic position and soils. All sites were covered with cyanobacterial soil crusts, with <1 per cent lichen cover at any of the sites. No vesicular horizons were observed at or below the soil surface. Four blocks of plots were designated for sites C1, C3 and D2 and six blocks for sites C2 and D1, for a total of 24 blocks. Within each block, two plots were designated, of which one was randomly chosen for trampling and the other left untrampled. This resulted in a total of 48 plots being used for this experiment.

Ground cover and soil characterization

Ground cover measures and soil characterizations were estimated in all 48 plots. Cover of rocks (>1 mm, by size class), plant litter, soil fines (expanse of particles less than 1 mm diameter), and cyanobacteria in the interspaces between plants were estimated with eight individual line transects per plot, spaced evenly over the wind tunnel's footprint and taken prior to wind measurement. A clear plastic ruler was placed at a 45° angle from the wind direction. The length occupied by the first 15 occurrences of any of the above variables was measured to the nearest 1 mm. This resulted in total transect length beneath the tunnel being 213-800 mm per wind tunnel footprint. For characterization of the soils at the site, ten samples of surface (0–0.5 cm) and subsurface (0–10 cm) were randomly collected from each plot and composited into one surface and one subsurface sample per plot. Surface soils were analysed for chlorophyll *a*, an indicator of cyanobacterial biomass. For this analysis, samples were kept cool and dark until they reached the laboratory. Samples were then extracted with dimethylsulphoxide (DMSO) in the dark for 45 minutes at 65 °C (Ronen and Galun, 1984), shaken, and centrifuged. The supernatant was immediately placed in a Turner Designs Inc. fluorometer,



Untrampled

Trampled

Figure 1. Photographs showing untrampled and trampled plots. This figure is available in colour online at www.interscience.wiley.com/journal/espl

where fluorescence, which is proportional to the concentration of the analyte, was measured. Fluorescence values were compared to a calibration curve obtained using commercially purchased standards of various concentrations of purified chlorophyll *a* dissolved in DMSO.

The 0–10 cm soils were analysed for soil texture. Clay was determined using the hydrometer method after dispersal with sodium hexametaphosphate (Gee and Bauder, 1986). The sand fraction was determined by washing the dispersed sample through a 53- μ m sieve. Silt was determined by adding the sand and clay fractions and subtracting that total from the complete sample. The sand fraction was further divided into the following fractions by sieving for the near-surface (0–10 cm) samples: 0.05–0.1 mm, 0.1–0.25 mm, 0.25–0.5 mm, 0.5–1 mm, and 1–2 mm.

Soil stability was determined using a modified field wet aggregate stability method described in Herrick *et al.* (2001). At nine points within each plot, soil samples of uniform dimensions (2–3 mm thick, 6–8 mm on each side) were collected from the surface (0–0.3 cm deep, which included biological and physical soil crusts) and subsurface (2-0–2.5 cm deep). The collected samples were placed on a screen, soaked in water a short time, and then dipped slowly up and down in the water, with the number of dips required to break apart the sample recorded as an index of the wet aggregate stability of the sample.

Trampling

Personnel using military issue lug-soled boots applied the trampling disturbance, resulting in a churned soil surface (Figure 1). Trampling of this kind is a common disturbance type at this location and throughout the Mojave Desert. Two people (c. 68 kg each) jogged through the plots 50 times, with a third observer counting passes and ascertaining that the entire plot had been evenly trampled.

Wind measurements

A portable, open-bottomed wind tunnel, $150 \text{ mm} \times 150 \text{ mm}$ cross-section by 2.4 m length, was used to generate a variable-speed turbulent boundary layer over the desert surface (Figure 2; Gillette, 1978). The tunnel used a 5:1 contraction section with a honeycomb flow straightener and a roughly conical diffuser attached to the working section. Wind speed data were measured twice using a Pitot tube at seven heights (0, 0.318, 0.635, 1.27, 2.54, 5.08, 7.62 and 10.16 cm) above the soil surface, midway across the end of the working section. The Pitot tube was calibrated prior to making measurements on each plot and corrected for temperature and pressure changes each day.

The threshold friction velocity (TFV) was defined as the velocity at which fragments were initially detached from the soil surface. Wind speed inside the wind tunnel was gradually increased until forward particle movement was observable across the soil surface. The wind-flow velocity was then recorded at the soil surface and at the seven heights to create an air-flow profile. Wind speeds were then increased until surface integrity of the



Figure 2. A photograph of the wind tunnel set-up, with arrows indicating where the air enters and where the sediment is captured. This figure is available in colour online at www.interscience.wiley.com/journal/espl

crusts was compromised, as indicated by the removal of soil particles, at which point an additional wind profile was recorded. Data for the mean horizontal wind velocity U (cm s⁻¹) versus height z (mm; wind profile data) were fitted to the function for aerodynamically rough flow (Priestley, 1959) using a non-linear least squares routine:

$$U_{*t} = kz \, \left(\mathrm{d}U_t / \mathrm{d}z \right)$$

where U^* t is friction velocity, and k is Von Karman's constant.

Immediately following the measurement of the final air-flow profile, the wind speed inside the tunnel was increased until air-flow velocity was 1180 cm s⁻¹. This speed represented a reasonable approximation of high spring wind speeds at this location. Wind speeds of 2300 cm s⁻¹ repeatedly occur near our site (Mojave River Sink, California weather station, www.wrcc.dri.edu). However, those wind speeds are measured at 200 cm off the ground, while ours were at 10 cm off the ground. The wind tunnel was run for 3 minutes and then stopped. During this time, all the sediment blown off the soil surface was trapped in or in front of a pre-weighed fibreglass filter (with a pore size of 1 μ m) located at the far end of the tunnel. Following the wind tunnel run, sediment in front of the filter was collected and weighed. The pre-weighed filter was then re-weighed, and the original filter weight subtracted to obtain the weight of the sediment retained within the filter. The two sediment weights were then combined to obtain the final sediment yield value. One wind tunnel run was performed in each plot, resulting in four to six values for the experimentally applied human trampled plots and four to six values for the undisturbed plots. These four to six values were then averaged to give two mean values (newly disturbed, undisturbed) for each site.

Data analysis

Data were log-transformed to achieve normality. A mixed-effects nested design model ANOVA test was used to determine if there was a significant effect of site type (control versus recently disturbed) on TFV, chlorophyll *a* content, soil surface stability, and sediment production. Paired *t*-tests were used to determine whether there was a significant effect of trampling within a site. Spearman's rank-order correlation coefficients and linear regressions were used to test the relationship between selected soil variables and TFV or sediment production. Stepwise multiple linear regression was used to determine the factors most responsible for wind erosion at the sites. Means were considered significantly different when P < 0.05. All tests were done using SPSS version 12.0 (SPSS, 2003).

Wind erodibility of soils

Sand fractions (%)									
indicate	e significant diff	erences acros	s sites at $P < 0$	05 Values are mean	ns \pm standard ei	rror			
Table	 Texture of s 	urface soils (C	–0·5 cm) from	i the control and p	reviously distur	bed sites. For ea	ch variable, d	ifferent letters	

Site	Sand (%)	Silt (%)	Clay (%)	Very coarse	Coarse	Medium	Fine	Very fine
CI	86·I ± 0·9 ^b	7·9 ± 0·7 ^b	6.0 ± 0.4^{ab}	$38.4 \pm 2.4^{\circ}$	31·2±0·9°	$ 6.5 \pm . ^{a}$	8.9 ± 0.5^{a}	4.9 ± 0.3^{a}
C2	$80 \cdot 1 \pm 1 \cdot 0^{a}$	12.8 ± 1.0°	$7 \cdot 1 \pm 0 \cdot 2^{bc}$	38·2 ± 1·3°	27.6 ± 0.7^{bc}	$ 6 \cdot \pm 0 \cdot 7^{a}$	10.5 ± 0.6^{ab}	7.7 ± 0.7^{ab}
C3	84.0 ± 0.9^{ab}	$7.7 \pm 0.2^{\circ}$	$8.3 \pm 0.8^{\circ}$	31.5 ± 2.5 ^{bc}	$23.9 \pm 0.4^{\circ}$	9·4 ± · ^{ab}	6·4 ± · ^{bc}	$8.8 \pm 0.3^{\circ}$
DI	87·7 ± 1·2 ^{bc}	$5 \cdot 1 \pm 0 \cdot 8^{ab}$	$7 \cdot 1 \pm 0 \cdot 4^{bc}$	24.5 ± 2.0^{ab}	24·4 ± 1·1 ^b	23·I ± 0·7ªb	20·I ± 0·3°	7.9 ± 0.2^{ab}
D2	92·5 ± 0·8°	2.7 ± 0.7^{a}	4.8 ± 0.4^{a}	18.9 ± 2.1^{a}	$ 3\cdot \pm \cdot ^a$	28·I ± 3·7 ^b	30.8 ± 2.8^{d}	9· ± ·3⁵

Table II. Means \pm standard error of chlorophyll *a* and soil stability values on untrampled surfaces. Chlorophyll *a* content, surface stability, and subsurface stability were all significantly higher in control compared to disturbed sites

Site	Chlorophyll <i>a</i> (µg/g soil)	Surface soil stability (0–0·3 cm)	Subsurface soil stability (2·2–2·5 cm)		
CI	3·23 ± 0·39	3·8 ± 0·5	3.5 ± 0.4		
C2	4.15 ± 0.36	5·7 ± 0·1	2.8 ± 0.2		
C3	2·4 ± 1·08	4.9 ± 0.4	1.5 ± 0.2		
DI	0.44 ± 0.18	I •6 ± 0• I	·4 ± 0·		
D2	0.29 ± 0.09	0.4 ± 0.3	1.2 ± 0.2		

Results

Soil texture

The disturbed sites had, on average, about 7 per cent more sand than the control sites, while having almost 6 per cent less silt (Table I). It is likely that these differences in soil texture are a result of the differential loss of silts from the recently disturbed sites via wind and water erosion.

Site effects – untrampled surfaces

Cyanobacteria crust cover could not be reliably quantified, as cyanobacterial biomass was so low it was not visually distinguishable from bare soil, and cyanobacteria also occurred under the many tiny rocks present on the soil surface. Therefore, we relied on chlorophyll measures to indicate the quantity of crust organisms present. When values for control (untrampled) sites were pooled and compared to the pooled values for recently disturbed sites, the control sites had significantly higher values than the recently disturbed sites for chlorophyll *a* (means = $3 \cdot 3$ versus $0 \cdot 37 \, \mu g/g$ soil, respectively; Table II), surface soil stability (means = $4 \cdot 8$ versus $1 \cdot 0$ units, respectively; Table II), subsurface stability (means = $2 \cdot 6$ versus $1 \cdot 3$ units, respectively; Table II), TFVs (means = $423 \cdot 6$ versus $154 \cdot 2$ cm s⁻¹; Figure 3), and rock cover (means = $63 \cdot 6$ versus $48 \cdot 2$ per cent; Figure 4). Control plots had lower sediment yield (means = $0 \cdot 04$ versus $0 \cdot 50$ g m⁻² s⁻¹; Figure 5) than the recently disturbed sites. Chlorophyll *a* and surface stability were significantly related ($R^2 = 0.80$, P < 0.001) when all sites were pooled.

Effects of trampling

Rock cover declined at all sites except D1 after trampling (Figure 4). Because trampling destroyed the surface stability of the plots, this variable was not remeasured after disturbance. Trampling significantly decreased TFVs at all sites, except at D2, when compared to the untrampled plots (the percentage decline in TFVs at C1 = 84 per cent, C2 = 72 per cent, C3 = 50 per cent, D1 = 43 per cent). Trampling reduced TFVs to equally low levels at all sites, regardless of previous disturbance history (Figure 3). The percentage decline of TFVs caused by trampling was more pronounced at the control sites (trampled = 50 per cent reduction, untrampled = 84 per cent reduction) compared to the recently disturbed sites (trampled = 24 per cent reduction, untrampled = 43 per cent). Untrampled sites showed a positive



Figure 3. Mean \pm standard error of TFV before trampling (dark bars) and after trampling (light bars) at control and recently disturbed sites. Statistical comparisons were done with log-transformed values. A significant difference between untrampled and trampled surfaces at the same site is indicated by an asterisk (P < 0.05). This figure is available in colour online at www.interscience.wiley.com/ journal/espl



Figure 4. Average rock cover (rocks > 1 mm) before trampling (dark bars) and after trampling (light bars) at the control and recently disturbed sites. A significant difference between untrampled and trampled surfaces at the same site is indicated by an asterisk (P < 0.05). This figure is available in colour online at www.interscience.wiley.com/journal/espl

relationship between chlorophyll *a* and TFVs ($R^2 = 0.58$, P = 0.01). However, this relationship was lost immediately after trampling ($R^2 = 0.01$, P = 0.66).

Sediment production increased significantly with trampling at all sites except C1 (Figure 5). The amount of sediment lost with trampling from the recently disturbed training sites was much higher (trampled = 1.98 g/m^2 , untrampled = 0.50 g/m^2) than the amount lost from the control sites (trampled = 0.34 g/m^2 , untrampled = 0.04 g/m^2). A significant but low, negative relationship between chlorophyll *a* and sediment production was present, before trampling ($R^2 = 0.35$, P < 0.0001) and moderate after trampling ($R^2 = 0.56$, P < 0.0001).

Stepwise multiple linear regression analysis including all measured variables at all sites showed untrampled TFVs were best predicted by the fine sand fraction, rock cover and subsurface soil stability combined ($R^2 = 0.91$, P < 0.034; Table III). The TFV after trampling was weakly predicted by clay content ($R^2 = 0.27$, P < 0.02). Sediment yield at the untrampled sites was best predicted by the coarse and medium sand fractions and subsurface soil stability combined



Figure 5. Mean \pm standard error of sediment produced from plots before trampling (dark bars) and after trampling (light bars) at control and recently disturbed sites. Statistical comparisons were done with log-transformed values. A significant difference between untrampled and trampled surfaces at the same site is indicated by an asterisk (P < 0.05). This figure is available in colour online at www.interscience.wiley.com/journal/espl

Table III.	Stepwise	multiple line	ear regression	models t	hat best p	predict T	FVs and	sediment	yield	among all	measured	variables	at all
sites comb	oined												

Dependent variables	Predictors	Model coefficients	R ²	Р
Untrampled TFV	Intercept	284.01		0.021
	Fine sand	-13.95	0.81	0.001
	Rock cover	235.37	0.82	0.027
	Subsurface slake	57.73	0.91	0.034
Trampled TFV	Intercept	-55.21		0.43
	Clay	24.69	0.27	0.02
Untrampled sediment yield	Intercept	52.53		0.67
	Coarse sand	-16.86	0.66	<0.0001
	Medium sand	13.74	0.76	<0.0001
	Subsurface slake	71.85	0.88	0.002
Trampled sediment yield	Intercept	53.44		0.20
	Fine sand	3.78	0.82	0.3
	Medium sand	3.94	0.86	0.02
	Coarse sand	-5.02	0.90	0.03

 $(R^2 = 0.88; P < 0.002)$. Sediment yield from trampled sites was best predicted by the coarse, medium and fine sand fractions $(R^2 = 0.90)$, with fine sand fractions being the most important determinant $(R^2 = 0.82)$.

Discussion

Polysaccharides extruded by biological soil crust organisms entrap and bind soil particles together, creating linked, large soil aggregates (e.g. Van den Ancker *et al.*, 1985; Danin *et al.*, 1989; Chartes, 1992; Belnap and Gardner, 1993; Eldridge and Greene, 1994), and moving these larger aggregates requires greater wind velocity than that required to move single soil particles (Gillette *et al.*, 1980; Marticorena *et al.*, 1997). Therefore, many studies have shown that the presence of biological soil crusts reduces soil erosion by wind (e.g. Dulieu *et al.*, 1977; Van den Ancker *et al.*, 1985; Tsoar and Møller, 1986; Danin *et al.*, 1989; Pluis, 1994; Williams *et al.*, 1995; Belnap and Gillette, 1997; Marticorena *et al.*, 1997; Belnap and Gillette, 1998; Leys and Eldridge, 1998). Even chemically killed crusts, if left undisturbed so that the polysaccharide material stays intact, appear to protect the soil surface from erosion at least in the short term (after which polysaccharide material probably degrades; Williams *et al.*, 1995). Similarly, our results show that wind erosion

decreases (as indicated by a decline in TFVs and an increase in sediment production) as biological soil crust biomass (as indicated by chlorophyll *a*) increases. Other factors can also be important in reducing wind erosion. In this study, increased rock cover, coarser soil particles, and subsurface soil stability (an indication of the inherent stability of the soil) also significantly decreased wind erosion. While physical crusts can also be important in stabilizing soils (Eldridge and Leys, 2003), we did not directly measure them and so are unable to quantitatively assess their importance at these sites.

When all factors were considered together, however, soil texture was the most important in predicting the wind erodibility of these sites. Greater amounts of fine sand in surface soils resulted in greater vulnerability to wind erosion, as it was related to lower TFV and greater sediment yield. The presence of coarse sands, on the other hand, reduced the amount of sediment produced, as coarse sand particles are large and difficult to move. This result appears to contrast with other studies on desert soils where biological crust cover and condition were the deciding factors in TFV and sediment production levels (e.g. Williams *et al.*, 1995; Belnap and Gillette, 1997, 1998).

A likely cause of this difference among studies was the amount of cyanobacteria and lichens present at the different sites. The biomass of the biological crust organisms present reflects the climate at the site, the time since past disturbance, and the severity of that disturbance. In hot deserts with very low precipitation, biological soil crusts are dominated by a low amount of cyanobacteria. The Fort Irwin sites, with a maximum of 0.006 mg chlorophyll *a* per gram soil, had close to an order of magnitude lower cyanobacterial biomass compared to many other sites in the Mojave Desert (maximum 0.046 mg chlorophyll *a* per gram soil) and sites in SE Utah (maximum 0.122 mg chlorophyll *a* per gram soil). Thus, a threshold of cyanobacterial biomass is likely required before it becomes the major determinant of site susceptibility to wind erosion. In addition, the Fort Irwin sites lacked soil lichens. Belnap and Gillette (1998) showed that lichens conferred much more stability to soils than cyanobacterial cover. This points out the importance of carefully defining the flora and biomass of biological soil crusts before broad statements are made regarding their role in stabilizing soils.

Soils are often much more susceptible to wind erosion after disturbance (reviewed in Belnap, 2003; Belnap and Eldridge, 2003). Cyanobacterial filaments, lichens and mosses are brittle when dry and crush easily under compressional or shear forces incurred by activities such as trampling or vehicular traffic. Such disturbances also crush physical crusts, subsurface soil aggregates, and the connections between aggregates, lowering the wind force required to detach particles from the soil surface. In addition, rock cover is often decreased as surface rocks are pushed below into the soil, leaving surface soils less protected (Belnap and Warren, 2002). In this study, we observed



Figure 6. An illustration of how this study can be used to inform land management decisions in areas where biological soil crust development is low. To determine whether a soil-disturbing use is to be allowed at similar sites in the Mojave, the manager would need to know the soil texture at the site and the acceptable limits of soil loss. Using the regression results that best predict sediment yield from trampled sites (Table III), a manager can then draw a line (Line A) from the point of acceptable soil loss to meet the regression line. At the point where Line A intersects the regression line, a vertical line (Line B) is drawn down to the *x*-axis. The point at which Line B intersects the *x*-axis is the amount of fine sand that can be present before the acceptable level of soil loss is exceeded.

Wind erodibility of soils

large differences in TFVs and sediment yield at the recently disturbed sites when compared to the control sites. This study also showed that new disturbance (via trampling in this case) had a greater effect at 'control' sites when compared to sites that had been recently disturbed. This finding contrasts with a study in southeastern Utah, USA, where disturbance applied to relatively well-developed crusts had less effect on TFVs than disturbance to crusts recovering from recent impact (Belnap and Gillette, 1997).

Land managers often need to decide whether to permit certain types of land use activities. In deserts, loss of soil stability, and the resultant loss of soil, is of concern. Therefore, ways to predict the susceptibility of soil surfaces to wind erosion are of value to managers. The results from this study indicate that at least 'ballpark' predictions are possible, as we obtained a linear relationship between sediment yield and site factors. Using the regression line of fine sand and sediment yield obtained by this study on trampled surfaces, a manager could set acceptable wind erosion limits and judge the vulnerability of a site accordingly, depending on the soil texture (Figure 6).

However, utilizing such an approach will require land managers to establish an upper limit on allowable soil loss over a given time period. Unfortunately, there is little information on what level might be appropriate. Eldridge and Leys (2003) suggest losses over 5 g soil/m² soil surface are to be avoided. This study and recent studies at both the plot (Belnap *et al.*, unpublished work) and landscape level (Chavez *et al.*, unpublished work) throughout the Mojave Desert show that most soil surfaces in this desert produce very little sediment unless they are disturbed, regardless of lithology, surface age, landscape position or sediment type (e.g. alluvial, aeolian). The exceptions are playa edges, sand dunes and lake basins that continue to receive sediment deposits (e.g. Owens Lake). Thus, most soil surface-disturbing activities in the Mojave Desert will accelerate soil losses above natural background levels. Dust input (Reheis, 2003) and rock weathering (Dregne, 1983) rates are currently very low. Therefore, soil formation rates are low as well. Thus, soil losses in desert regions should be considered irreplaceable within the time frame of most management plans and actions. All US land management agencies have a mandate to allow use while sustaining the potential of the land to recover from that use (e.g. National Park Service's Organic Act, Bureau of Land Management's National Environmental Protection Act). Given the vulnerability of Mojave Desert soils to wind erosion after soil surface disturbance and the soil-disturbing nature of most types of land use, maintaining this mandated balance will be difficult, if not impossible.

Conclusion

All previous studies, as well as this one, have demonstrated that biological soil crusts play a role in reducing soil loss by wind. However, the extent to which this occurs differs among deserts. In hot deserts, soil texture can play a dominant role in the susceptibility of a soil surface to wind erosion. This is in contrast to sites where higher precipitation allows higher biological crust biomass to develop and where this biomass is the main determinant of soil erosion rates.

When surfaces are newly disturbed, their vulnerability to wind erosion increases dramatically. The biological and physical crusts are crushed, soil aggregate structure is destroyed, and rocks are pushed below the surface. In this study, sites with recent (<3 years) previous disturbance were more vulnerable to wind erosion than those with a more distant (>20 years) disturbance history. Because current dust inputs are generally low in the Mojave Desert, accelerated soil losses due to surface disturbance are unlikely to be replaced in the near future.

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The potential roles of biological soil crusts in dryland hydrologic cycles

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Abstract:

Biological soil crusts (BSCs) are the dominant living cover in many drylands of the world. They possess many features that can influence different aspects of local hydrologic cycles, including soil porosity, absorptivity, roughness, aggregate stability, texture, pore formation, and water retention. The influence of biological soil crusts on these factors depends on their internal and external structure, which varies with climate, soil, and disturbance history. This paper presents the different types of biological soil crusts, discusses how crust type likely influences various aspects of the hydrologic cycle, and reviews what is known and not known about the influence of biological crusts on sediment production and water infiltration versus runoff in various drylands around the world. Most studies examining the effect of biological soil crusts on local hydrology are done by comparing undisturbed sites with those recently disturbed by the researchers. Unfortunately, this greatly complicates interpretation of the results. Applied disturbances alter many soil features such as soil texture, roughness, aggregate stability, physical crusting, porosity, and bulk density in ways that would not necessarily be the same if crusts were not naturally present. Combined, these studies show little agreement on how biological crusts affect water infiltration or runoff. However, when studies are separated by biological crust type and utilize naturally occurring differences among these types, results indicate that biological crusts in hyperarid regions reduce infiltration and increase runoff, have mixed effects in arid regions, and increase infiltration and reduce runoff in semiarid cool and cold drylands. However, more studies are needed before broad generalizations can be made on how biological crusts affect infiltration and runoff. We especially need studies that control for sub-surface soil features such as bulk density, micro- and macropores, and biological crust structure. Unlike the mixed effects of biological crusts on infiltration and runoff among regions, almost all studies show that biological crusts reduce sediment production, regardless of crust or dryland type. Published in 2006 by John Wiley & Sons, Ltd.

KEY WORDS arid; desert; infiltration; microbiotic crusts; runoff; semiarid; water cycles; water erosion

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INTRODUCTION

It is well known that many soil factors influence local hydrologic regimes. The most often discussed variables controlling the dynamics of sediment production and runoff versus infiltration include factors such as soil texture, degree of soil aggregation, soil structure, plant and plant litter cover, rock cover, and physical crusting. Less understood and discussed is how the presence of biological soil crust (BSC) communities (consisting of soil surface-dwelling cyanobacteria, green algae, microfungi, bacteria, lichens, and bryophytes) influences local hydrologic dynamics. BSCs can profoundly influence many soil surface characteristics known to affect local hydrologic patterns (reviewed in Warren, 2003a,b), including soil texture, aggregation, cohesiveness, absorptivity, roughness, cracking, micro- and macropore formation, water retention, and patterns of infiltration, as well as the composition and architectural structure of vascular plant communities. Little is known about the relative importance of these features among themselves or relative to sub-surface soil characteristics, as

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few experiments have utilized the same equipment, measured the same variables across sites, or successfully distinguished the influence of crusts from other site variables.

This paper reviews what is known about how biological crusts influence soil surface features and local hydrologic processes and presents a conceptual model for how the modification of soil surface features likely influences local hydrologic patterns. It is hoped that this discussion and the conceptual framework presented will provide structure and stimulus for a more systematic investigation into how biological crusts affect local hydrologic cycles.

AN OVERVIEW OF BIOLOGICAL SOIL CRUSTS

Biological soil crusts are created by an intimate association between soil particles and cyanobacteria, green algae, microfungi, bacteria, lichens, and bryophytes which live within, or immediately on top of, the uppermost millimetres of soil (Belnap and Gardner, 1993). These organisms, and the extracellular polysaccharide materials associated with them, connect soil particles together, creating a coherent living crust that covers the surface of many dryland regions. Biological soil crusts have had many names, including cryptogamic, cryptobiotic, microbiotic, and microphytic soil crusts.

Distribution of biological soil crusts

Biological soil crusts organisms have a very wide distribution. They occur on most soil types and in almost all vegetative communities where sunlight can reach the soil surface. They have low moisture requirements and a high tolerance of extreme temperatures and light, thus enabling them to survive under conditions that limit vascular plant growth (Belnap *et al.*, 2003a). Because of these traits, they are often the dominant ground cover in low-productivity environments such as hyperarid, arid, semiarid, sub-humid, alpine, and polar regions, which constitute over 40% of the world's terrestrial land mass (Figure 1). Biological crusts also occur in localized areas in more mesic regions (e.g. pine barrens, serpentine soils, temperate steppe). Only the tropical evergreen rain forests appear to lack BSCs (Büdel and Lange, 2003).

Soils in dryland regions generally have a pH of 7 or greater. This factor, combined with the relatively high potential evapotranspiration (PET) found in these areas, results in the soil surface being mostly dominated by cyanobacteria, lichens, and mosses. Under these conditions, the biomass and cover of green algae, microfungi, and other bryophytes (e.g. liverworts) are quite limited. For this reason, we will only discuss cyanobacteria, lichens, and mosses in the following review. However, when considering the influence of biological crusts on hydrologic processes, the function of green algae and microfungi is similar to cyanobacteria, and the function of other bryophytes is similar to lichens, such as liverworts. Thus, it is not expected that the fundamental principles discussed below will show much change if the more common dryland species are replaced by those found in relatively more mesic areas.

Types of biological soil crusts among climatic regions

The appearance, biomass, and species composition of BSCs vary widely among climatic regimes. These differences in external and internal structure result in distinct crust types, with each type having a different effect on ecological and hydrologic processes. Multiple classification schemes for crust types have been proposed (reviewed in Belnap *et al.*, 2003a). The classification system presented here is based on factors that influence runoff, infiltration, and sediment production and is therefore helpful in discussing how crusts may affect hydrologic function. This system defines four types of biological crust (Figure 2).

Smooth crusts occur in hyperarid hot drylands (e.g. Atacama, Sahara deserts) where soils never freeze and where PET is very high (Figure 2). The crust biota in smooth crusts is dominated by a thin layer of cyanobacteria and fungi that live on or just below the soil surface, with rare pockets of lichens and mosses in specialized microhabitats. Soils are generally young, coarse, and relatively unweathered. When the individual



Approximate equatorial scale 1:115 million

Figure 1. Patterned areas represent regions where biological soil crusts are likely to influence local hydrologic processes. Cumulatively, these lands represent 40% of the Earth's terrestrial surface

soil particles are bound together by the crust biota, the smoothness of the soil surface is increased. Very low moisture availability results in a low biomass and thus low absorptivity of crust organisms, with relatively high soil surface porosity and low surface roughness.

Rugose crusts occur in dryland regions where soils do not freeze, but with lower PET than hyperarid deserts (e.g. low-elevation Sonoran, Mojave, Australian deserts; Figure 2). Rugose crusts are dominated by a thin layer of cyanobacteria and fungi. In drier regions of these deserts, they contain sparse patches of lichens and mosses growing on the relatively even soil surface. As moisture increases within these regions, lichen and moss cover increases as well, although the soil surface still remains fairly flat. Overall low moisture results in moderately low crust biomass, soil surface roughness, and crust absorptivity, whereas soil surface porosity is moderately high.

Pinnacled crusts occur in mid-latitude cool desert regions (e.g. low-elevation Colorado Plateau, midlatitude China deserts, high-elevation Sonoran and Mojave deserts) where soils freeze and PET is lower than in hot deserts (Figure 2). Pinnacled crusts are dominated by relatively thick layers of cyanobacteria with up to 40% lichen and moss cover. This crust type is characterized by strikingly pedicelled mounds formed as soils uplifted by frost heaving are differentially eroded by downward-cutting water. These castle-like mounds can be up to 15 cm high, with thin tips 4-10 mm across. Crust biomass, crust absorptivity, and soil surface roughness are high in this crust type, with relatively low soil surface porosity.

Rolling crusts occur in colder, lower PET regions (e.g. northern Great Basin, high-latitude deserts) than pinnacled crusts (Figure 2). Lichens and mosses heavily dominate these thick crusts. The upward frost heaving of the soil is counteracted by a cohesive, thickly encrusted mat of lichens and mosses. This mat presents an erosion-resistant surface that prevents differential downward cutting, creating a roughened, slightly rolling crust surface. The low PET in these regions allows for very high crust biomass and surface absorptivity, with low soil surface porosity and moderate soil surface roughness.



Figure 2. Classification of biological crust types based on flora and external morphology. The flora of BSCs change with rainfall timing and amount. In hyperarid deserts, biological crusts are dominated by cyanobacteria, whereas in dryland regions with lower PET, they are dominated by lichens and mosses. The external morphology of biological crusts also changes with climate. In hyperarid regions, biological crusts are flat. Decreasing PET and freezing soils increase the surface roughness of crusts

Types of biological soil crusts within a given climatic region

Within a given climatic zone, many factors can influence the external morphology of BSCs. Crusts with similar species and biomass are flatter when they occur on clay and silty soils compared to those on adjacent coarser soils. In soils with weak crystalline structures (e.g. soils derived from calcite and gypsum), extracellular polysaccharide materials combine with the dissolved minerals when soils are wet to create very strong microbial sheaths that are part organic and part inorganic materials. The internal strength of these soils resists winter frost heaving, and they do not form the highly dissected surfaces that may be found in adjacent sandy soils. Cyanobacteria generally dominate soils that are very sandy (>90%), very salty, or have a high content of shrink-swell clays, regardless of the climatic zone. Lichen cover generally increases with an increase in the amount of carbonate, gypsum, and/or silt in the soil (Büdel and Lange, 2003).

In soils with heavy physical crusting, the surface morphology of crusts is primarily controlled by soil physical and chemical characteristics, and the biological components have only a limited effect. If only cyanobacteria are present under these circumstances, the resultant crusts are smooth. If lichens and mosses colonize as well, the slight roughening of the soil surface creates a rugose or rolling crust. Pinnacled crusts seldom form in soils with a high degree of physical crusting.

Internal structure of biological soil crusts

The internal structure of soil crusts varies with the crust flora. Cyanobacteria and fungi, ubiquitous to all crust types, provide most of the cohesive quality of the BSCs. Bare soils are first colonized by large, mobile filamentous cyanobacteria (e.g. *Microcoleus vaginatus*; Figures 3(a), 4) that live 1–4 mm below the soil



Figure 3. (a) *Microcoleus vaginatus* in sandy soils (bar = $10 \mu m$). (b) When wetted (using freeze substitution), sheaths and filaments swell and cover the soil surface (bar = $100 \mu m$). (c) Sheaths adhere firmly to the sand grain surfaces, binding the grains together (bar = $100 \mu m$). (d) Soil aggregate formed by cyanobacterial sheaths (bar = $100 \mu m$). (e) Multiple sheaths wrap around a sand grain, holding it firmly in place (bar = $10 \mu m$). (f) Cyanobacterial sheaths hold together multiple soil aggregates (bar = 5 mm). Images (a) through (e) are scanning electron micrographs of BSCs. Image (f) is a photograph

surface. However, during wet periods, they can cover the soil surface (Figure 3(b)). Later, smaller and less mobile cyanobacteria colonize (e.g. *Nostoc, Scytonema*). These smaller species live on or just below the soil surface, creating layers of species in the soils (Garcia-Pichel and Belnap, 1996; Belnap, 2003a). The sticky, polysaccharide outer sheaths of the cyanobacteria wind throughout the uppermost soil layers (Figure 3(c)), linking soil particles together, forming soil aggregates (Figure 3(d)). These aggregates themselves are then further linked together by cyanobacterial strands (Figure 3(e), (f)).



Successional Sequence

Figure 4. Colonization sequence for biological crust species. Arrows indicate colonization events; the length of the line indicates relative recovery time for each successional group. Species indicative of large filamentous cyanobacteria are *Microcoleus* spp.; for small cyanobacteria, *Nostoc* spp. and *Scytonema* spp.; very early successional lichens, *Collema* spp.; early successional lichens and mosses, *Placidium* spp. and *Pterygoneurum* spp.; mid successional lichens and mosses, *Psora* spp., *Fulgensia* spp.; late successional lichens and mosses, *Acarospora* spp., *Panneria* spp.

Once the soil surface is stabilized by cyanobacteria, lichens and mosses colonize if climate conditions permit (Figure 4). Unlike the soil cyanobacteria, which grow within the soil, lichens and bryophytes have most of their biomass above the soil surface (Figure 5), which protects underlying soils from raindrop impact and resists detachment of particles during overland flow events. Lichens and bryophytes also have anchoring structures (rhizoptae, rhizinae, and rhizomorphs; Poelt and Baumgärtner, 1964; Sanders, 1994) that penetrate down into the soil as deep as 14 mm (Belnap *et al.*, 2003a). In addition, multi-branched, subterranean moss protonemata are interspersed throughout the soil crust matrix. Combined, these structures form a dense, subterranean network of tissue that is intimately connected with soil particles and that strongly contributes to soil stability (Belnap and Gardner, 1993; Belnap, 2003a).

Effects of disturbance and climate change on external morphology and internal structure of crusts

The intensity, type, and time since disturbance can control both the external and internal structure of biological soil crusts. Crustal components are brittle and easily crushed, especially when dry. Once buried, these photosynthetic organisms die. Damage to buried sheath material cannot be repaired, as living cyanobacteria are no longer present to secrete new sheath material. Most soil surface disturbances leave surfaces flattened relative to the previously roughened surface (Figure 2), and early re-colonization is exclusively by the large cyanobacterial species (Figures 3(a), 4). Recovery of both the external and internal structure of crusts occurs in the sequence outlined above, with the final developmental stage determined by climate (Figure 4). Biological soil crust organisms are also sensitive to other types of disturbance, including


Figure 5. Photos of lichens and mosses on desert soil surfaces. Note that both lichens and mosses have substantial tissue above the surface that can completely cover soil pores. Cover can be continuous (a), discontinuously clumped (b), or more evenly, but still discontinuously (c) spread across the soil surface

air pollution, herbicides (Zaady et al., 2004; Belnap et al., 2003b), and climate change, including changes in precipitation (Belnap et al., 2004) and increased air temperatures (Belnap et al., 2006).

BIOLOGICAL CRUSTS CAN INFLUENCE HYDROLOGIC PROCESSES

Soil texture

Relatively unweathered, coarse-textured soils cover large amounts of global dryland surfaces. In these soils, particles deposited by aeolian processes can represent up to 60% of soil fines (Danin and Yaalon, 1982; Reynolds *et al.*, 2001). Airborne silts and clays are trapped by sticky cyanobacterial sheaths, by surface roughness created by biological crusts, and by protruding moss stems and lichen thalli. This results in a thin layer of silt and clay on the soil surface that is often lacking where biological crusts are absent (Verrecchia *et al.*, 1995). Silt and clay particles increase the absorptivity of the soil. However, they can also decrease soil porosity (Brady and Weil, 1996). It is predicted that dust-trapping efficiency will increase with increasing surface roughness, cyanobacterial biomass, and lichen-moss cover. Therefore, the dust-trapping ability of the soil surface is expected to increase in the following order: bare soil < smooth crust < rugose crust < pinnacled crust < rolling crust (Figure 6).

Absorptivity of biological crust organisms

All BSC biota absorb water, but to varying degrees. Cyanobacteria absorb up to 10 times their volume of water and 8–12 times their dry weight (Campbell, 1979; Verrecchia *et al.*, 1995). Water absorption by lichens and mosses varies greatly among species. Gelatinous lichens and mosses can expand their cover and biomass by up to 13 times or more when wetted (Galun *et al.*, 1982), whereas crustose and squamulose lichens absorb smaller amounts of water (Blum, 1973). Mosses can absorb water directly, trap water in specialized leaf structures, and differentially channel water to their stems with special leaf arrangements (Catcheside, 1980).

Crust types vary widely in their thickness. Smooth and rugose crusts tend to be thin, whereas pinnacled and rolling crusts are much thicker, with occasional polysaccharide sheath material or moss anchoring structures found up to 10 cm below the soil surface. Biomass also increases as PET decreases. Therefore, the degree to which biological crusts affect soil absorptivity will depend on crust features as controlled by climatic factors. Unfortunately, crust absorptivity has not been quantified in any systematic way for either individual species or crusts as a mixed community. However, because cyanobacteria, mosses, and lichens all absorb water, it is expected that an increase in biomass and cover of these organisms will increase absorptivity of the crusts. Thus, absorptivity of different soil surface types is expected to increase in the following order: bare soil < smooth crust < rugose crust < pinnacled crust < rolling crust (Figure 6).

Soil surface porosity and the formation of micro- and macropores

Biological crust organisms, by their very presence on the soil surface and by their ability to swell upon wetting, can clog soil pores and thus reduce soil porosity (Avnimelech and Nevo, 1964; Campbell, 1979; Eldridge and Greene, 1994; Verrecchia *et al.*, 1995; Kidron *et al.*, 1999). This is especially true when the crust organisms are concentrated on the soil surface (Figure 3(b)). However, cyanobacteria occur as strands, thus leaving spaces at the soil surface. Therefore, cyanobacteria are less likely to clog pores than lichens and mosses, which are large enough to cover soil pores completely (Figure 5(a)). However, the cover of any of these organisms is seldom continuous (Figure 5(b–c)). Because cyanobacteria occur on the soil surface, high intensity raindrop impact can break apart aggregates formed by the cyanobacterial filaments, allowing pores to clog (Faust, 1970). Unlike most cyanobacteria, lichen tissue and moss stems completely protect underlying soil aggregates. Data suggest that porosity at the soil surface decreases as cyanobacterial biomass and lichen/moss cover increase (Figure 6), especially once lichen and moss cover exceeds a critical threshold (Eldridge, 2003).



Figure 6. Conceptual diagram of the possible influence of different crust types on soil features that affect local hydrologic cycles

Counteracting the tendency to clog soil pores, biological crust organisms are known to increase aggregation via soil carbon additions. This creates micropore channels, which are known to increase water infiltration (Greene, 1992; Eldridge *et al.*, 2001). These micropore channels are also stabilized by crust organisms when soils are exposed to rainfall or overland flow (McIntyre, 1958; Bond and Harris, 1964; Rogers, 1989; Eldridge *et al.*, 2001). Therefore, as the numbers of cyanobacterial filaments and anchoring structures increase with decreasing PET and thus biological crust cover, the number of soil aggregates and micropores are expected to increase as well (Figure 6).

Soil micropores and macropores are also created by burrowing soil invertebrates, many of which feed on the cyanobacteria, lichens and mosses found in BSCs. These soil invertebrates include mites, collembolans, nematodes, rotifers, tardigrades, isopods, snails, mole crickets, tenebrionid beetles, protozoans, termites, and ants. Studies show that the diversity and abundance of soil invertebrates increase as lichen and moss cover increases (reviewed in Belnap, 2003b).

Because of larger numbers of filaments, lichen-moss anchoring structures, greater soil carbon, and burrowing invertebrates, an increase in micropore formation is expected with increased cyanobacterial biomass

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and lichen/moss cover. Therefore, it is expected that pore formation on different soil surfaces will increase in the following order: bare soil < smooth crust < rugose crust < pinnacled crust < rolling crust (Figure 6). However, we have no reliable data on this. In addition, we have no data on the conditions under which pore clogging by crust organisms retards infiltration more or less than the formation and stabilization of pores increase infiltration.

Differential infiltration patterns

As discussed above, different soil biota can influence infiltration differently. Cyanobacteria generally occur just below the surface in strands with spaces between them (Figure 3(a)), while lichen and moss tissue can have low to high coverage of the soil surface (Figure 5(a-c)). Thus, water is expected to infiltrate more evenly in bare soil, a smooth cyanobacterial crust type, or in a continuous lichen–moss crust than in rugose and pinnacled crusts where lichens and mosses occur in patches. However, biomass within any crust type is also concentrated in patches, and differential infiltration patterns have been observed at a very small scale (e.g. Bond and Harris, 1964).

Soil surface roughness

The presence or lack of soil surface roughness can have a large influence on water retention times at a given site (Thurow, 1991). Smooth crusts flatten the soil surface and thus reduce water retention times relative to uncrusted surfaces (Yair, 1990). In contrast, retention time is greatly increased in crusts with high pedicels when compared to crusts having little pedicellation (Barger *et al.*, unpublished data; Belnap *et al.*, unpublished data). This is likely due to the large increase in path length experienced by water travelling over a pinnacled soil crust compared to a smooth crust (Figure 7, Belnap *et al.*, 2005). The only experiment assessing the effect of rugose crusts on retention time without the complication of disturbance (see Past Studies: How Crusts Affect Runoff and Infiltration below for further discussion on the undesired side effects of disturbance treatments) showed time to ponding was positively related to crust cover ($R^2 = 0.35$), but there was no correlation with time to runoff (Eldridge *et al.*, 1997). There are no known measures for rolling crusts. If it can be assumed that surface roughness, and thus tortuosity, dominates retention time, then it is expected that retention time will change with the soil surface type, and increase in the following order: smooth crust < bare soil < rugose crust < rolling crust < pinnacled crust (Figure 6).

Surface area for infiltration

Because smooth and rugose crusts are relatively flat, they offer little increase in the amount of soil surface area available for water infiltration. Pinnacled crusts represent the other extreme, with an increase of 100% or more in surface area on the upslope side of a typical mound (Figure 2). Rolling crusts are expected to be intermediate between rugose and pinnacled crusts (Figure 6).

Association with physical (mechanical, chemical, and vesicular) crusts

Physical crusts are transient soil surface layers which range in thickness from less than 1 mm to a few centimetres and which are structurally different than the material immediately beneath them. Most physical crusts form due to one or a combination of the following factors: the impact of raindrops, compressional forces such as animal trampling or vehicular traffic, evaporative processes (forming chemical crusts), and trapped gas bubbles (forming vesicular crusts). Biological crusts are often associated with varying degrees of physical crusting, which is known to restrict infiltration and increase runoff (Romkens *et al.*, 1990; Eldridge, 2003; Warren, 2003a). However, very little is understood about the relationship between physical and biological crusts, and there is no known data on the threshold where the strength or thickness of the physical crust impedes infiltration relative to the various aspects of the biological crusts that may enhance (or impede, in the case of smooth crusts) infiltration. Strong physical crusting is more often associated with fine-textured



Figure 7. The path length of water leaving a site with smooth crusts is much shorter than the path length of water leaving a site with pinnacled crusts. Note that the mounds in a pinnacled crust are parallel to each other, affecting the direction of water flow

soils relative to more sandy soils. Therefore, it could be predicted that physical crusts are more likely than biological crusts to control infiltration rates on fine-textured soils. However, it has also been argued that the inherent lack of micropores in fine-textured or physically crusted soils (compared to coarse-textured soils) means that pore formation by biological crusts has a larger impact on infiltration rates of fine-textured soils than sandier soils (Warren, 2003b). Unfortunately, there is little known data to inform this debate.

Soil surface cracking

Polysaccharide secretions by crust organisms can increase the density of surface cracks on fine-textured soils (Danin *et al.*, 1998; Kidron *et al.*, 1999). In addition, the patchy nature of crust biomass concentrations can lead to differential drying between the upper and lower surfaces of the crust, resulting in upward curling of the polygon margins (e.g. Durrell and Shields, 1961; Danin *et al.*, 1998). This cracking and lifting upwards

of the soil surface can result in greater infiltration into a surface that is otherwise fairly impermeable (Kidron *et al.*, 1999). In addition, the roughness of the cracked surface lessens water velocity and allows more time for infiltration to occur. However, there is little information on the density of polysaccharides required to enhance cracking or uplifting of soil polygons, above that inherent to the soil alone.

Patterns in biological soil crust mounds

Mound formation in pinnacled crusts is initiated by ice needles pushing biologically crusted soils upwards (Belnap, 2003a). The crust organisms provide sufficient cohesion to stabilize the mounds, even after the ice needles melt. Once the surface is roughened, crust organisms preferentially colonize the east-northeast (ENE) aspects of the mounds in the northern hemisphere (George et al., 2000; Bowker et al., 2002), as it is the most favourable aspect for maximizing carbon gain in these organisms (Belnap, unpublished data). This greater biomass makes the ENE aspect less erodible than the other aspects, especially the west-southwest aspect. Continued greater growth and less erosion on the ENE result in mounds with their long axes facing ENE and running parallel to each other. If the mounds are at an angle to the slope, the path length of water leaving a site is greatly increased relative to a non-mounded slope (Figure 7) or to a slope where the mounds run parallel to the slope. The orientation of the mounds can also determine the path water takes as it leaves a site, thus influencing where it ultimately infiltrates into the soil. This patterning of soil crust mounds can mimic, on a microscale, the patterning of banded vegetation (d'Herbès et al., 2001) and is expected to have a similar effect on the hydrology at the appropriate scale (Greene et al., 2001). However, unlike banded vegetation, we do not understand the relationship between the length of the mounds or the distance between them and site characteristics likely to influence this patterning (e.g. slope degree, aspect, timing and intensity of precipitation, soil texture). Rugose and rolling crusts sometimes form small mounds, and in the northern hemisphere, these mounds are also oriented ENE. The formation process of these mounds has not been studied, although it is likely that differential growth also creates these phenomena.

Vascular plant communities

Biological crusts can influence many characteristics of vascular plant communities, including species composition, plant density, plant size, and community architecture. Plants, in turn, intercept, direct, and slow runoff water, thus influencing the location and amount of water retained on a site (Loik *et al.*, 2004; Ludwig *et al.*, 2005). The type and amount of influence biological crusts exert on vascular plant communities are determined by what crust type is present.

Smooth crusts increase the probability that seeds will be blown or washed from plant interspaces to nearby obstructions (e.g. plants, large rocks), as they act to flatten and smooth the soil surface (Prasse, 1999). Thus, seedlings are only infrequently found in interspaces on the smooth crust type. Instead, plants generally germinate under the canopy of nearby 'nurse' plants. Furthermore, smooth crusts are also the only crust type found to inhibit the germination of selected plant species (Boeken *et al.*, 1998), although very few species have been tested. Smooth crusts can significantly increase water runoff to downslope vegetation. In hyperarid areas, this runoff is critical to plant survival; when the crusts in the interband areas are removed, downslope plants die from lack of water and nutrients. As plants die, the banding effect of the vegetation is lost, as is the ability to retain water and nutrients at the local scale (Eldridge *et al.*, 2000; Eldridge *et al.*, 2001).

Pinnacled and rolling crusts affect vascular plants differently than smooth crusts as they retain seeds and other resources (e.g. water, organic matter) in plant interspaces, where the seeds can germinate and establish (Belnap *et al.*, 2003b). Wind tunnel experiments show, however, that when crust mounds are flattened, seeds skid off to nearby obstructions rather than staying in the plant interspace (Belnap, unpublished data). As mentioned above, the orientation of crust mounds can direct water toward, or away from, an individual plant, thus affecting survival of the plant. Seed germination and plant success are either enhanced or not affected by pinnacled and rolling crusts, with no known cases of native plants being suppressed (Belnap *et al.*, 2003b). Pinnacled and rolling crusts have a high cover of nitrogen-fixing species, which increases soil fertility, plant

density, and plant biomass in crusted soils when compared to uncrusted soils (Belnap *et al.*, 2003b). Pinnacled and rolling crusts also appear to increase the resistance of an ecosystem to invasion by exotic annual grasses (Larsen, 1995; Howell, 1998), thus conserving the hydrologic cycles associated with the native perennial plant communities. In wet years, the annual plants decrease water runoff and sediment production relative to the native perennial plants, but in drought years, the annuals often fail to germinate, leaving extensive areas of soils unprotected.

Very little is known about the influence of rugose crusts on vascular plant communities. These communities generally contain a high biomass of nitrogen-fixing cyanobacteria. It has been shown that nitrogen fixed by biological crusts is utilized by associated vascular plants (reviewed in Belnap, 2003c), and thus it likely results in greater plant biomass. Rugose crusts have been found to exclude the invasion of annual grasses, as do pinnacled and rolling crusts (Crisp, 1975). Unfortunately, we have no information on how this crust type might structure perennial plant placement on the local landscape.

Soil moisture retention time

Increases in crust biomass and lichen-moss cover darken soil surfaces, which increases soil temperatures (Belnap *et al.*, 2003b). Therefore, greater crust biomass may result in greater evaporative losses of soil moisture. Alternatively, decreases in soil porosity associated with increased crust cover and biomass may lessen evaporative losses. There have only been a few studies on this topic, with conflicting results. Booth (1941) found there was greater soil moisture under biologically crusted surfaces compared to bare surfaces 2 days after rainfall. Rushforth and Brotherson (1982) and George *et al.* (2003) also found soil moisture was higher under lichen crusted soils compared to bare soils. Harper and Marble (1988) found that when lichen and moss cover was less than 61%, there was no difference between crusted and uncrusted soils. However, soils with a lichen and moss cover exceeding 85% dried more quickly than bare soils. Given the wide range of climate, soil, and crust types, we need more data on the effect of biological crusts before any general conclusions can be drawn. On the basis of what data we have, it is expected that soil moisture retention will vary with crust type in the following order: smooth < rugose < rolling < pinnacled (Figure 6).

Possible feedbacks among water, crusts, and soil surface features

There are many feedback loops among crust and soil features that can influence local hydrologic processes (Figure 8). For instance, the formation of mounds in pinnacled crusts slows water and increases surface roughness, thereby increasing soil infiltration. Greater soil moisture allows for greater crust carbon and nitrogen fixation, which results in greater crust biomass. Greater crust biomass increases soil surface absorptivity, soil aggregates, soil micropore formation and stability and, up to a point, may also increase soil moisture retention. The loop is closed as these factors in turn lead to greater mounding and crust biomass. Eventually, as soil biota increase soil fertility, vascular vegetation structure and biomass are increased, which further facilitates water infiltration. This model also applies to smooth crusts. However, as smooth crusts reduce surface roughness and surface porosity, their presence will also reduce water infiltration. In hyperarid areas where smooth crusts at the local scale (see discussion above). If smooth crusts are a result of disturbance, the reduction of water infiltration will reduce vascular plant biomass. In either case, the other relationships described in the model still hold.

BIOLOGICAL CRUSTS AND SOIL LOSS

Water velocity

The effect of BSCs on water velocity has been found to be the same as the effect of crusts on water retention time. Smooth crusts connect sand grains together, flattening and smoothing the soil surface. This



Figure 8. A conceptual model of the feedback loops in deserts connecting biological soil crusts (BSC), water and nutrient cycles, and vascular plants. The solid lines represent linkages that have been explicitly studied; the dotted lines represent hypothesized connections. It is important to note that the effect of smooth biological crusts on water infiltration and surface roughness is the opposite of other crust types (see text), and thus the type and direction of linkages noted in this model can vary with crust type

facilitates an increase in the velocity of water leaving a site (Yair, 1990). In contrast, the extreme soil surface roughness created by pinnacled crusts greatly slows time to runoff (Barger *et al.*, unpublished data; Belnap *et al.*, 2005). As discussed above, rugose crusts appear to influence time to ponding but not time to runoff (Eldridge *et al.*, 1997). There is no known information on how rolling crusts affect water velocity. Given that their surfaces are highly absorptive and of intermediate roughness between rugose and pinnacled crusts, they are expected to slow water velocity more than rugose crusts but less than pinnacled crusts.

Soil aggregation and linkages between particles

As discussed in several sections above, soils colonized by BSCs are filled with a network of cyanobacteria and microfungal filaments, as well as the anchoring structures of mosses and lichens (Figure 3(a-f)). This provides these soils with a tremendous resistance to movement by water (e.g. Durrell and Shields, 1961; Bond and Harris, 1964; Schulten, 1985; Belnap and Gardner, 1993; Rogers and Burns, 1994; Mazor *et al.*, 1996). Biological soil crusts also contribute significant amounts of organic carbon to arid soils via carbon fixation (Beymer and Klopatek, 1991) and decaying organic matter (Danin and Ganor, 1991), which also contributes to aggregate formation and thus stability. In fact, the organic mass of algal crusts can exceed that of vascular plants in some deserts (Rodin and Bazilevich, 1967). The ability of biological crusts to stabilize soils can exceed that of physical crusts (McCalla, 1946; Eldridge and Kinnell, 1997). As the number of cyanobacterial filaments and lichen and moss anchoring structures increases (Figure 4), the ability of these organisms to stabilize the soils is also increased (reviewed in Warren, 2003a, b).

Because lichen tissue and moss tissue actually protrude above and cover the soil surface, these organisms can offer complete protection to underlying soils from raindrop impacts. Cyanobacterial crusts, on the other hand, offer less protection to the soil surface, as the bulk of the cyanobacteria reside just under the surface. Although they weave a protective web throughout the soil that often connects to soil particles at the surface, raindrops still directly impact these soil particles. The type of cyanobacterial species present also affects the protective ability of cyanobacterial crusts. For instance, the filamentous *Scytonema* is more effective at

stabilizing surfaces than the unicellular *Nostoc* (Kidron *et al.*, 1999). Therefore, as cyanobacterial biomass and lichen–moss cover increase, it is likely that resistance to soil erosion from raindrop impact and overland flow increases and sediment production declines. Therefore, erosion resistance is least in smooth crusts, more in rugose crust, even more in pinnacled crusts and the highest in rolling crusts (Figure 6).

Surface cracking

As discussed above, cyanobacterial crusts can increase surface cracking of fine-textured soils, and differential drying of the upper and lower layers of the crust can result in an upward curling of the polygon margins (Durrell and Shields, 1961; Danin *et al.*, 1998). This upward lifting decreases velocity of runoff water, reducing its erosive force (Kidron *et al.*, 1999).

PAST STUDIES: HOW CRUSTS AFFECT RUNOFF AND INFILTRATION

There has long been a debate in the literature on how the presence of BSCs influences water infiltration and runoff. A considerable literature reports that the presence of crusts increases infiltration and decreases runoff (e.g. Booth, 1941; Fletcher and Martin, 1948; Osborn, 1952; Faust, 1970; Loope and Gifford, 1972; Blackburn, 1975; Brotherson *et al.*, 1983; Harper and St. Clair, 1985; Greene and Tongway, 1989; Eldridge, 1993; Perez, 1997; Seghieri *et al.*, 1997); or reduces infiltration and increases runoff (e.g. Bond and Harris, 1964; Roberts and Carson, 1971; Dulieu *et al.*, 1977; Brotherson *et al.*, 1983; Graetz and Tongway, 1986; Dekker and Jungerius, 1990; Greene *et al.*, 1990; Abaturov, 1993; Bisdom *et al.*, 1993; Danin, 1996; Mazor *et al.*, 1996; Kidron and Yair, 1997; Eldridge *et al.*, 2000). However, other studies show no effect on either process (e.g. Faust, 1970; Dobrowolski and Williams, 1994; Eldridge *et al.*, 1997; Williams *et al.*, 1999). When summarizing all these studies, Warren (2003a) suggested that overall, biological crusts decreased water infiltration in sandy soils (>66% sand) and increased infiltration where clays exceeded 15%. However, almost all the studies discussed were in hot deserts, where there was no surface roughening by soil crusts. In addition, there was a great deal of variability within the studies on those finer-textured soils. Of the 13 studies presented, 7 showed that the presence of biological crusts increased infiltration, 4 showed no effect, and 2 showed biological crusts decreased infiltration.

Most studies examining the effect of biological crusts on hydrologic cycles compare crusted soils that have not been disturbed to soils where the researchers removed the crusts by various methods (e.g. trampling by humans or livestock, scalping the surface soil, driving over with vehicles or tanks, fire). Unfortunately, in addition to the removal of biological crusts, such applied disturbances result in many changes to the structure of surface and sub-surface soils (Eldridge, 2003; Warren, 2003a). Disturbance to the soil surface breaks soil aggregates, crushes macropores, disrupts physical and chemical crusts, and compacts soils. Removal of the crusts necessitates removing the top few millimetres to centimetres of soil. Therefore, subsequent experiments encounter a surface with altered soil texture, structure, and physical crusting relative to the original surface.

Using fire to kill BSCs can create hydrophobic soils, seal surfaces, and alter soil chemistry. Killing the crusts chemically still leaves polysaccharide materials in place, which are able to stabilize the soils. Thus, the complications created by applied disturbance make it extremely difficult to reach any conclusion about how crusts affect infiltration and runoff. Instead, these studies tell us how disturbance affects previously crusted soils. In addition, the role of biological crusts on infiltration and runoff may be greatly influenced by site conditions existing before the disturbance is applied. For instance, Eldridge *et al.* (1997) suggested that biological crusts increase infiltration on degraded sites, but do not affect infiltration on sites in good condition.

Another factor that makes it difficult to draw conclusions from previous studies (even comparing among undisturbed controls of the various experiments) is the lack of reported information on soil features known to influence water infiltration and runoff such as (but not limited to) the relative cover of the crust biota by species, cyanobacterial biomass, soil surface roughness, soil texture, bulk density, the degree of other types of crusting (physical, vesicular, or chemical), surface and sub-surface soil aggregate stability, percentage of

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shrink-swell clays, calcrete formation, depth to bedrock, and the number of macropores. Without this type of information, it is impossible to separate the effect of biological crusts from other soil factors, as there are many that could easily override any influence of the biological crusts (e.g. a high percentage of heavy shrink-swell clays, the presence of thick vesicular crusts, a high number of macropores; Blackburn, 1975; Dobrowolski and Williams, 1994; Warren, 2003a). Results from previous studies are also difficult to compare because most studies used different instruments, methods, and even measured different variables. Many studies also utilized methods or plots too small to allow all factors, especially soil surface roughness, to influence the results. Lastly, most studies were done in hot deserts, with little data from cool or cold deserts.

Of the 41 published studies reviewed for this paper, only 8 used a gradient of existing crust types to avoid at least some of the confounding variables introduced when surfaces are disturbed to remove crusts. Of these 8, only 5 studies utilized rainfall simulators on plots large enough to integrate most or all of the factors influencing infiltration and runoff. Four of these were conducted on smooth cyanobacterial crust (Faust, 1970; Verrecchia *et al.*, 1995; Kidron and Yair, 1997; Eldridge *et al.*, 2000) and one on rugose crusts (Eldridge *et al.*, 1997). There are also two unpublished studies on pinnacled crusts (Barger *et al.*, unpublished data; Belnap *et al.*, unpublished data). Whereas all these studies reported sufficient detail on the crusts and some reported vital information on soil structure, none of these studies quantitatively measured factors such as physical crusting or soil macropores. This makes it difficult to assess if the results obtained were the influence of crusts or other soil features.

However, there were consistent results among the studies within a particular crust type. All four studies on smooth crusts found that the presence of algal crusts reduced infiltration and increased runoff. The two unpublished studies on pinnacled crusts both found that as crust development increased (as measured by species richness, biomass, and surface roughness of the biological crust), so did total infiltration. The one study on rugose crusts in Australia showed no effect of soil crusts on runoff. Despite this consistency among crust types, we still need far more data before any generalizations are made about the influence of BSCs on infiltration and runoff.

To address the above issues, we need studies designed to explicitly address how biological crusts influence infiltration and runoff relative to other soil factors, without influencing these factors by applying disturbance. Such experiments need to use standardized equipment and measures on sample areas that (1) are large enough to integrate all the ways crusts may influence infiltration and runoff or (2) have specific characteristics that allow separation of individual factors influencing infiltration and runoff (e.g. the relative effect of clogging vs creating micropores). In addition, such studies need to avoid disturbance that may impact other surface and sub-surface soil characteristics. One approach would be to measure infiltration and runoff on a range of naturally occurring crust covers (*sensu* Eldridge *et al.*, 1997). Another would be to inoculate soils with similar surface and sub-surface characteristics with crust organisms (*sensu* Faust, 1970), with experiments performed after the crusts are formed. However, all studies need to control for underlying soil factors if we are to truly elucidate the role of biological crusts. We also need new, creative ways to approach this question. For instance, Ladyman *et al.* (1993) reasoned that greater infiltration would transfer more calcium carbonate to depth in calcareous desert soils. They then used pH changes between the surface and sub-surface soils to investigate relative infiltration among soil crust types.

PAST STUDIES: HOW CRUSTS INFLUENCE SEDIMENT PRODUCTION

In contrast to the conflicting results on how biological crusts affect infiltration and runoff, there is a general consensus among studies in all regions that biological crusts significantly reduce sediment production from experimental sites (e.g. Booth, 1941; Fletcher and Martin, 1948; Osborn, 1952; Faust, 1970, 1971; Mücher *et al.*, 1988; Chartres and Mücher, 1989; Tchoupopnou, 1989; Greene *et al.*, 1990; Kinnell *et al.*, 1990; Eldridge, 1993; Eldridge and Greene, 1994; Eldridge and Kinnell, 1997). There are a few exceptions, but they are rare and appear restricted to smooth crusts on sand dunes (Warren, 2003b). As with the research

on infiltration and runoff, most of these studies compare undisturbed crusts with those disturbed by the researcher, making it difficult to draw definitive conclusions. However, because almost all studies obtained the same result, information on sediment production appears more reliable than that on infiltration and runoff. In addition, the studies that did not rely on disturbance treatments (e.g. Tchoupopnou, 1989; Yair, 1990; Eldridge and Greene, 1994; Eldridge and Kinnell, 1997) all found soil stability increased as crust biomass, cover, and development increased.

CONCLUSIONS

Although previous studies have highlighted many aspects of BSCs that can, or are likely to, influence local hydrologic patterns, the role of these organisms in upland hydrologic patterns is far from well understood. The most fundamental question that remains unanswered is the relative contribution of different crust types to infiltration and runoff relative to other soil factors such as texture and sub-surface structure. Answering this question will require carefully executed studies, creative thinking, and perhaps a change in the scale of studies.

Future changes in land use and climate are likely to have a negative effect on the presence and development of BSCs. Increased human use of drylands is expected to convert many lichen-moss crusts to cyanobacterial crusts and to flatten many currently roughened surfaces. In addition, increasing air temperature is likely to decrease lichen cover in many crusts. Therefore, it is probable that the current influence of BSCs on infiltration, runoff, and sediment production will be greatly altered in the future.

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GOLDEN EAGLES IN THE U.S. AND CANADA: STATUS, TRENDS, AND CONSERVATION CHALLENGES

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ABSTRACT.—We reviewed the literature to assess status and population trends and to identify mortality factors affecting Golden Eagle populations in the U.S. and Canada. Nesting populations in Alaska and Canada are stable, but some nesting populations in the western U.S. have declined. Small but steady declines in the intermountain West have been associated with shrub loss and declining jackrabbit populations; declines in southern California have been attributed to urbanization. Migration counts in the eastern U.S. suggest a decline in Golden Eagles from the 1930s to the early 1970s, with a stable or increasing trend since the early 1970s. No significant trends in migration counts were reported for Golden Eagles in the western U.S. since the mid-1980s. Western migration count sites on the continental divide in the Rocky Mountains at or just north of the U.S.-Canadian border (49–51°N latitude) show potential to provide information on trends of Golden Eagle populations from Alaska and western Canada. Most eagle mortality is human related. This paper illustrates the need for more effective monitoring of Golden Eagle populations in North America.

KEY WORDS: Golden Eagle; Aquila chrysaetos; status; monitoring; mortality; U.S.; Canada.

Aguilas reals en E.U.A. y canadá: estado, tendencias y retos para su conservación

RESÚMEN.—Revisamos la literatura para evaluar el estado y las tendencias poblacionales y para identificar los factores de mortalidad que afectan las poblaciones de águila real en E.U.A. y Canadá. Las poblaciones que anidan en Alaska y Canadá están estables, pero algunas poblaciones que anidan en el oeste de E.U.A. han declinado. Pequeñas, pero continuas declinaciones en el oeste íntermontañoso han sido asociadas con la perdida de arbustos y con el decline en las poblaciones de liebres; el declive en el sur de California ha sido atribuido a la urbanización. Conteos migratorios en el este de E.U.A. sugieren un decline en las águilas reals desde los años 1930s hasta principios de los 1970s, con una tendencia estable o a incrementar desde el principio de los 1970s. Ninguna tendencia significativa en conteos de migratorios fue reportada para las águilas reals en el oeste de E.U.A. desde mediados de los 1980s. Los sitios de conteo de migración del oeste sobre la divisoria continental en las montañas rocosas en o justo al norte de la frontera E.U.A.-Canadá (49–51° latitud N) tiene potencial para proveer de información sobre las tendencias de las poblaciones de águilas reals de Alaska y el oeste de Canadá. La mayoría de la mortalidad de las águilas esta relacionada con los humanos. Este articulo ilustra la necesidad de un monitoreo mas efectivo de las poblaciones de águila real en Norte América.

[Traducción de César Márquez y Victor Vanegas]

Until recently Golden Eagles (*Aquila chrysaetos*) were considered abundant in North America with stable populations (Hamerstrom et al. 1975, Palmer 1988). However, some studies, particularly those from migration count sites in the U.S. (e.g., Bednarz et al. 1990, Hoffman et al. 1992), have raised questions about trends of Golden Eagle populations. Only four nesting Golden Eagle pairs are known in the eastern U.S in Maine, Tennessee, and Georgia with two pairs the result of introduction efforts in Tennessee and Georgia (Kochert et al. 2002). In addition, recent requests by Native

Americans to the U.S. Fish and Wildlife Service to harvest Golden Eagles for religious purposes have prompted the need to assess the status of the species in North America and to assess threats to populations (Bart et al. 1999). In this paper, we report information on the status and trends of Golden Eagle populations in the U.S. and Canada, and we discuss mortality factors affecting eagle populations.

Methods

We obtained information from published and unpublished literature and personal interviews with individuals

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Table 1. Trends in number of occupied nesting territories at four long-term survey areas in the U.S.

LOCATION	YEARS	N^{h}	Trend	Source
Interior Alaska	198899	58-76	Stable	McIntyre and Adams 1999, McIntyre 2001
Southwestern Idaho	1971–99	28–35	Decline*	Steenhof et al. 1997, USGS, unpubl. data
Northeast Colorado	1972 - 90	7-10	Decline	Leslie 1992
Southern California	1895-1999	40-85	Decline	Bittner and Oakley 1999

^a Number of territories.

* P < 0.001.

conducting long-term surveys of Golden Eagles. We used a variety of data including long-term nesting surveys, the Breeding Bird Survey (Peterjohn 1994), Christmas Bird Counts (Sauer et al. 1996), and migration counts. Other sources included modeling efforts and other literature syntheses.

To assess long-term trends in territory occupancy and productivity, we selected studies that spanned more than 10 yr and extended into at least the mid-1980s. Four studies fit the criteria for occupancy (Table 1), and four fit criteria for productivity (Table 2). Continuous studies of both occupancy and productivity occurred only in the Snake River Birds of Prey National Conservation Area (NCA) in southwestern Idaho (Steenhof et al. 1997, USGS unpubl. data) and in Denali National Park in interior Alaska (McIntyre and Adams 1999, McIntyre 2001). Occupancy data from San Diego County, California span more than 100 yr and were collected by several investigators (Bittner and Oakley 1999), including Dixon (1937) and Scott (1985). Leslie (1992) compared occupancy in northeastern Colorado during two seasons 18 yr apart. We obtained productivity information for Utah from Keller and Smith (1998) and Bates and Moretti (1994) (Table 2). In addition, we used the number of egg-laying pairs during 20 seasons in central Oregon (Anderson 1985).

RESULTS

Nesting Territory Occupancy. Of four areas tracked for long-term occupancy of eagle territories, all except interior Alaska experienced de-

clines (Table 1). The number of occupied territories in southwestern Idaho declined significantly between 1971 and 1994 ($r^2 = -0.54$, P < 0.001; Steenhof et al. 1997). Declines of nesting eagles in southwestern Idaho were associated with loss of shrubs and black-tailed jackrabbit (Lepus californicus) habitat due to widespread fires (Kochert et al. 1999). Nesting eagles in San Diego County decreased dramatically from an estimated 85 pairs in 1900 to 40 occupied territories in 1999 (Bittner and Oakley 1999). Large-scale declines occurred between 1956-80, and subtle declines occurred through 1999. These declines were related to extensive residential development (Bittner and Oakley 1999). The decline reported for northeastern Colorado (10 to 7 pairs) should be interpreted with caution because of the small sample size and low frequency of sampling (Leslie 1992). The number of nesting attempts in central Oregon declined significantly ($r^2 = -0.69$, P < 0.001) between 1966-84 (Anderson 1985). It is not clear if this decline was the result of a decrease in occupancy or in the proportion of pairs that laid eggs.

Eagle Productivity. In contrast to territory occupancy, no long-term trends in productivity were reported except in north-central Utah (Table 2).

Table 2. Trends in Golden Eagle productivity in four long-term survey areas in the U.S. Productivity is young fledged per pair except for north-central Utah where it is young per egg-laying pair.

Location	YEARS	N	Trend	Source
Interior Alaska	1988–99	58–76	None	McIntyre and Adams 1999, McIntyre 2001
Southwestern Idaho	1971-99	2835	None	Steenhof et al. 1997, USGS unpubl. data
North-central Utah	1977-98	31-240	Decline*	Keller and Smith 1998
Eastern Utah	1981-92	39	None	Bates and Moretti 1994

* P = 0.02.

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Table 3. Golden Eagle trends from Breeding Bird Surveys, 1966–98.

Region	Trend	N^{a}	Р
All U.S. ^b	2.4	271	0.23
Pacific region	4.3	99	0.17
Southwest region	-6.6	21	0.25
CMP^c	2.8	151	0.36
Canada	-7.1	5	0.56
Survey wide	1.9	276	0.33

^a Number of routes with eagle observations.

^b Excluding Alaska.

^c Central mountains and plains.

Although eagle productivity has fluctuated with changes in the major prey in Alaska, southwestern Idaho, and eastern Utah, the number of the young fledged per occupied territory showed no trends over time (Bates and Moretti 1994, Steenhof et al. 1997, McIntyre and Adams 1999). However, the proportion of young fledged per egg-laying pair declined slightly but significantly ($r^2 = -0.22$, P = 0.02) in the desert (lower elevation) study area of north-central Utah (Keller and Smith 1998). This decline in productivity may reflect loss and degradation of native sagebrush (jackrabbit) habitats (Keller and Smith 1998).

Breeding Bird Surveys. Breeding Bird Surveys (BBS) show no trend for nesting Golden Eagles on either a regional or continental scale from 1966-98 (Table 3). Long-term data from BBS routes are available only in the southern portions of the Canadian provinces, and these results may not be reliable because only five routes had eagle observations (Table 3). Data from Alaska and the Yukon and Northwest Territories of Canada where Golden Eagles are abundant (Kirk and Hyslop 1998, McIntyre 2001) were not included in these analyses because BBS did not establish routes in these regions until the 1980s (Peterjohn 1994) and the number of routes and routes with eagle sightings are low. Most BBS routes follow roads (Peterjohn 1994) and because Golden Eagles generally nest in remote areas (Palmer 1988), the BBS is not the most reliable method to assess trends of nesting Golden Eagles.

Trends Based on Other Information. Golden Eagle nesting populations and productivity in Canada are likely stable; evidence for this assessment includes considerable unpublished information (Kirk and Hyslop 1998). In eastern Canada, nestTable 4. Golden Eagle trends from Christmas Bird Counts, 1959–88.

REGION	Trend	P
Survey wide	-1.0	< 0.05
States with declines		
Idaho	-1.4	< 0.001
Oregon	-2.4	< 0.001
Kansas	-3.7	< 0.05

ing populations have been found recently at Hudson Bay in northern Quebec (Morneau et al. 1994) and in the Labrador Peninsula. Nesting populations in southwestern Saskatchewan and the Yukon Territory are stable, with the latter being a large population (estimated 900–1000 pairs). Long-term productivity of eagles in the Northwest Territories is also stable (Kirk and Hyslop 1998). White (1994) reported that the status of Golden Eagles in the western U.S. was variable: stable in some areas and possibly declining in others. Hunt et al. (1999) modeled the breeding Golden Eagle population at Altamont Pass in central California and concluded that the population was either stable or decreasing.

Winter Surveys. According to results of Christmas Bird Counts, Golden Eagles declined significantly throughout the U.S. and Canada (Ontario and British Columbia) from 1959–88 (Table 4). Counts in Idaho, Oregon, and Kansas declined significantly, while other survey regions showed no significant trend. However, Christmas Bird Counts have limited value for detecting Golden Eagle trends because of the low number of individuals counted on each survey, inconsistencies among years in survey efforts and area surveyed, and the fact that most surveys are in suburban, exurban, or rural settings where eagles are least likely to occur.

Aerial surveys coordinated by the U.S. Fish and Wildlife Service (USFWS) provide potentially useful information on wintering Golden Eagle densities and adult:immature ratios (USFWS unpubl. data). Between 1972–80, 124 000 km² were sampled from random transects in Colorado, Idaho, Montana, New Mexico, Utah, and Wyoming during January–February. Only the area in southern Idaho was surveyed after 1980 and for more than 10 yr (Kochert et al. 1984). This 18 000-km² area was also surveyed in October from 1972–78. Counts averaged 2.56 more eagles during midwinter than in October, suggesting an influx of migrant birds. The southern Idaho area contained both resident



Figure 1. Densities of Golden Eagles wintering in southern Idaho, 1973-84.

birds and migrants from Alaska and Canada during the winter (Fuller et al. 1995, Craig and Craig 1998, McIntyre 2000). Wintering densities in southern Idaho correlated strongly with black-tailed jackrabbit abundance (Kochert 1980). Because jackrabbit populations cycle about every 10 yr (Johnson and Peek 1984), inferences from data sets covering less than 10 yr can be misleading. Eagle counts from 1973–80 showed a significant decline in southern Idaho (r = -0.80; P = 0.02) that coincided with a jackrabbit decline (Kochert 1980), but longer-term analyses that included the jackrabbit recovery showed that winter eagle densities were stable from 1973–84 (Fig. 1).

Migration Count Sites in the Eastern U.S. and Canada. We assessed trends of migrating Golden Eagles in the eastern U.S. and Canada from six migration count sites (Table 5). Passage rates (number of Golden Eagles per 10 hr of observation) declined significantly at Hawk Mountain, Pennsylvania between 1934–72 but remained relatively stable between 1973–86 (Bednarz et al. 1990). From 1987–99, trends for Golden Eagles at Hawk Mountain have been stable or increasing (L. Goodrich pers. comm., Hawk Mountain Sanctuary unpubl. data). Data from Ontario (Hussell and Brown 1992) and five migration sites in the eastern U.S. (Titus and Fuller 1990) suggest at least a stable trend for Golden Eagle counts from the early 1970s to the late 1980s.

Migration Count Sites in the Western U.S. and Canada. Unlike migration count sites in the eastern U.S., continuous counts in the western U.S. span little over a decade (Table 6). Passage rates at four migration count sites showed no trend from the mid-1980s to late 1990s (Table 6). These sites occur south of 42°N latitude, and eagles that pass through them are probably a mix of northern migrants and dispersing resident birds or short-distance migrants (J. Smith pers. comm.). These Hawkwatch International sites report possible changes in eagle age ratios that may reflect deteriorating conditions in the western U.S. (J. Smith pers. comm.). Passage rates of immature Golden Eagles at the Wellsville Mountains in northern Utah were significantly lower from 1987-97 than from 1977-79.

Raptor migration count sites on the continental divide in the Rocky Mountains just north of the U.S.-Canadian border show potential for monitor-

Table 5. Golden Eagle trends at migration count sites in the eastern U.S. and Canada.

LOCATION	YEARS	Season	Trend	Source
Hawk Mountain, Pennsylvania	1934–72	Autumn	Decline	Bednarz et al. 1990
	1973–86	Autumn	None	Bednarz et al. 1990
Niagara Peninsula, Ontario	1975–90	Autumn	Increase	Hussell and Brown 1992
5 Eastern U.S. sitesª	1972–87	Autumn/Spring	None	Titus and Fuller 1990

^a Includes Hawk Mountain, Pennsylvania; Hawk Ridge, Minnesota; Whitefish Point, Michigan; Derby Hill, New York; and Cape May, New Jersey.

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 Table 6. Golden Eagle population trends at four migration count sites in the western United States.^a

LOCATION	Season	Years	Trend
Wellsvilles, Utah	Autumn	1987–97	none ^b
Goshutes, Nevada	Autumn	1983 - 97	none
Manzanos, New Mexico	Autumn	1985 - 97	none
Sandias, New Mexico	Spring	1985 - 98	none

 ^a Source: Hoffman et al. unpubl. data, J. Smith, pers. comm.
 ^b Passage rates for immatures were significantly lower from 1987– 97 than from 1977–79.

ing trends because of the large number of eagles that pass over them (Sherrington 1993). For example, fall counts at Mount Lorette (50°58'N) in southern Alberta averaged 4014 Golden Eagles (range 3706–4599) between 1993–96, and spring counts averaged 3707 (range 2461–4213) between 1993–98 (Sherrington 1998, 1999). Although counts have been conducted since 1984 at Windy Point (50°40'N) and 1992 at Mount Lorette (Sherrington 1998), data have not been analyzed for trends.

Conservation Challenges. The greatest conservation challenge in managing Golden Eagle populations is offsetting the adverse effects of human activity. Of Golden Eagles found dead from the early 1960s to the mid-1990s, 73% died from human-related causes, including accidental trauma (27%), electrocution (25%), shooting (15%), and poisoning (6%; Franson et al. 1995). Accidental trauma included collisions with cars, fences, wires, and wind turbines. At least 28-43 Golden Eagles are killed each year by turbine blade strikes in the Altamont Pass Wind Resource Area in west-central California; of 61 eagle deaths investigated in the Diablo Range between 1994–97, 37% resulted from turbine strikes, 5% from car strikes, and 3% from fence collisions (Hunt et al. 1999). Golden Eagles continue to be electrocuted in the western U.S and Canada where Harness (1997) reported 272 eagle electrocutions between 1986-96. Electrocution accounted for 16% of the Golden Eagle deaths in the Diablo Range, California between 1994-97 (Hunt et al. 1999).

Lead accounted for most poisoning deaths of Golden Eagles. Elevated lead levels (>0.20 ppm) occurred in 36% of 162 eagles sampled in 1985– 86 from southern California (Pattee et al. 1990). Elevated levels also occurred in 46% of 281 wintering eagles captured in southeastern Idaho between 1990-97 (Craig and Craig 1998), and 56% of 86 spring migrants in Montana trapped between 1985-93 (Harmata and Restani 1995). Sources of lead have not been documented definitively, but are likely from lead shot or bullets in hunter-killed upland game birds and mammals (Wayland and Bollinger 1999), particularly deer (Pattee et al. 1990) and ground squirrels (Harmata and Restani 1995) with waterfowl as a secondary source. Mortality from ingested shot and bullet fragments occurs occasionally (P. Redig pers. comm.). Blood lead levels of recaptured wintering individuals in Idaho did not decrease over 1-5 yr, suggesting repeated or continual exposure to lead in the environment (Craig and Craig 1998). Four (13%) of 31 dead Golden Eagles examined from 1990-96 from the Canadian Prairie Provinces had been poisoned and three (10%) were sublethally exposed to lead (Wayland and Bollinger 1999). In Idaho, seven of 16 dead Golden Eagles necropsied between 1977-86 were lead poisoned (Craig et al. 1990). Agricultural pesticides, mainly organophosphates and carbamates, accounted for most of the remaining poisoning deaths. In the latter cases, eagles often died by consuming other animals that were poisoned or by consuming baits placed to kill other wildlife.

DISCUSSION

Nesting Golden Eagles. Although data provide conflicting evidence on population trends, available information suggests that nesting populations in Alaska and Canada are stable and, for the most part, doing well. The status of nesting Golden Eagles in the western U.S. is less clear. Although some data, such as the BBS, suggest stable populations throughout the western U.S., some populations have declined. Areas like the Snake River Birds of Prey National Conservation Area may have experienced a decrease in carrying capacity (Steenhof et al. 1997). Shrub loss and declining jackrabbit populations have been associated with small, but steady, declines in the intermountain West; declines in southern California have been attributed to urbanization. Although some nesting populations in the western U.S. have decreased, productivity has not declined, except in one population. This agrees with observations of other eagle species where lower quality (or less productive) territories are abandoned in some declining populaMARCH 2002

tions before productivity at higher quality territories declines (Ferrer and Donazar 1996).

Conclusions from Migration Counts. Migration counts in the eastern U.S. suggest a decline in Golden Eagles from the 1930s to the early 1970s, with a stable or increasing trend since the early 1970s. No significant trends were reported for Golden Eagles in the West since the mid-1980s. However, recent increases in adult detection rates and a decrease in migratory immatures have raised concern about conditions for breeding birds and possible lowered reproduction of Golden Eagles in parts of the western U.S. (J. Smith pers. comm.).

Golden Eagle population trends from migration counts should be assessed judiciously because of inconsistencies in data collection among years and count sites, inconsistencies and biases in assessing passage rates, and variability in counts and passage rates caused by weather and eagle behavior (Gould and Lewis 1998, Fuller and Bates 1999). In addition, the origins and destinations of most birds seen at migration count sites are unknown. Significant declines at a migration site could reflect problems throughout the range or merely at an isolated nesting or wintering area. It is difficult to develop management strategies to address possible causes of declines.

Western migration count sites on the continental divide in the Rocky Mountains at or just north of the U.S.-Canadian border (49–51°N latitude) show potential to provide information on trends of Golden Eagle populations from Alaska and western Canada. Large numbers of Golden Eagles pass through these sites, and information from satellite telemetry studies suggests these migration count sites may be on a flight path for Golden Eagles migrating from Alaska and western Canada (Fuller et al. 1995, McIntyre 2000).

Recommendations for Monitoring. Information we present in this paper illustrates the need for more effective monitoring of Golden Eagle populations in North America. We recommend that long-term nesting surveys continue, specifically in Denali National Park (McIntyre 2001), the Snake River Birds of Prey NCA (Steenhof et al. 1997), and San Diego County, California (Bittner and Oakley 1999). Continuous data from these areas provide valuable insights about eagle responses to different environmental problems in diverse geographical areas. We recommend that survey areas be developed for monitoring nesting eagles in Canada, particularly in areas that have been surveyed in the past (see Kirk and Hyslop 1998). Long-term data sets from areas such as north-central Utah (Keller and Smith 1998) should be analyzed and evaluated to determine if these areas should become additional long-term monitoring sites. The area in central Oregon studied by Anderson (1985) also should be resurveyed to ascertain if the population is still depressed or whether it has rebounded. We recommend monitoring the major prey (e.g., black-tailed jackrabbits) concurrently with eagle nesting surveys, specifically in those areas with background prey data; i.e., the Snake River NCA (Steenhof et al. 1997) and Denali National Park (McIntyre and Adams 1999).

We recommend that migration counts continue in the western Rocky Mountains >50°N latitude because they have potential to reflect trends in western Canada and Alaska. Counts at raptor migration count sites should continue to be evaluated (e.g., Gould and Lewis 1998, Fuller and Bates 1999) to determine if they provide meaningful data about status and trend of eagle populations. Information also is needed about the origin and destination of eagles passing through migration count sites.

Counts of Golden Eagles along midwinter Bald Eagle (*Haliaeetus leucocephalus*) survey routes also may provide long-term trend data. More than 300 Golden Eagles have been counted annually on 220 standard routes in 28 states since the mid-1980s (USGS unpubl. data). These January counts occur in Bald Eagle wintering habitat, which may not be prime Golden Eagle habitat. The feasibility of using numbers and age classes of Golden Eagles counted on mid-winter Bald Eagle survey routes for trend analyses should be assessed.

Winter aerial surveys along transects also could provide useful information about population trends, if they are conducted over at least 10 yr to span a complete jackrabbit population cycle. Data from USFWS aerial surveys in six states during the 1970s might provide valuable baseline data on winter eagle densities and age ratios, if the surveys were resumed. These surveys are repeatable because they were conducted on random transects and sampled in a consistent fashion each year. They also are relatively inexpensive to conduct; in southern Idaho, we surveyed 1600 km of transects, using 20 hr of aircraft time. These aerial surveys, like the midwinter Bald Eagle counts, sample populations that contain both the resident and migrant birds. It is extremely difficult to attribute whether change in status is a result of a change in the resident or migrant population or both.

An accurate evaluation of eagle population status requires knowledge about status and trend of floaters (nonterritorial, nonbreeding adults) in a population in addition to the nesting segment of the population (Hunt 1998, Hunt et al. 1999, Bart et al. 1999). Stable populations contain an adequate number of floaters that readily replace breeding adults. Although difficult to obtain, accurate assessment of the floating segment is critical for assessing status of populations. Detecting decreases in the proportion of floaters provides early warning of population declines (Hunt 1998, Bart et al. 1999). Research is needed to develop a feasible means to efficiently gather information on the proportion of floaters in populations.

Fall aerial surveys show potential for assessing changes in resident eagle populations in the western U.S. Surveys conducted in the early fall when young are dispersing from their nesting areas and just prior to arrival of migrants include all segments of the population, including floaters, in the survey area. Like the winter aerial surveys, these fall surveys are repeatable and inexpensive, and they should be conducted for at least 10 yr. Fall surveys have potential for migratory populations if surveys are conducted after young disperse, but before migration.

Another way to monitor Golden Eagle populations is to monitor the threats they face. Because most eagle mortality is human-related, monitoring causes of death including electrocution, collisions, and lead levels should continue.

Standard protocols for inventory and monitoring must be established and followed to effectively assess status and trends of North American Golden Eagle populations. We found it difficult to make adequate assessments because of inconsistencies among sites and years and, even worse, inconsistencies among years within sites. The North American Raptor Monitoring Strategy (Anonymous 1997) may provide the necessary vehicle to address these problems. A goal of this strategy is to develop standard protocols for monitoring various raptor species, including Golden Eagles. Local declines of Golden Eagles and a recent request from Native Americans to harvest this species in the southwestern U.S. have prompted the need for a range-wide inventory and long-term monitoring of Golden Eagle populations in North America. Populations must be monitored consistently throughout the species' range, and well-designed inventory and monitoring protocols are essential to ensure the future long-term stability of the Golden Eagle in North America.

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Research Article



Golden Eagle Population Trends in the Western United States: 1968–2010

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ABSTRACT In 2009, the United States Fish and Wildlife Service promulgated permit regulations for the unintentional lethal take (anthropogenic mortality) and disturbance of golden eagles (Aquila chrysaetos). Accurate population trend and size information for golden eagles are needed so agency biologists can make informed decisions when eagle take permits are requested. To address this need with available data, we used a log-linear hierarchical model to average data from a late-summer aerial-line-transect distance-sampling survey (WGES) of golden eagles in the United States portions of Bird Conservation Region (BCR) 9 (Great Basin), BCR 10 (Northern Rockies), BCR 16 (Southern Rockies/Colorado Plateau), and BCR 17 (Badlands and Prairies) from 2006 to 2010 with late-spring, early summer Breeding Bird Survey (BBS) data for the same BCRs and years to estimate summer golden eagle population size and trends in these BCRs. We used the ratio of the density estimates from the WGES to the BBS index to calculate a BCR-specific adjustment factor that scaled the BBS index (i.e., birds per route) to a density estimate. Our results indicated golden eagle populations were generally stable from 2006 to 2010 in the 4 BCRs, with an estimated average rate of population change of -0.41% (95% credible interval [CI]: -4.17% to 3.40%) per year. For the 4 BCRs and years, we estimated annual golden eagle population size to range from 28,220 (95% CI: 23,250-35,110) in 2007 to 26,490 (95% CI: 21,760-32,680) in 2008. We found a general correspondence in trends between WGES and BBS data for these 4 BCRs, which suggested BBS data were providing useful trend information. We used the overall adjustment factor calculated from the 4 BCRs and years to scale BBS golden eagle counts from 1968 to 2005 for the 4 BCRs and for 1968 to 2010 for the 8 other BCRs (without WGES data) to estimate golden eagle population size and trends across the western United States for the period 1968 to 2010. In general, we noted slightly declining trends in southern BCRs and slightly increasing trends in northern BCRs. However, we estimated the average rate of golden eagle population change across all 12 BCRs for the period 1968–2010 as +0.40% per year (95% CI = -0.27% to 1.00%), suggesting a stable population. We also estimated the average rate of population change for the period 1990-2010 was +0.5%per year (95% CI = -0.33% to 1.3%). Our annual estimates of population size for the most recent decade range from 31,370 (95% CI: 25,450-39,310) in 2004 to 33,460 (95% CI: 27,380-41,710) in 2007. Our results clarify that golden eagles are not declining widely in the western United States. © 2013 The Wildlife Society.

KEY WORDS Aquila chrysaetos, Breeding Bird Survey, golden eagle, hierarchical model, populations, trend, United States.

In 2009, the United States Fish and Wildlife Service (Service) published regulations under the Bald and Golden Eagle Protection Act (16 United States Code 668–668d; hereafter Act) that established conditions under which the

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Service could permit lethal take and disturbance of bald (*Haliaeetus leucocephalus*) and golden eagles (*Aquila chrys-aetos*). The Act delegates to the Secretary of the Interior the ability to permit take of the eagles "necessary for the protection of other interests in any particular locality" after determining the take is "compatible with the preservation of the bald eagle or golden eagle." The regulations define take to mean pursue, shoot, shoot at, poison, wound, kill, capture, trap, collect, destroy, molest, or disturb. In the 2009

regulations, the Service established that compatibility with mandates of the Act are accomplished if permitting activities do not result in a net decrease in the number of breeding pairs of either species of eagle (using 2009 as the baseline) within regional geographic management units, which in the case of the golden eagle are Bird Conservation Regions (BCR; U.S. North American Bird Conservation Initiative Monitoring Subcommittee 2007, U.S. Fish and Wildlife Service 2009). Direct counts of the number of golden eagle breeding pairs are not available and the number varies annually with environmental conditions (Kochert et al. 2002); therefore, the Service relies on trends in estimates of total golden eagle population size and demographic models that use those population estimates to assess whether the management objective of a stable breeding population is being achieved (U.S. Fish and Wildlife Service 2009).

This permitting threshold created a need for accurate population trend and size data for both species of eagle so Service and other agency biologists could make informed decisions when eagle take permits were requested. This had been problematic in the case of the golden eagle because available data had been sufficient for only coarse estimates of population size with no measure of uncertainty. The lack of robust population data was 1 factor that led the Service to conclude it could not authorize additional take above that existing at the time the eagle take regulations were published without potentially violating the preservation standard in the Act (U.S. Fish and Wildlife Service 2009). This decision has been controversial, particularly in the western United States where permits to unintentionally take golden eagles in association with renewable energy development are needed.

We integrated data from golden eagle population surveys conducted by Western Ecosystems Technology (WEST) and the Service (hereafter the western United States summer golden eagle survey, or WGES; Good et al. 2007, Nielson et al. 2012) and the North American Breeding Bird Survey (hereafter BBS) using a log-linear hierarchical model (Sauer and Link 2011, Zimmerman et al. 2012). Our broad objectives were to help clarify our understanding of the status of the golden eagle in the conterminous western United States. We studied the summer golden eagle population in the conterminous western United States roughly west of the 100th meridian; we stratified this population by BCR for analyses (Fig. 1). The BBS is a well-known survey intended to provide early-summer population change information for over 420 species of birds from the late 1960s to the present over much of North America (Sauer and Link 2011). Given its timing, the BBS provides information on golden eagles before young have fledged from nests over most of the western United States, hence it is a pre-recruitment survey. Population estimates from the BBS are controversial because they lack estimates of detection (Thogmartin et al. 2006), and the BBS is considered to have deficiencies because of low precision and low abundances with respect to assessing trends of golden eagle populations (http://www.mbr-pwrc. usgs.gov/cgi-bin/atlasa10.pl?03490&1&10, accessed 4 Nov 2012). The WGES was initiated in 2003 as a pilot study, and was designed to estimate population size of golden eagles.

Adjustments were made following the pilot study and the survey has been conducted annually using a consistent protocol and sample of survey transects since 2006 by WEST with funding from the Service (Good et al. 2007, Nielson et al. 2012). This aerial transect-based survey focuses on late summer, post-breeding golden eagles in the Great Basin (BCR 9), Northern Rockies (BCR 10), Southern Rockies/Colorado Plateau (BCR 16), and Badlands and Prairies (BCR 17) BCRs, which collectively cover about 80% of the golden eagle's range in the conterminous western United States (U.S. Fish and Wildlife Service 2009).

Both WGES and BBS counts of golden eagles exist for BCRs 9, 10, 16, and 17 for the years 2006–2010; we refer to these BCRs as the overlap BCRs. The WGES has produced estimates of golden eagle density for the overlap BCRS for the years 2006-2010 (Nielson et al. 2012), and the BBS has generated estimates of golden eagle population trends for the period 1968-2008 (Sauer and Link 2011). Our specific objectives in integrating data from the WGES and BBS were to 1) collectively apply all available survey data to inform regional trend estimates; 2) assess whether the BBS and WGES were providing similar golden eagle population trend estimates for the time periods and BCRs of overlap; and if so, 3) develop an adjustment factor to scale the BBS counts of birds per route in the spring to density estimates postbreeding, which would allow us to estimate golden eagle population size and trend over the time series of the BBS (1968–2010) or for parts of that interval for both the overlap BCRs and other BCRs in the conterminous United States west of the 100th meridian.

We present the methods and results from the composite analysis of WGES and BBS golden eagle population data, and compare those findings with those from other recent golden eagle population analyses and assessments. In that context we also consider recent published estimates of golden eagle population trends from regression analyses of autumn western United States golden eagle migration counts (Bildstein et al. 2008). The original analysis of those data suggested migratory populations of golden eagles over much of the western United States have declined since the mid-1980s, and in particular from 1995 to 2005 (Farmer et al. 2008). However, recent analyses suggest migratory behavior of some North American raptors may be changing in response to climate change (Rosenfield et al. 2011, Buskirk 2012), and we wanted to assess whether this might be a factor in the golden eagle trends reported by Farmer et al. (2008). In addition to providing insights into golden eagle population change over the analysis period, our results also extend the utility of the hierarchical model developed by Sauer and Link (2011) in generating estimates of population numbers through the incorporation of estimated detection probabilities from the WGES.

STUDY AREA

The WGES was conducted in the United States portions of BCRs 9, 10, 16, and 17, which collectively cover the majority of the interior conterminous western United States (Fig. 1). Military lands, elevations >3,048 m, water bodies



Figure 1. Map of our study area showing Bird Conservation Regions (BCRs), the geographic regions by which we stratified our analyses of golden eagle surveys. Shaded BCRs were included in our study.

>30,000 ha, and large urban areas accounting for 6.03% of these BCRs were not sampled in the WGES. The BBS provides information for the entire western United States; we used BBS data for each BCR west of the 100th meridian in the conterminous United States (Table 1). Thus, we used

Table 1. Bird Conservation Region (BCRs) areas used in our analysis ofgolden eagle surveys, 2006–2010.

BCR ^a	Area (km ²) ^b
9—Great Basin	671,710
10—Northern Rockies	504,133
16—Southern Rockies/Colorado Plateau	477,753
17—Badlands and Prairies	360,113
5—Northern Pacific Rainforest	175,866
11—Prairie Potholes	414,819
33—Sonoran and Mojave Deserts	216,255
34—Sierra Madre Occidental	123,571
32—Coastal California	155,169
15—Sierra Nevada	48,340
18—Shortgrass Prairie	381,839
35—Chihuahuan Desert	176,139

^a Analysis used only United States portions of BCRs.

^b We filtered BCR areas to exclude military lands, elevations >3,048 m, water bodies >30,000 ha, and large urban areas to be compatible with the areas used by Nielson et al. (2012). Overall, this resulted in a 6.03% reduction in area compared to the unfiltered BCR areas.

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both WGES and BBS data from overlap BCRs 9, 10, 16, and 17, and BBS data only from the non-overlap BCR 5 (Northern Pacific Rainforest), BCR 11 (Prairie Potholes), BCR 15 (Sierra Nevada), BCR 18 (Shortgrass Prairie), BCR 32 (Coastal California), BCR 33 (Sonoran and Mojave deserts), BCR 34 (Sierra Madre Occidental), and BCR 35 (Chihuahuan Desert).

METHODS

We used a log-linear hierarchical model (Sauer and Link 2011) to estimate population sizes and trends, and to integrate data from the WGES and the BBS. The WGES was conducted by WEST, flying fixed-wing aircraft along transects at a speed of about 161 km/hr. For complete details on the design of the WGES, see Good et al. (2007) and Nielson et al. (2012). We used WGES data from 2006 through 2010 in these analyses; we did not use data from the pilot year of 2003 as it may not be comparable, following the recommendation of Nielson et al. (2012). In each year, WEST flew between 203 and 216 standardized transects (Table 2). Transect length was typically 100 km, but differences in the number and length of transects occurred for various reasons (e.g., in some years forest fires precluded flying all or portions of some transects). These variations

 Table 2.
 Length (km) of transects flown by year on the western United States summer golden eagle survey (WGES) in Bird Conservation Regions (BCRs)

 9, 10, 16, and 17.

BCR	2006	2007	2008	2009	2010	Total
9	6,016	5,857	5,770	5,915	5,911	29,469
10	4,606	4,570	4,546	4,728	4,557	23,007
16	3,966	3,998	3,975	3,807	3,939	19,685
17	3,143	3,245	3,129	3,147	3,201	15,865
Total	17,731	17,670	17,420	17,597	17,608	88,026

were accommodated by treating transects as sampling units in the log-linear hierarchical models. These surveys were conducted from 15 August to 15 September, after juvenile golden eagles had fledged but before autumn migration (Fuller et al. 2001).

Surveys were flown at different altitudes because of topography. Specifically, rugged portions of transects were flown at a higher altitude (150 m above-ground level; AGL) compared to relatively level portions (107 m AGL). During 2006, 2007, 2009, and 2010, 2 observers were situated on the right side of the aircraft (1 in the front seat and 1 in the rear) and 1 observer in the rear left side of the aircraft. During 2008, only 1 observer occupied the right side of the aircraft (in the front) on 68 of 213 transects. Observers counted all golden eagles, attempted to place each eagle in an age class, estimated the perpendicular distance of observed eagles from the transect, and recorded whether eagles were perched or flying. Using these data and a combination of distance sampling (Buckland et al. 2001) and mark-recapture methods (Borchers et al. 2006), Nielson et al. (2012) estimated population sizes and detection functions for golden eagles in each of the 4 BCRs covered by the WGES. Considering the various combinations of observer position (back-left, front and back-right, and front-right only), flight height (AGL), and eagle behavior (flying vs. perched), we recognized 9 different detection categories for our analysis of WGES data. In our analysis, we used the estimated average probability of detection within 1,000 m of the aircraft for each detection category to relate counts of golden eagle groups during the WGES to density estimates.

The BBS was conducted from the ground at points along road transects (different from WGES transects) from April through June. Each route was 39.4 km long and survey points were placed at 0.8-km intervals. Protocol dictated that observers counted every bird that was not a dependent juvenile heard or seen within 400 m for a 3-minute period at each point. However, we were not confident that observers consistently followed protocol with respect to the distance, so we did not incorporate the area sampled in analysis of the BBS data. We used BBS data from 1968 to 2010 for this analysis, but calculated trend estimates for 2 time periods: 1968-2010 and 1990-2010. We included the former period to present our best estimate of trend for the complete range of years for which we have data. We present the limited trend because early years of the BBS provided relatively small sample sizes for analysis, and these small sample sizes can lead to imprecise results and to an inability to distinguish patterns within the period. The years 1990-2010 had much

greater BBS coverage and commensurately larger golden eagle sample sizes, and the estimates of annual change over this period were unaffected by the imprecise estimates from the earlier years. Past analyses of BBS data have assigned routes to strata defined by BCR and state or province. To maintain consistency with the design of the WGES, we defined strata based on BCR only, except that we split out British Columbia and Alberta from BCRs 10 and 11 because the WGES did not survey areas outside the United States.

Many juvenile golden eagles encountered during the WGES in a given year were not available to be sampled during the BBS survey in that year, as the BBS primarily occurred before juvenile golden eagles fledged. Initially we considered analyzing the juvenile and non-juvenile age class data separately, but uncertainty over how to treat golden eagles classified as an unknown age in the WGES precluded this approach. Therefore, we combined all golden eagles observed during the WGES to a single age class.

The hierarchical models we used to derive population indices accommodate the stratification and the repeated sampling (i.e., counts are conducted along the same transects each year for the respective surveys) design of both surveys (Sauer and Link 2011, Nielson et al. 2012). The model used for the BBS was

$$\log(\lambda_{i,j,t}) = S_i + \beta_i T_t^* + \gamma_{i,t} + \omega_j + \eta E_{j,t} + \varepsilon_{i,j,t}$$

where we assumed that counts of eagles from each transect were samples from an overdispersed Poisson distribution with expected value λ that was specific for each BCR (*i*), route-observer combination (*i*), and year (*t*). The S and β represent BCR-specific intercept and slope parameters for underlying trends over the entire time series. Following Sauer and Link (2011), we centered years on the median value (i.e., $T_t^* = t$ – median year). We also included BCRand year-specific random effects (γ) to model annual indices as offsets from the underlying trends, a random effect for observer and BBS route combinations (ω) to account for repeated sampling along the same routes by the same observers each year, and a fixed effect of first-year observers (η) to account for inexperience and learning by observers during the survey. The $E_{j,t}$ was an indicator variable that was assigned a 1 if an observer conducted a BBS route *j* for the first time (in year t) and a 0 otherwise (e.g., observer experience). We included an overdispersion parameter (ε) to account for extra Poisson variation. Following Sauer and Link (2011), we weighted BBS indices for each BCR by the proportion of routes that recorded ≥ 1 golden eagle since the survey's inception. Because we did not have an estimate of detection probability or area sampled, the model for the BBS data yields an annual index to population size quantified as the number of birds per route (Sauer and Link 2011).

Although the model structure for the WGES was similar to the BBS model, the WGES model statement accommodated differences in survey design. For the WGES, WEST 1) employed observers that were carefully trained and had a year of pilot surveys, which allowed us to ignore the first-year observer effect; 2) estimated detection probability, which allowed us to adjust the counts for undetected individuals; and 3) surveyed a defined area along a systematic sample of transects across the overlap area, which enabled us to estimate an actual density (see Table S1, available online at www.onlinelibrary.wiley.com). Our modeling approach was similar to Zimmerman et al. (2012), except that we included detection rate directly in the main model, whereas they used a visibility correction factor when calculating derived statistics. Specifically, the structure of our model for the WGES data was

$$\log(\lambda_{i,j,a,b,c,t}) = \log(A_{j,a,b,c}) + \log(P_{a,b,c}) + S_{i,c} + \beta_{i,c} T_t^* + \gamma_{i,c,t} + \omega_{i,c} + \varepsilon_{i,j,a,b,c,t}$$

where A represented the area sampled for each detection class along transects and P represented the detection probability. Area sampled was based on the assumption of a 1,000-m buffer on each side of the aircraft minus the area underneath the plane where vision was blocked, which was 25 m over flat terrain and 40 m over rugged terrain for each side of the aircraft (i.e., total buffer width was 1,950 m and 1,920 m over flat and rugged terrain, respectively). The indexing for the WGES data was slightly different than the model for the BBS data. Although *i* still indexed BCR, *j* represented individual transects for the WGES data (i.e., our sampling unit). The indices a, b, and c are associated with detection classes. Detection probabilities varied by 1) for perched golden eagles, gentle terrain flown at 107 m versus rugged terrain flown at 150 m, indexed by a above; 2) side of the airplane (left side had 1 observer in the rear, the right side had 2 observers most years, and 1 observer in the front for some transects in 2008) indexed by b above; and 3) behavior (flying vs. perching birds) indexed by *c* above. Although the detection probability of perched birds varied by altitude

flown, we found no effect of altitude on detection of flying birds (Table 3). Separate linear regressions $(S_{i,c} + \beta_{i,c}T_t^* + \gamma_{i,c,t})$ of the trend and separate random transect effects $(\omega_{j,c})$ were estimated for perched and flying birds.

We used Bayesian methods to make inferences about unknown parameters in the models. We used the Markov chain Monte Carlo (MCMC) method implemented in program WinBUGS (Lunn et al. 2000) to estimate posterior distributions of unknown parameters (Table S1, available online at www.onlinelibrary.wiley.com, which also provides prior distributions for each of the unknown parameters). We incorporated uncertainty associated with the detection probabilities by sampling a P (detection probability) from a normal distribution with means and variances estimated by Nielson et al. (2012; see Table 3). We ran 3 chains for 40,000 iterations and used the first 36,000 iterations for a burn-in period and made inferences using the final 4,000 iterations for each of the chains. Therefore, our final summary statistics are based on a total of 12,000 iterations. We inspected history plots and used R to estimate convergence. R convergence measures <1.1 suggested convergence (Gelman and Hill 2007), and all model results reported here had \hat{R} values ≤ 1.03 .

We used the MCMC procedure to estimate the posterior distributions of several derived parameters. We computed annual indices of golden eagles from each survey in each BCR as functions of the model parameters. For the BBS, we derived annual indices (I) of birds per route from parameters and variance components as

$$I_{i,t} = z_i \exp(S_i + \beta_i T_t^* + \gamma_{i,t} + 0.5\sigma_{\omega}^2 + 0.5\sigma_{\varepsilon}^2)$$

where z represented a weighting factor based on the proportion of routes in that strata (Sauer and Link 2011). We estimated annual estimates of birds per km^2 from the WGES as

$$n_{i,t,c} = \exp(S_{i,c} + \beta_{i,c}T_t^* + \gamma_{i,t,c} + 0.5\sigma_{\omega_c}^2 + 0.5\sigma_{\varepsilon_c}^2)$$

Note that perched birds were indexed as c = 1 and flying as c = 2, and we summed these 2 densities to estimate a total density for eagles in each BCR for each year based on the WGES data (n_{it}) .

Similar to Zimmerman et al. (2012), we needed to scale data from 1 survey to the level of the other to integrate results from the 2 surveys. We chose to scale the BBS data to the

Table 3. Detection probabilities and standard errors (SE) for the different observation categories in the western United States summer golden eagle survey (WGES) in Bird Conservation Regions (BCRs) 9, 10, 16, and 17 from 2006 to 2010.

		Detection probability (SE) ^a	
	Eagle flying	Eagle	perched
Observer position in aircraft	All terrain ^b	Gentle ^c	Rugged ^c
Left (rear)	0.437 (0.071)	0.443 (0.033)	0.325 (0.010)
Right (front and rear)	0.511 (0.060)	0.556 (0.033)	0.419 (0.091)
Right (front only; 2008)	0.304 (0.059)	0.426 (0.032)	0.283 (0.090)

^a Detection probabilities were estimated as the mean of detection functions from distance sampling over a 1-km range.

^b Terrain and altitude did not influence detection probabilities for flying golden eagles.

^c Flight altitude was 150 m above-ground level over rugged terrain compared to 107 m above-ground level over gentle terrain.

level of the WGES because the goal of this analysis was to derive a population estimate. To transform the BBS indices of birds per route during the breeding season to estimates of density post-fledging, we adjusted the BBS levels for the overlap BCRs to the WGES for all years using the ratio of the sum of WGES densities over all overlap years (*nDen* in Table S1, available online at www.onlinelibrary.wiley.com) to the sum of the BBS indices over all overlap years (*n* in Table S1, available online at www.onlinelibrary.wiley.com) for each BCR (i = 9, 10, 16, and 17):

$$\text{Scale}_i = \frac{n_{i,.,.}}{I_i}$$

The purpose of the scale factor is to adjust the results of the 2 surveys to a common level to enable results to be combined during years of overlap. In addition to combined inference for overlap years, historical BBS results should be scaled to be consistent with combined results to make inferences regarding population size and trends for years prior to implementation of the WGES. More complicated models for aggregation could be considered, with parameters to control for 1) differences in units (i.e., BBS population index and WGES density) and approach (road counts vs. aerial counts); 2) mortality of birds throughout the summer; and 3) movements of birds to and from the conterminous western United States during the summer. These factors are accounted for implicitly by the scale factor in our analyses, but even with data and a model to directly account for these added features we would still need to estimate a constant scale factor to adjust the BBS index to the density scale of the WGES. We adjusted the BBS indices in the non-overlap BCRs using an overall scaling factor averaging the overlap BCR-specific scaling factors, and based variability in these estimates on the MCMC simulations. These constant scale factors maintained the trend information in the BBS data and were the best available for adjusting BBS indices for the years prior to the WGES.

After scaling the BBS data to represent densities, we calculated composite estimates as the means of scaled BBS and WGES densities for each year and BCR. The WGES did not begin until 2006, so the composite BBS densities for years prior to 2006 were only the BBS estimates scaled by the adjustment for the respective BCR in the overlap regions (i.e., prior to 2006, we had no WGES estimate to average with the scaled BBS index). We then calculated the population estimate by expanding the composite density estimates by the total area in each BCR. We generated area estimates that excluded military lands, elevations >3,048 m, water bodies >30,000 ha, and large urban areas. Overall, we excluded 6.03% of the total area.

We calculated trends by BCR and for all BCRs combined as the average population change from 1968 to 2010 and 1990 to 2010 based on the composite population index as suggested by Sauer and Link (2011):

$$B_i = \left(rac{N_{i,2010}}{N_{i, ext{year1}}}
ight)^{1/(2010- ext{year1})}$$

where i indexes BCR, year1 represents the first year (i.e., 1968 or 1990), and N is the composite population size for each year, reported as a percent relative change.

We compared our results relative to population size and trends for golden eagles in the western United States to prior published assessments, including the previous analyses of the WGES by Nielson et al. (2012). With respect to trends in numbers of autumn migrant golden eagles, we hypothesized that if migration behavior was changing in response to climate change that negative trends in autumn counts of golden eagles would be greater at southern than more northern hawk watch sites. A complete assessment of this hypothesis was not possible as we were unable to obtain raw data from all pertinent hawk watch sites for analysis in this paper. Given this, we were not able to separate the locationspecific trends from the overall trend, but we were able to evaluate this hypothesis in a preliminary context by plotting the summary trend results from Smith et al. (2008: 226–227) against latitude, and fitting a locally weighted scatterplot smoothing (LOWESS) line to the trend data and to upper and lower 95% confidence limits for each site. We used the locfit package and scb function (http://CRAN.R-project. org/package=locfit, accessed 18 Jun 2012) in R (version 2.15.0, http://www.r-project.org/, accessed 18 Jun 2012) for this analysis.

RESULTS

From 2006 to 2010, 780 golden eagles were detected on approximately 88,000 km of transects that were surveyed in the 4 BCRs covered by the WGES (Table 2). Golden eagle detection probabilities on the WGES across the 9 detection classes ranged from 0.28 to 0.56 (Table 3). Hierarchical model estimates from the WGES for the total population of golden eagles in all BCRs tended to be slightly larger than distance sampling estimates, but broad overlap occurred in the credible intervals (Fig. 2).

Golden eagles are generally seen at low abundances throughout their range on BBS routes, though our analysis included 3,977 golden eagle detections on BBS routes over all 12 BCRs over the study period (Tables S2 and S3). As BBS data only index trends, the scaling factors derived from the WGES analysis for each BCR allowed us to adjust the scale of BBS estimates from golden eagles per route to golden eagles per km² (Table 4). The scaling factors were similar among BCRs 9, 10, and 16. The scaling factor in BCR 17 was approximately 3 times greater than the other BCRs, which resulted from a relatively high density of eagles observed in that BCR by the WGES ($\bar{x} = 0.009, 0.015$, 0.008, 0.027 birds/km² in BCRs 9, 10, 16, and 17, respectively) compared to the BBS index of birds per route $(\bar{x} = 0.322, 0.362, 0.225, 0.253 \text{ in BCRs } 9, 10, 16, \text{ and } 17,$ respectively). In other words, the WGES estimated almost double the density of golden eagles in BCR 17 compared to any of the other BCRs, whereas the BBS survey counted more birds per route in BCRs 9 and 10 than BCR 17. We plotted the scaled BBS data against the densities estimated from the WGES to compare trends between the 2 surveys (Fig. 3). Credible intervals of yearly estimates and patterns of



Figure 2. Comparison of population estimates from our hierarchical model to those derived from distance sampling (Nielson et al. 2012) from the western United States summer golden eagle survey in Bird Conservation Regions (BCRs) 9, 10, 16, and 17, 2006–2010. Error bars represent the 90% credible intervals.

population change of overlap BCRs were generally consistent between surveys. Declines in WGES results in BCR 17 over the period 2006–2009 were not significantly different from the no-change indicated by BBS results, and more positive

Table 4. Factors used to scale the Breeding Bird Survey (BBS) counts of golden eagles per route to the level of golden eagles per km^2 as estimated from the western United States summer golden eagle survey (WGES), for the 4 Bird Conservation Regions (BCRs) and years of overlap (2006–2010) for the 2 surveys.

BCR	Median scaling factor (95% CI)
9	0.028 (0.020, 0.039)
10	0.042 (0.029, 0.062)
16	0.034 (0.023, 0.052)
17	0.106 (0.069, 0.168)
Overall	0.053 (0.041, 0.071)

trends from WGES results in BCR 10 were likewise not significantly different from the less positive BBS results.

We expanded the 4 overlap BCR density estimates to provide estimates of composite population size and credible intervals for these BCRs (Fig. 4). As in the non-combined estimates, credible intervals of the composite population index were larger for BCR 17. However, average coefficients of variation for BCRs 9, 10, 16, and 17 were 21%, 21%, 25%, and 25%, respectively, indicating that the variability of BCR 17 scaled with the higher index of golden eagles there (i.e., indices were 2–4 times higher in BCR 17 than in the other 3 BCRs).

Population estimates for BCRs other than 9, 10, 16, and 17 were based solely on BBS data, which were scaled to the level of the WGES using the overall scaling factor (Fig. 5, Table S4). Our analysis indicates some support for population increases in the Northern Rockies and Prairie



Figure 3. Comparison of trends in golden eagle density for years and Bird Conservation Regions (BCRs) of survey overlap by the Breeding Bird Survey (BBS) and Western Golden Eagle Survey (WGES). Error bars represent the 95% credible intervals.

Pothole BCRs (10 and 11, respectively), and slight declines in some of the southern BCRs (15, 16, 32, 33). However, in nearly all cases credible intervals included 0, indicating limited support for decreasing or increasing populations in these BCRs. The overall trend estimate from 1968 to 2010 for all BCRs combined (including both the combined results from the 4 overlap strata and the BBS-only strata) was +0.4% per year (95% CI = -0.27% to 1.00%), suggesting the population was stable over the period (Figs. 5 and 6). Our estimate of overall trend for the period 1990–2010 was +0.5% per year (95% CI = -0.33% to 1.3%).

Our LOWESS-fit plot of trends in counts of autumn migrant golden eagles by latitude showed stronger negative trends from 1995 to 2008 at hawk watch sites south of 40° north latitude than a sites further north (Fig. 7).

DISCUSSION

These data represent the first comprehensive, integrated analysis of the 2 most appropriate existing datasets to assess

the golden eagle's status in the western United States and are therefore of interest for comparison with previous findings. Kochert and Steenhof (2002) provided a broad overview of migration count, BBS, Christmas Bird Count, and local population study data for golden eagles throughout North America. They concluded that golden eagle populations in Alaska and Canada were likely stable, but that some breeding populations in the western United States were evidencing declines. Nielson et al. (2012) analyzed the WGES trend data from 2006 to 2010 and concluded those data showed no evidence of a trend in overall numbers of golden eagles in BCRs 9, 10, 16, and 17. Our findings from the composite analysis of BBS and WGES data for the overlap BCRs parallel those of Nielson et al. (2012) for the period of the WGES, but also suggest the study population has been generally stable in those BCRs since the late 1960s. Moreover, our analysis of BBS data for the other BCRs in western North America suggests golden eagle populations are generally stable there as well. Our overall estimates of



Figure 4. Integrated Breeding Bird Survey and Western Golden Eagle Survey estimates of golden eagle population size in Bird Conservation Regions (BCRs) 9, 10, 16, and 17. Dashed lines represent the 95% credible interval.

golden eagle population trends were similar for the 2 time periods of analysis, so these findings were not an artifact of the relatively imprecise estimates over the early years of the BBS.

The level of imprecision and scale of our estimates certainly leaves room for the local declines described by Kochert and Steenhof (2002), and point estimates of trend for BCRs 15, 16, and 34 were <0 in our analysis. However, point estimates of trend from our analysis were above 0 for BCRs 5, 9, 10, 11, 17, and 18. Thus, although our results overall suggest golden eagle populations are and have been stable for the past 43 years in the western United States, the direction of golden eagle population change may differ at the BCR level. In addition, the amount of annual change estimated in some BCRs is greater than what might be expected from mortality and fecundity alone. This suggests that other factors, such as geographic shifts in the summer distribution of golden eagles from southern to northern BCRs among years, may be contributing to the population change estimates at the BCR level.

Our composite estimates for BCRs 9, 10, 16, and 17, both in terms of golden eagle population trends and size, compare favorably with prior distance sampling analyses of the WGES data (Nielson et al. 2012). We note that our estimates were slightly greater than those based on distance sampling alone because of transformation to the log scale and the addition of variance components for calculating derived parameters for our log-linear model, the inclusion of a sample unit random effect in our repeated measures analysis, and the slightly larger expansion areas used in our analysis. However, credible intervals for the 2 approaches greatly overlapped and inferences were consistent.

Our inferences regarding trend in all cases are based on BCR-specific information. The scaling factor, which we derived from the overlap BCRs only, merely scaled results from 1 survey to the other and had no affect on the trend



Figure 5. Trend estimates by Bird Conservation Region (BCR) and total survey area for golden eagles based on Breeding Bird Survey indices (BCRs 5, 11, 15, 18, 32, 33, 34, and 35) and integrated population estimates (BCRs 9, 10, 16, and 17). The black lines represent trends for the 1968–2010 period and the gray lines represent the trend from 1990 to 2010. Error bars represent 95% credible intervals.

estimate. Scaling permitted the conversion of golden eagles observed per BBS route to golden eagles per km², and controlled for population differences due to timing of surveys (i.e., the BBS survey was largely a pre-fledging survey

whereas the WGES was a post-fledging survey). Inclusion of the BBS data allowed us to extend the time series trend beyond the years of the WGES in the overlap BCRs and make predictions about population size in BCRs outside of





Figure 6. Trend in golden eagle population estimates for all western United States Bird Conservation Regions (BCRs) combined, 1968–2010. Estimates for all BCRs from 1968 to 2005 are from the Breeding Bird Survey (BBS), as are estimates for all BCRs but 9, 10, 16, and 17 from 2006 to 2010. Estimates for BCRs 9, 10, 16, and 17 for 2006–2010 are composite estimates using both BBS and western United States summer golden eagle survey data. The middle line is the median, and upper and lower dotted lines represent the 95% credible intervals.

Figure 7. Trends in counts of autumn migrant golden eagles at 10 hawk watch sites in the western United States, as reported in Smith et al. (2008; Table 3). Periods of observation vary by site, but range from 1985 to 2005. The middle line is the mean, and the upper and lower dotted lines represent the 95% confidence intervals reported in Smith et al. (2008).

the overlap area. We have advanced our understanding of golden eagle populations in these BCRs, and implemented a method for incorporating detection rates into the Sauer and Link (2011) hierarchical model. The close correspondence in direction and magnitude between BBS and WGES trends in BCRs 9, 10, 16, and to a lesser degree, 17, for the overlap years of 2006–2010 suggest the BBS may provide more useful information on golden eagle population change than previously thought (Kochert and Steenhof 2002). This also lends support for our use of BBS data to provisionally estimate golden eagle trends in other BCRs in the western United States.

Smith et al. (2008) and Farmer et al. (2008) reviewed migration count data from autumn hawk watch sites in western North America, and reported negative count trends over the most recent decade at many count sites and concluded migratory golden eagle populations in western North America were undergoing recent declines. Our reassessment of their results suggests a latitudinal pattern may exist in the trends in counts of autumn migrant golden eagles in western North America. Such a pattern implies that factors other than, or in addition to, population change may be operating to affect autumn counts of migrant golden eagles. We hypothesize that this pattern may be a consequence of changes in migratory behavior that result in fewer golden eagles arriving at southern hawk watch sites during the time those sites are operating. This could occur if fewer golden eagles left northern breeding areas, if they migrated shorter distances, or if migration were delayed in time, such as has been reported for the sharp-shinned hawk (Accipiter striatus; Rosenfield et al. 2011) and other raptors in eastern North America (Buskirk 2012). This hypothesis should be explored further with full data from these hawk watch sites. Counts of migrant golden eagles also represent a larger area than is covered by the WGES or our BBS samples (e.g., golden eagles from breeding areas across all of Canada and Alaska), and population trends in the portion of the migrant population not included in our analyses were possibly different from those of golden eagles summering in the western United States.

Historically, the golden eagle population in the conterminous United States was estimated at between 10,000 and 100,000 individuals (Hamerstrom et al. 1975), but this estimate was not based on actual surveys. Rich et al. (2004) estimated about 30,000 golden eagles occurred in parts of the United States and Canada sampled by BBS routes. Good et al. (2007) estimated 27,392 golden eagles (90% CI: 21,352-35,140) occurred in the WGES area in 2003. Nielson et al. (2012) updated the estimate of Good et al. (2007) for the WGES area for the years 2006-2010; annual estimates of total population size ranged from a low of 19,286 (90% CI: 15,802-23,349) in 2008 to a high of 24,933 (90% CI: 20,296–30,664) in 2007. The Service adopted an estimate of 30,193 golden eagles in the conterminous western United States in its final environmental assessment addressing unintentional take regulations under the Bald and Golden Eagle Protection Act; this estimate was derived from a combination of the WGES results through 2008 for BCRs 9,

10, 16, and 17, and estimates in Rich et al. (2004) for the other western BCRs (U.S. Fish and Wildlife Service 2009). Our population estimates from the composite model for the overlap BCRs for 2006-2010 range from a low of 26,490 (95% CI: 21,760-32,680) in 2008 to a high of 28,220 (95% CI: 23,250-35,110) in 2007, slightly greater than the estimates of Nielson et al. (2012). Our overall golden eagle population estimates for the western United States must be regarded cautiously in light of the underlying assumptions. However, our annual estimates since 2001 (31,370 [95% CI: 25,450-39,310] in 2004 to 33,460 [95% CI: 27,380-41,710] in 2007) compare favorably with the Service's 2009 estimate (U. S. Fish and Wildlife Service 2009) and the Partner's In Flight estimate, though the latter included parts of Canada not covered by our estimate (Rich et al. 2004), and our estimate excludes 6.03% of the area in the western United States.

Two issues with our approach warrant further discussion. First, for the years and BCRs where we had both BBS and WGES data, we were able to directly calculate scaling factors to scale the BBS data to estimate golden eagle density. Factors accounted for by the adjustment in these BCRs and years included 1) differences in units between the BBS and WGES due to a lack of detection probability and lack of a well-defined sampling area associated with BBS counts, 2) possible bias in the BBS estimates given the counts are conducted from roads, 3) addition of fledged young to and mortality of breeding birds from the golden eagle population of each BCR between the time of the BBS and WGES, and 4) immigration and emigration of birds between the 2 surveys. As noted previously, we considered omitting juvenile golden eagles counted on the WGES from the composite estimates, and then estimating trends and density of juveniles separately. However, we were uncertain how to treat unknown-age golden eagles seen on the WGES under that approach. In some years and in some BCRs the number of unknown-aged eagles was at the same level as the number of juveniles; therefore, the treatment of unknowns had influential consequences on estimates of juvenile population size and trend. After comparing various approaches, we decided that pooling age classes and thus incorporating the correction for the addition of juveniles to the population between the BBS and WGES into the scaling factor was the most defensible method.

The second issue involves application of the scaling factor used to scale the BBS counts to golden eagle density. The overall scaling factor was similar for BCRs 9, 10, and 16, but about 3 times greater in BCR 17. We are uncertain why BCR 17 was different, but this demonstrates that the adjustment can vary considerably among BCRs. However, the overall scaling factor reflects the differences among groups, as it has a large credible interval that overlaps the credible intervals of all the BCR estimates except BCR 9. The overall scaling factor allows us to scale BBS data for non-overlap years and BCRs to an abundance estimate, and that abundance estimate reflects the uncertainty in the scaling factor. Even though uncertainty reflected in the composite estimate reduces the precision, the population size estimates we calculated are based on survey data and have direct management relevance, as estimates of population size are essential for the Service's permitting of eagle take. The golden eagle population size estimates currently being used by the Service for the non-overlap BCRs are based on outdated estimates from biological data for which measures of uncertainty are lacking (Rich et al. 2004, U.S. Fish and Wildlife Service 2009). Accordingly, comparative population estimates using current data, for which explicit assumptions can be described, and which are amenable to testing are desirable for the non-overlap BCRs.

A fundamental assumption underlying our population estimates for the 8 non-overlap BCRs is that the overall adjustment factor for BCRs 9, 10, 16, and 17 is relevant for these BCRs and years. This assumption could be tested by independent surveys in these BCRs and generating additional BCR-specific adjustment factors for comparison. In the meantime, considering the variation in adjustment factors we found for the 4 overlap BCRs, the population estimates presented here for the non-overlap BCRs should be regarded cautiously and with due consideration of the wide confidence intervals surrounding the annual estimates and range in the adjustment factors for the 4 overlap BCRs. Improving population estimates for non-overlap BCRs may also be possible by using information presented in our supplemental tables in conjunction with other information (e.g., BCR-specific landscape-scale habitat information) to better match scaling factors for non-overlap BCRs to the most similar overlap BCR.

Hierarchical models provide a very general framework for modeling survey data, and we chose to use models that conformed as close as possible to present BBS analyses (Sauer and Link 2011) but used the information and results from analysis of WGES data (Nielson et al. 2012). During the development of the model, we considered alternative forms to assess whether we could improve performance. Alternatives we evaluated included approaches where we modeled the trend with a common linear regression or a common random walk (Durbin and Koopman 2001) for both surveys, estimated a single trend with random effects for perched and flying birds, and included a BCR-transect-year random effect and estimated BCR-specific variances. These alternative models resulted in only minor changes to our results and did not influence inferences from our study.

MANAGEMENT IMPLICATIONS

Our findings have potential implications for the issuance of golden eagle take permits under the Act by the Service. In 2009, the Service concluded that golden eagle populations might be declining and were not robust enough to support additional permitted take. Consequently, the Service severely restricted availability of such permits. Our results clarify that golden eagles are not declining, at least widely and at the present time, in the western United States, though we acknowledge occupied breeding areas may be declining locally or regionally as described by Kochert and Steenhof (2002). However, our findings do not address the question of whether golden eagles have the demographic resiliency to absorb additional mortality and maintain their stable population trajectory. Additional demographic research and modeling is needed to address this question. Our results also show promise relative to use of a combination of BBS and aerial surveys in generating credible population size estimates for golden eagles on a landscape scale. Population size estimates and an understanding of the uncertainty in those estimates are necessary to assess the population-level significance of any authorized take of golden eagles. An important next step is to conduct WGES-like aerial counts in 1 or more of the non-overlap BCRs to develop additional BCR-specific adjustment factors for comparison with those presented here for BCRs 9, 10, 16, and 17. Such an analysis would help clarify the applicability of an overall adjustment factor for BBS counts in other BCRs, and provide information useful in deciding whether aerial surveys comparable to the WGES are necessary in every BCR for which population estimates are needed.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.

Table S1. WinBUGS code used to integrate information from the Breeding Bird Survey (BBS) and western United States summer golden eagle survey (WGES).

Table S2. Number of golden eagles counted on Breeding Bird Survey (BBS) routes by Bird Conservation Region (BCR) from 1968 to 2010. Data from Canadian potions of BCRs that extend into Canada are excluded.

Table S3. Numbers of Breeding Bird Survey (BBS) routes for Bird Conservation Regions (BCRs) used in this analysis that have been surveyed from 1968 to current. Counts in Canadian portions of BCRs that extend into Canada are omitted.

Table S4. Golden eagle population estimates for all western United States Bird Conservation Regions (BCRs), 1967– 2010. For the overlap BCRs (9, 10, 16, and 17) and years (2006–2010) the estimates are composites derived from the BBS and WGES. For other BCRs and years, estimates are derived from the BBS only, using the overall adjustment factor derived for the composite estimates to scale to density.