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A review of trail-related fragmentation, unauthorized trails, and other aspects of recreation ecology in protected areas

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Expanding levels of authorized and unauthorized non-consumptive recreation increasingly threaten sensitive biological resources in areas protected primarily or solely to conserve them. The majority of the documented effects on wildlife from non-consumptive recreation are negative. From a review of 84 papers in the recreation ecology literature about the effects of recreation on wildlife, the following topics emerged as warranting full consideration: trail-related internal fragmentation and expansion of the effect zone; the proliferation and use of unauthorized trails; disturbance thresholds; population-level effects; distinguishing facets of mountain biking; interpretation of observed behavioral responses by wildlife to recreation; magnitude and duration of responses; comparisons of effects among types of recreation and of results among studies; cumulative and synergistic effects; habituation; and the complexity of recreation ecology. Knowledge of these topics must inform efforts to cease the extant recreation-related exploitation of protected areas and to prevent it in the future. These efforts include: securing urgently needed perpetual monitoring, management, and enforcement commensurate with recreational pressure in dual-role protected areas to ensure the perpetuation of viable populations of focal sensitive species; preventing further use and proliferation of unauthorized trails; restoring areas damaged by inappropriate trails (i.e., unauthorized trails, unnecessarily redundant designated trails, and trails to be decommissioned); using science-based disturbance thresholds to develop management measures for recreation; using the best available science to guide all policy and decision-making about (1) the siting, design, and alignment of trails, and (2) the types, levels, and timing of recreation under consideration; and, planning separate protected areas and recreational areas in the future.

Key words: dual-role protected areas, effect zone, disturbance thresholds, internal fragmentation, mountain biking, non-consumptive recreation, perpetual monitoring/management/enforcement, recreation ecology, recreation-related disturbance to wildlife, unauthorized trails

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Conservation of habitats is a key strategy for conserving biodiversity worldwide (Pickering 2010a; Soulé and Noss 1998). The core function of many areas in California protected for conservation is to ensure that the wildlife species living in them thrive in what is the nation's most biologically diverse state (CDFW 2015).[1] Areas protected for conservation (protected areas) include locally owned lands (e.g., county and city reserves), state-owned lands (e.g., ecological reserves, wildlife areas, state parks), federally owned lands (e.g., national wildlife refuges, wilderness areas), and privately owned lands (e.g., conservation easements, conservancy lands, mitigation banks and lands). Here, the focus is on protected areas conserved primarily or solely for the perpetuation of viable populations of sensitive species (i.e., species whose persistence is jeopardized).[2] These protected areas often serve a dual role of conserving biodiversity and providing nature-based recreational and educational opportunities for millions of people, despite the evidence that even non-consumptive recreation[3] may not be compatible with protected areas' core function (Reed and Merenlender 2008; Larson et al. 2016; Dertien et al. 2018; Reed et al. 2019).

Recreation ecology is the scientific study of the ecological effects of outdoor recreation and nature-based tourism activities and their effective management in natural or semi-natural environments (Monz et al. 2013; Gutzwiller et al. 2017).[4] Studies in recreation ecology have shown that the majority of documented responses of wildlife species to recreation are negative (Steven et al. 2011; Larson et al. 2016; Hennings 2017; Patten and Burger 2018). Recreation-related disturbance to wildlife is recognized as a threat to global biodiversity, and as having wide-ranging and, at times, profound implications for wildlife individuals, populations, and communities (Dertien et al. 2018). Documented negative effects include detrimental changes to behavior, reproduction, growth, immune system function, and levels of stress hormones, and ultimately the survival of individual animals and persistence of wildlife populations and communities.

In this review, several topics about recreation ecology became apparent as warranting full consideration.[5] These topics are (1) the major issues of trail-related fragmentation and

1 Wildlife means all wild animals: insects, fish, amphibians, reptiles, birds, and mammals.

2 These areas include areas protected pursuant to Natural Community Conservation Plans and/or Habitat Conservation Plans (NCCPs/HCPs). An NCCP is a comprehensive, single- or multi-jurisdictional plan that provides for regional habitat and species conservation at an ecosystem level while allowing local land use authorities to better manage growth and development. Upon issuing an NCCP Permit, the California Department of Fish and Wildlife (CDFW) can authorize take of certain state listed species and other species of concern, subject to the terms of coverage under the NCCP (CDFW 2015). An HCP is the federal counterpart to an NCCP; the U.S. Fish and Wildlife Service prepares HCPs and issues HCP permits. The terms and conditions under which an NCCP/HCP's protected areas are conserved establish the types and levels of public access that are permitted (Burger 2012). The types and levels of public access vary among the NCCP/HCP protected areas from no access to guided-only access to open access.

3 In contrast to consumptive recreation (e.g., hunting, fishing), non-consumptive recreation is generally assumed not to directly extract a resource; it includes nature and wildlife viewing, beach-going, kayaking, hiking, biking, horseback riding, and wildlife photography (Reed and Merenlender 2008; CDFW 2016; Gutzwiller at el. 2017). From here forward, "recreation" means non-consumptive recreation, unless otherwise stated.

4 From here forward, "management" includes monitoring, management, and enforcement. The level of enforcement necessary depends on the level of continual management implemented; generally, the more the management, the less enforcement is necessary. In addition, monitoring and management encompass both the natural resources and human users of the protected areas.

5 The author read 71 articles and 13 reports about the recreation-related effects on wildlife; this paper does not cite all of them. All the articles are published in peer-reviewed journals. Some of the reports were peer reviewed and all were written by or contributed to by professionals in the fields of biology or ecology, though none of the reports were published in peer-reviewed journals to this author's knowledge (e.g., Burger 2012; Hennings 2017; Dertien et al. 2018; Reed et al. 2019). And, the totals exclude documents that are not explicitly about recreation-related effects on wildlife (e.g., Taff et al. 2019) and all newspaper articles.

expansion of the effect zone, unauthorized trail creation and use,[6] disturbance thresholds, population-level effects, and distinguishing facets of mountain biking, and (2) the following aspects of recreation ecology: the interpretation of observed behavioral responses by wildlife to recreation, magnitude and duration of responses, comparisons of effects among types of recreation and of results among studies, cumulative and synergistic effects, habituation, and the complexity of recreation ecology.

This paper discusses the issues identified above to inform efforts to cease the extant recreation-related exploitation of protected areas and to prevent it in the future. These efforts include: securing urgently needed perpetual management of recreation commensurate with recreational pressure to ensure the perpetuation of viable populations of focal sensitive species[7] as intended upon establishment of the protected areas; preventing further use and proliferation of unauthorized trails; restoring areas damaged by inappropriate trails (i.e., unauthorized trails, unnecessarily redundant designated trails, and trails to be decommissioned); using science-based disturbance thresholds; using the best available science to guide all policy and decision-making about the siting, design, and alignment of trails, and about the types, levels, and timing of recreation under consideration; and, planning separate protected areas and recreational areas in the future. This paper discusses the above-listed aspects of recreation ecology for consideration in designing field studies and while reviewing recreation ecology literature.

Trail-related disturbance: fragmentation, edge effects, and expansion of the effect zone

External fragmentation.—There is much peer-reviewed literature on the ecological effects of fragmentation, a process by which once-contiguous areas of habitat are physically separated by human disturbance creating a network of isolated habitat patches (Soulé et al. 1988; Ballantyne et al. 2014; Vickers et al. 2015; Cheptou et al. 2017). Most fragmentation research worldwide has concentrated on progressive losses of natural habitat through removal of vegetation as a result of development, agriculture, and resource extraction. Physical fragmentation, in conjunction with other related factors (e.g., duration of isolation of habitat fragments, low vagility of species, loss of genetic diversity), causes the isolated areas of habitat to experience a decay of species diversity over time due to local extinctions (Soulé et al. 1988). Consequently, fragmentation is a major threat to biodiversity (Cheptou et al. 2017). This fragmentation is considered external to the protected areas within a landscape, though it influences the viability of protected areas with respect to wildlife conservation.

Internal fragmentation.—Recreational trails themselves can fragment habitat, thereby causing fragmentation that is internal to the areas they traverse (Pickering 2010a; Leung et al. 2011; Burgin and Hardiman 2012; Pickering and Norman 2017). Because of their linear nature, trails can have a greater negative effect than if the affected terrain were consolidated in a more compact form (Pickering 2010a). Complex networks of trails within protected areas

6 The literature refers to illegally created trails and constructed trail features variously as unauthorized, informal, social, unofficial, off-trail, visitor-created, user-created, and demand trails. "Unauthorized" is the term of choice here because it is the only term among these that clearly denotes the illegality of the creation and use of such trails and features.

7 Focal species are organisms whose requirements for survival represent factors important to maintaining ecologically healthy conditions; types of focal species include keystone species, umbrella species, flagship species, and indicator species. Focal species are identified for the purpose of guiding the planning and management of protected areas in a tractable way (Soulé and Noss 1998, Marcot and Flather 2007). Here, the term "focal species" is intended to include those species encompassed by the guild surrogate approach of conservation; this approach entails one member or a subset of members serving as a surrogate for other members of the guild (Marcot and Flather 2007).

can cumulatively affect nearly as much area as the above-mentioned external fragmentation (Ballantyne et al. 2014). Substantial evidence exists that trails may act as barriers to the movement of animals due to behavioral avoidance, the presence of a physical barrier, or development of a home range along the physical barrier (Burgin and Hardiman 2012). Trail density is a main factor influencing how wildlife respond to trail users and the ability of wildlife to disperse or reach seasonally important habitats such as breeding grounds (D'Acunto et al. 2018). Particularly when resulting from unauthorized trails or poorly sited and/or designed official trails, internal fragmentation can compound the negative effects of the external fragmentation in the surrounding landscape. The arterial spread of multiple cleared areas for trails within protected areas may cause losses of plant communities and ultimately result in long-term degradation of protected areas across large areas (Ballantyne et al. 2014).

Effects of trail presence on wildlife.—A likely consequence of internal fragmentation within protected areas is that the mere presence of trails, even in the absence of humans, can compromise protected areas' ability to sustain sensitive species (Pickering and Norman 2017; Baker and Leberg 2018). This is partly due to edge effects in the area of transition between two contrasting habitats, where resulting changes can occur in species abundance, community structure, and/or predation and parasitism (Zurita et al. 2012). Edge effects are major drivers of change in many fragmented landscapes (Laurance et al. 2007) and factor into the observations that internal fragmentation can restrict movement of some native animals and plants among habitat fragments and enhance the movement of invasive species along the trails (Barros and Pickering 2017). Baker and Leberg (2018) found that the presence alone of roads and trails, and not necessarily how often humans use them, had a significant negative effect on the occupancy of most of the 11 mammalian carnivore species they studied. Trails also potentially expose native animals to predators, including feral species such as the red fox (Vulpes vulpes), that penetrate natural areas by moving along the trails (Burgin and Hardiman 2012): a study on the effects of mountain biking on golden-cheeked warblers (Dendroica chrysoparia) found that the indirect effects from fragmentation and alteration of habitats from mountain biking trails may reduce the quality of the warblers' nesting habitat by increasing the vulnerability of warbler nests to predation by rat snakes (Elaphe obsoleta) and other edge-adapted predators (Davis et al. 2010). Edge effects associated with trails are known to affect other avian species similarly and to reduce the local abundance and nesting frequency of certain avian species, increase the incidence of nest parasitism by cowbirds, and affect avian vocalizations (Hennings 2017). The penetration of edge effects into the areas adjacent to trails is an aspect of internal fragmentation that underscores the ecological cost of unauthorized trails (Pickering and Norman 2017).

Trails expand the zone of effect.—Another notable consequence of trails is the expansion of the zone of effect of recreational disturbance to wildlife as habitats become more open, as occurs from the proliferation of unauthorized trails (Reed et al. 2019). In this context, "effect zones" are areas within which wildlife is disturbed by recreational activities on trails; effect zones encompass and extend beyond the area influenced by edge effects. The expanse of effect zones likely varies depending on the types and intensities of recreation and therefore may not be consistent across a trail network (Reed et al. 2019). Particularly in urbanized areas where protected areas are already highly confined in the surrounding urban matrix, the expansion of the effect zones further dissects and internally fragments what are already essentially habitat 'islands' (Balantyne et al. 2014; Pickering and Norman 2017).

The expansion of effect zones occurs in all protected areas with widespread trails irrespective of the sizes of the protected areas. For small protected areas (~300 ha) with dense trail networks, an effect zone of several hundred meters on either side of the trails can encompass a substantial proportion of the protected areas (Reed et al. 2019). In this way, effect zones reduce the proportion of a protected area that is suitable for various wildlife species (Reed et al. 2019), and can result in no contiguous areas across a protected area free from recreation-related disturbance to wildlife (Dertien et al. 2018).

The higher the level of recreation in protected areas, the greater the potential there is for the effects of trails and their use to extend beyond habitat loss and individual-level effects (behavioral and physiological) on wildlife into population- and community-level effects, including depletion of floral and faunal populations, alteration of trophic and community structures, and reduction of biodiversity (CDFW 2015). If habitat is available, wildlife may move to areas farther from trails, areas beyond the effect zone, to avoid recreation-related disturbance (Reed et al. 2019). However, the greater the proportion of a protected area occupied by effect zones, the fewer options there are for wildlife to move to areas outside the effect zones.

Unauthorized trails and technical trail features

General.—The implications to wildlife conservation of the disturbance to wildlife from trail-related fragmentation and expansion of effect zones are particularly grave with respect to unauthorized trails and recreational activities. The creation and use of unauthorized trails and technical trail features (TTFs) are commonplace and present concerns about the sustainability of biological resources in protected areas worldwide (Marion and Wimpey 2007; Newsome and Davies 2009; Ballantyne et al. 2014; Havlick et al. 2016; Barros and Pickering 2017).[8] Though most unauthorized trails and TTFs are readily visible and accessible, they are not officially planned or designed, approved for construction, managed, or part of a formally designated trail network (Davies and Newsome 2009; Leung et al. 2011; Hennings 2017). All user groups tend to create and use unauthorized trails, and there are several motivations for doing so, such as wanting access to trails closer to home or to engage in off-trail activities (Hennings 2017).

Though other recreationists venture off of designated trails, mountain bikers increasingly create unauthorized trails as they seek more challenging, wider-ranging, or free-riding opportunities (Havlick et al. 2016), or want a shortcut to reach specific destinations or to connect existing trails (Davies and Newsome 2009). If a trail is not sited in a place where bikers want to go, the off-trailing that results eventually forms trails (Davies and Newsome 2009).

Unauthorized trails expand the negative effects of human recreation on the flora and fauna of any protected area (Dertien et al. 2018). Similar to the above-discussed problems associated with internal fragmentation, unauthorized trails and recreational activities can negate the ecological benefits of both well-planned designated trails/trail networks and of prohibitions on access and activity (e.g., avoidance of breeding areas and seasonal access restrictions). The proliferation of unauthorized trails is often more responsible for trail-based fragmentation than formally designated trails (Ballantyne et al. 2014).

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8 TTFs are created on mountain biking trails to increase the challenge of the ride. Examples of TTFs are jumps, ditches, mounds, bridges, ramps, ladders, drop offs, see saws, and 'skinnies' (i.e., narrow features that can be traversed) (Davies and Newsome 2009; Pickering et al. 2010c; Quinn and Chernoff 2010; Ballantyne et al. 2014; Havlick et al. 2016; Hennings 2017; Pickering and Norman 2017).

Even where unauthorized trails occupy a relatively small proportion of a landscape, they can be quite detrimental if in vital habitat; sensitive species whose territories or home ranges include the affected area(s) may be prevented via displacement or loss of habitat connectivity from accessing limited and essential resources (Gutzwiller et al. 2017). Wildlife can be more disturbed by off-trail than on-trail recreationists. For example, Taylor and Knight (2003) compared how mule deer (*Odocoileus hemionus*) respond to hikers and bikers using designated trails and one randomly chosen off-trail route. The deer exhibited a 70% probability of flushing from on-trail recreationists within 100 m from designated trails, whereas they exhibited a 96% probability of flushing within 100 m of recreationists located off trails, and their probability of flushing did not drop to 70% until the distance from the recreationists reached 390 m.

Examples.—Examples of protected areas affected by unauthorized trails include: 19 Natural Community Conservation Plan/Habitat Conservation Plan (NCCP/HCP; see footnote #2) protected areas in San Diego County, California where unauthorized trails comprise a mean of 45% (range: 8–85%) of the 1,206 km of trails mapped (Reed et al. 2014); an 829-ha area of the endangered Tall Open Blackbutt Forest in southeast Queensland, Australia, where 57% (26.5 km) of the 46.1 km of recreational trails was unauthorized when mapped in 2013 (Ballantyne et al. 2014); and, a 237-ha protected area in Argentina where 94% of the 19 km of trails found was unauthorized, resulting in landscape-level fragmentation and loss of vegetation (Barros and Pickering 2017). Another example of a protected area affected by unauthorized trails is the 191-ha Carlsbad Highlands Ecological Reserve in San Diego County. Though mountain biking is prohibited in this reserve, in addition to the 4 km of legal hiking trails in the reserve are also 27.4 km of unauthorized mountain biking trails and TTFs (E. Pert, South Coast Region, Regional Manager, California Department of Fish and Wildlife [CDFW], personal communication, 2019; Figure 1). This ecological reserve, so designated in 2000, comprises a critical component of an NCCP/HCP protected area and supports coastal sage scrub (a sensitive plant community), grasslands, thread-leaved brodiaea (*Brodiaea filifolia*, listed as threatened and endangered under the Federal and California endangered species acts, respectively), and several sensitive wildlife species: the federally threatened coastal California gnatcatcher (*Polioptila californica*), sharp-shinned hawk (*Accipiter striatus*), golden eagle (*Aquila chrysaetos*), white-tailed kite (*Elanus leucurus*), turkey vulture (*Cathartes aura*), and grasshopper sparrow (*Ammodramus savannarum*).[9]

Managing unauthorized trail creation and use.—Managing the rapid proliferation of unauthorized mountain biking trails and TTFs and their use is challenging. Even if only a small proportion of bikers is involved, the resulting vandalism can have serious ecological consequences as is well reflected in the statement, "[g]enerally when you ask people to stay out of the area no matter what the reason is, 80-90% obey you, [b]ut if you get 10% who don't obey you, you haven't done any good" (Bill Andree, retired district wildlife manager of Colorado Parks and Wildlife; Peterson 2019).

In the aforementioned Carlsbad Highlands Ecological Reserve, enforcement and education are necessary to substantially reduce the illegal riding, but the bikers monitor

9 Of CDFW's 136 ecological reserves (ER) statewide, biking is allowed on eight. About ERs, Title 14, California Code of Regulations §630(a) states, "All ecological reserves are maintained for the primary purpose of developing a statewide program for protection of rare, threatened, or endangered native plants, wildlife, aquatic organisms, and specialized terrestrial or aquatic habitat types. Visitor uses are dependent upon the provisions of applicable laws and upon a determination by the [Fish and Game] commission that opening an area to such visitor use is compatible with the purposes of the property."

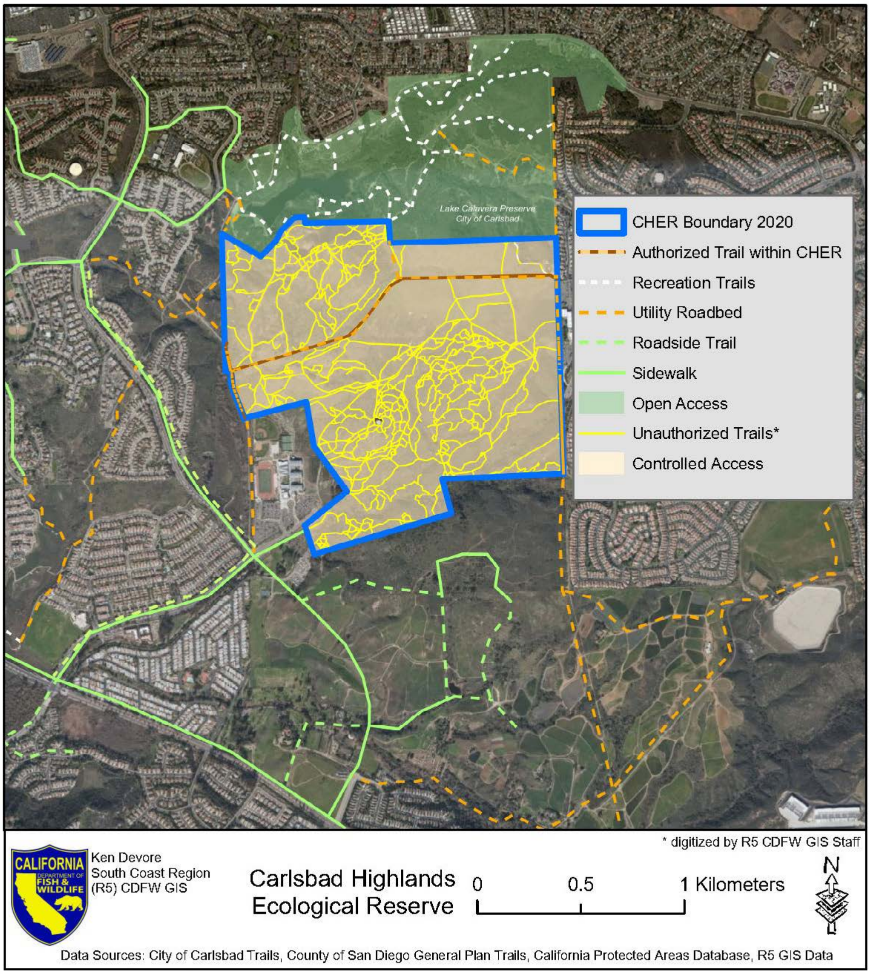

Figure 1. Carlsbad Highlands Ecological Reserve, Carlsbad, California. The yellow lines represent the unauthorized trails. Their associated effect zones occupy most, if not all of, the Ecological Reserve. (Credit: Ken Devore, South Coast Region (R5), GIS, CDFW 2017).

enforcement activity and recommence riding in the ecological reserve when enforcement officers leave (E. Pert, CDFW, personal communication, 2019). A similar protected area is the 350-ha Del Mar Mesa Preserve (Preserve) in the City of San Diego; the Preserve supports rare and endangered species such as Del Mar Manzanita (*Arctostaphylos glandulosa* ssp. *crassifolia)*, Orcutt's brodiaea (*Brodiaea orcutti)*, San Diego button celery (*Eryngium aristulatum* var. *parishii)*, San Diego mesa mint (*Pogogyne abramsii*), San Diego fairy shrimp (*Branchinecta sandiegonensis)*, and the California gnatcatcher, and was the subject of a study the City conducted to determine whether enforcement by CDFW Wildlife Officers (wardens) is an effective method to curb unauthorized trail uses (SANDAG 2015; Greer et al. 2017). Of the 32.22 km mapped trails on a 257-ha portion of this Preserve, 21.98 km are considered unauthorized (Reed et al. 2014). Prior to the study, City Park Rangers had conducted regular educational efforts in the field an average of 3–4 times monthly over a 17–month period. Despite the Rangers' efforts, non-compliance became the social norm as more users followed expanding numbers of unauthorized trails (Greer et al. 2017). The subsequent period of the CDFW Wildlife Officers' enforcement comprised 810 hours during a 12-week period with an unpredictable schedule. Prior to enforcement activities, the majority (78.7%) of the use within the study area was illegal, and over 85.5% of the illegal use was mountain biking. Illegal mountain biking decreased quickly during the enforcement period by 66.0% over the study period and stayed low during the 43-day post-enforcement period, while legal mountain biking remained the same. Other illegal use also decreased significantly, while other legal uses doubled (Greer et al. 2017). Greer et al. (2017) cite decades of research indicating that a combination of soft (i.e., education) and hard (e.g., warnings, citations, arrests, confiscation of bikes) enforcement is the most effective approach to promoting compliance. They assert that education becomes less effective in areas with chronic unauthorized trail creation and use.

Overall conclusions from Greer et al.'s (2017) study follow: (1) soft enforcement aimed at public education and redirecting social norms was not sufficient to curb unauthorized trail use in the Preserve; (2) open space enforcement by CDFW Wildlife Officers was determined to be effective in reducing unauthorized use in the Preserve; (3) the threat of sanctions (hard enforcement) has a more general utility and effectiveness in curbing non-compliant behavior than outreach to promote "awareness-of-consequence" of user actions (soft enforcement). The authors also concluded that social media has great potential to engage and educate the public on environmental issues, and that its use in combination with community policing can be a powerful tool to: redirect user attitude and subsequent behavior through peer-to-peer education about environmental impacts; answer questions regarding authorized uses; and, warn users of potential sanctions for non-compliance. They recommend the implementation of a social media component prior to and during enforcement efforts to help educate recreationists and reduce misinformation and recreationists' distrust of managers and enforcement personnel (Greer et al. 2017).

Paucity of information available.—Despite the global proliferation and use of unauthorized trails and TTFs and their far-reaching effects on wildlife in protected areas, there is a paucity of information of any depth available on such effects. The impacts of unauthorized trails and TTFs have been rarely documented (Marion and Wimpey 2007; Davies and Newsome 2009). A comprehensive literature search prior to 2010 produced only eight studies documenting the effects of unauthorized trails (Pickering et al. 2010c). Since then, additional studies have assessed the effects on vegetation from unauthorized trails, with little elucidation about their effects on wildlife. The proliferation, use, and wildlife-related effects of unauthorized trails remain understudied and insufficiently addressed. For protected areas where the creation and use of unauthorized trails and TTFs are prevalent, it is infeasible to fully assess the recreation-related effects on wildlife without including these activities and their effects. Yet, these effects have a great potential to impair the ability of protected areas to meet their conservation objectives.

Disturbance thresholds

Disturbance thresholds are predetermined levels of various measurable indicators above or below (depending on the indicator) which wildlife is disturbed (Hennings 2017).

These thresholds may be used to establish management measures such as minimum widths of spatial buffers between recreational trails and wildlife. Exceedance of a threshold may trigger the implementation of further management measures (Hennings 2017). Examples of disturbance thresholds are distance between people and wildlife or between trails and nesting sites (i.e., the distance within which wildlife species avoid people or trails), density of active trails above which wildlife alters its use of habitat, number of recreationists per day over which wildlife abundance decreases, duration of recreation, and number of recreational events per unit time (Hennings 2017; Dertien et al. 2018).

Thresholds should be set at levels equal to or more protective of predetermined levels of disturbance, and should be responsive to trends in changing conditions as identified by monitoring (Hennings 2017). Data from studies of recreational activities can be used to estimate quantitative thresholds of disturbance to wildlife (Dertien et al. 2018); however, determining these thresholds requires very specific empirical data (Rodríguez-Prieto et al. 2014).

While determining and using disturbance thresholds would be ideal for managers to optimize management decisions (Rodríguez-Prieto et al. 2014), they are difficult to determine for broad application. For example, thresholds established for distance to trail are not necessarily adequately protective of the focal species under all conditions in which they occur; a general rule of minimum thresholds for distance to trail cannot be established for some species, as individual variability within species can be high and can differ among populations, types of topography, and frequencies and types of human intrusion (González et al. 2006). As a result, the literature about recreation-related disturbance to wildlife provides limited information about quantitative thresholds for distance to trail (Dertien et al. 2018). Though their sample sizes (i.e., number of articles reviewed with such information) are accordingly small, Dertien et al. (2018) found the following examples of such thresholds: wading birds and passerines were generally affected at distances less than 100 m; larger-bodied species such as hawks and eagles had threshold effect distances greater than 400 m; small rodent species avoided areas within 50-100 m of trails or people; and some carnivores and ungulates had minimum effect distances up to 350-1000 m from trails and people.

As another example of a spatial buffer, Dertien et al. (2018) recommend a 200-m minimum buffer for ungulates; however, this would be insufficient for the circumstances of Taylor and Knight's (2003) study in which they found that mule deer showed a 96% probability of flushing within 100 m of recreationists located off trails, and the probability of their flushing did not drop to 70% until perpendicular distance reached 390 m. Two additional factors that influence the determination of spatial buffers are the density of the trail networks and the above-discussed effect zones. The smaller a protected area is and the denser its trail networks are, the greater the proportion of the protected area is occupied by effect zones, and the less likely it is that spatial buffers will protect the focal species from recreational disturbance (Wilcove et al. 1986; Ballantyne et al. 2014).

Land managers should consider both trail density and the level of human recreation before deciding on disturbance thresholds, since thresholds that work at lower levels of human activity may be ineffective when activity levels increase (D'Acunto et al. 2018). D'Acunto et al. (2018) simulated the success of trail closure strategies on reducing disturbance from Off Road Vehicles and pedestrians to nesting golden eagles during laying and incubation, focusing on eagle flushing behavior from the nest and alteration of foraging flight. They found that, for current levels of human recreation, the restrictive buffer (i.e. all trails closed within the buffer) was best at reducing flushing of incubating eagles, while closing all but the popular trails was best for foraging eagles. When the simulated human recreation was increased, trail density was the main factor influencing eagle flushing frequency.

Hennings (2017) reports the following thresholds for levels of human recreation (i.e., number of users) from four studies: for guanacos (*Lama guanicoe*), about 250 visitors per day, above which the number of birds observed declined; for sanderlings (*Calidris alba*), 20 visitors per day; for songbirds, eight out of 13 species showed thresholds ranging from 8-37 visitors per ha; and, for Mexican spotted owls (*Strix occidentalis lucida*), around 50 hikers per day. Regardless of any threshold effects, the majority of the research indicates that more visitors will generally cause more wildlife effects (Hennings 2017). However, since recreational impacts vary nonlinearly with use in a variety of ecosystems, a small number of visitors can have a disproportionate impact on sensitive species (Reed and Merenlender 2008).

Other aspects of recreation ecology to consider

Interpretation of observed behavioral responses.—It is possible to misconstrue the reasons for and implications of observed responses by wildlife to recreational activity. Traditionally and intuitively, species or individuals showing strong negative responses (e.g., readily flee or avoid) to human disturbance are those assumed to most need protection from disturbance. However, species with little suitable habitat available nearby cannot show marked avoidance of disturbance even if the fitness costs of the disturbance are high (e.g., reduction of survival or reproductive success; Gill et al. 2001). Conversely, species with many nearby alternative sites to move to are likely to move away from disturbance even if the fitness costs of the disturbance are low (Gill et al. 2001). It should not be assumed that the most responsive animals are the most vulnerable (Beale and Monaghan 2004). For example, in a controlled study of the behavioral responses of a shorebird (ruddy turnstone, *Arenia interpres*) to human disturbance (an approaching observer), Beale and Monaghan (2004) found that birds in better condition (i.e., supplemented with food) had longer flight initiation distances (i.e., flushed sooner) from the disturbance and searched for predators more frequently than control birds (i.e., not supplemented with food).[10] That is, birds responding most were actually the least likely to suffer any fitness consequences associated with the human presence; this is opposite from the response generally expected when behavior is used as an index of disturbance effects. Birds that had the most to lose by flushing, or otherwise changing their behavior in a manner that reduced feeding time, showed the least behavioral response; this could be interpreted incorrectly as meaning that these birds were not disturbed. Gill et al. (2001) assert that the absence of an obvious behavioral response does not rule out a population-level effect. In the same vein, it may be that species occurring in protected areas that are remnant fragments within urban landscapes are forced to utilize all components of the fragments, irrespective of their land-use intensity and land cover. This may occur if animals have nowhere else to go, and may be an explanation for instances when total relative abundance of birds is greater in urban and suburban reserves than in exurban reserves (Markovchick-Nicholls et al. 2008).

In addition to the reasons Gill et al. (2001) provide for an absence of detected effects, other possible reasons for finding no recreation-related effects include that there

10 Flight initiation distance is the distance from an approaching threat (e.g., recreationist) at which an animal begins to move away to escape from the threat.

may be a negative effect but it is not detected due to methodological issues. For example, the response variable examined (e.g., behavior versus physiology) and/or the number of replicates used compared to the amount of variation in the traits measured may not reveal the actual response of the species studied or the associated longer-term population-level effects (Steven et al. 2011). Furthermore, some studies may not include sufficiently high levels of human activity to detect responses from species that can tolerate lower levels of disturbance (Reed et al. 2019).

Threatened, endangered, and sensitive species.—Current research of recreation-related effects on wildlife does not include many species of urgent conservation concern (Larson et al. 2016). As many rare and isolated species tend to be specialists, anthropogenic activities could have a greater detrimental effect on the distribution, breeding success, and survival of individuals of these species (Beale and Monaghan 2004b; Bennett et al. 2013) than found in studies involving less sensitive species. Studies do not always reveal the strongest effects because the most disturbance-sensitive species are naturally rare in number or are already gone from disturbed sites (Hennings 2017). While recreation may not be the primary reason for the sensitive status of such species, it is a threat worth understanding for types of recreation that occur in the protected areas designated to conserve them (Larson et al. 2016).

Magnitude and duration of wildlife responses to recreation.— It is known that the nature (e.g., behavioral, physiological), magnitude, and duration of recreation-related disturbance to wildlife depend on a variety of factors, including, but not limited to, frequency and type of recreation, distribution of recreational use, season(s) of use, and environmental conditions (Marzano and Dandy 2012). Evaluating the effectiveness of measures to manage recreation can be complicated by the intensity of recreational use of a protected area because levels of use influence the magnitude of recreation-related effects on wildlife (Reed and Merenlender 2011). But studies do not always quantify the levels of recreational uses. Likewise, research seldom provides insight to the duration of wildlife species' response (e.g., nest abandonment, interruption of foraging/hunting, breeding, fleeing) to human disturbance (Marzano and Dandy 2012; Burger 2012; Larsen et al. 2016) or degree of response (e.g., how far wildlife moves away from human disturbance at a greater energetic cost and resulting in less availability of habitat). The same is true for the spatial scale at which wildlife response occurs (Burger 2012).

Generalized comparisons of effects among types of recreation.—It is clear from the literature that recreation in protected areas, particularly in more urbanized areas, can negatively affect wildlife (Larsen et al. 2016). However, it is difficult to make defensible generalized comparisons of the effects on wildlife among different types of recreation, partly because of the diversity of recreational activities, study methodologies, and observed responses (Monz et al. 2013). A comparison of results among similar studies indicates that sweeping conclusions about the effects of urbanization and human activity on wildlife need to be made with caution and are likely to be species-specific (Markovchick-Nicholls et al. 2008). For example, applying this caution to one species, the U.S. Fish and Wildlife Service (2000) concludes that attempts to ascribe relative importance, distinguish among, or generalize the effects of different human activities on bighorn sheep (*Ovis canadensis*) behavior are not supportable, given the range of potential reactions reported in the literature and the different variables impinging on given situations. Therefore, generalized comparisons of the effects on wildlife among different types of recreation are ill advised. The differences among types of recreation in their effects on wildlife are less important than the negative association for wildlife of human presence, irrespective of type of recreation (Patten and Burger 2018).

Despite the difficulty of making well-founded comparisons of the effects on wildlife among different types of recreation, comparisons are made. Among the types of recreation examined in the literature, the ecological effects of hiking and biking are most often compared. For studies done in the United States, this reflects the 22% increase to 8.3 million from 2006 to 2015 in mountain bikers, and the 24% increase to 37.2 million hikers during the same time period (Hennings 2017). And, notwithstanding the foregoing caveat about generalized comparisons, Hennings (2017) underscores that photographers, people with small children, bird watchers, and people engaging in loud conversations may be especially detrimental to bird communities because they are unpredictable and generally alarming. Photographers and wildlife watchers tend to stop, look directly at wildlife, and even follow them around, triggering stronger antipredator responses than people who simply pass by; photographers also tend to seek out rare species and look for nests. Also, curious, excited children tend to run around and shout in an unpredictable fashion (Marzano and Dandy 2012; Hennings 2017).

An absence of differences among effects.—The absence of differences among recreational activities' effects on wildlife does not equate to no effects. There can be similar levels of both benign or significant effects. For instance, in a study of bison (*Bison bison*) and pronghorn (*Antilocapra americana*), the authors found little difference in wildlife response (i.e., alert distance, flight initiation distance, or distance moved)[11] to hikers versus mountain bikers, but both species exhibited a 70% probability of flushing when within 100 m from trails with recreationists present (Taylor and Knight 2003).

Cumulative and synergistic negative effects.— The negative effects of recreation on wildlife compound, and may also act synergistically with, those from other influences (Larson et al. 2016; Reed et al. 2019). The cumulative negative effects of all anthropogenic influences on wildlife complicate efforts to minimize the effects and assess their population-level consequences (Pirotta et al. 2018). However, recreation ecology studies typically do not factor in other anthropogenic influences to which wildlife in protected areas are exposed (Pickering et al. 2010c; Erb et al. 2012; Messenger et al. 2014; Reed et al. 2019). Other anthropogenic influences include climate change and its associated effects on natural disasters; fires and other natural or human-caused disasters; consumptive recreation; non-recreational human activity such as habitat loss or alteration, the associated lack of connectivity, and the resulting loss of genetic diversity; poor air and/or water quality; invasive species; roads; vehicles; artificial light; prey declines; reverse zoonoses; drones; and noise (e.g., from vehicles, planes, ships, and boats). Recreation-related cumulative effects may be important if, for instance, the densities of different types of recreationists influence predator use of sites more than does the density of any one type of recreationist alone (Gutzwiller et al. 2017).

Wildlife habituation to human activity.—Habituation is a form of tolerance in which, as the result of a lack of negative consequences, there is a waning of response to a repeated, neutral stimulus (Whittaker and Knight 1998; Pauli et al. 2017). Habituation allows wildlife to use their energy for normal fitness-enhancing behaviors such as resting, foraging, and mating instead of fleeing when confronted with human activities that result in neutral outcomes (Whittaker and Knight 1998; George and Crooks 2006; Reilly et al. 2017). Habituation is

11 Alert distance is the distance from a stimulus at which an animal initiates vigilance behavior (Guay et al. 2016 in Reed et al. 2019); more specifically in this context, it is the distance between a recreationist and an animal when the animal first becomes visibly alert to the recreationist. Distance moved is the distance an animal travels from its initial position until it stops (Taylor and Knight 2003).

an apt description for crows (*Corvus* spp.) ignoring a scarecrow, or a red fox ignoring the human activity in a suburban area (Whittaker and Knight 1998). Citing several authors' work, Martínez-Abraín et al. (2008) identify level and frequency of disturbance, species, location, size and diet of species, and age of individual animals as factors that affect the degree of wildlife habituation to human disturbance.

The ability to habituate to predictable and recurrent human use of recreational trails may be an important behavioral adaptation for wildlife (González et al. 2006; Martínez-Abraín et al. 2008). However, habituated urban wildlife might be less likely to avoid contact with humans, which may increase the probability of human-wildlife conflicts and of attraction to anthropogenic food sources; both circumstances are considered problematic in many urban areas (Whittaker and Knight 1998; George and Crooks 2006). Wildlife habituation to humans may also increase wildlife aggression toward humans, or render wildlife more vulnerable to predators, hunters, poaching, or roadkill (Whittaker and Knight 1998; George and Crooks 2006; Marzano and Dandy 2012). Habituation of adult individuals may be associated with negative consequences for their offspring since habituation of adult animals does not translate to immediate habituation of juveniles (Reilly et al. 2017).

True habituation is not easily measured, and what appears to be habituation is often not (Hennings 2017). Apparent habituation is not a true measure of whether people are disturbing wildlife (Hennings 2017). Wildlife can experience significant stress without fleeing, and when this is misconstrued as habituation, disturbance effects on wildlife are underestimated (Hennings 2017). Care must be taken to avoid attributing a lack of observable response by wildlife to human presence as habituation (Beale and Monaghan 2004). Wildlife that seem not to avoid recreational disturbance may experience stress or be unable to leave a site if, for example, there is no suitable habitat nearby (Gill et al. 2001; Beale and Monaghan 2004; Markovchick-Nicholls et al. 2008).

While habituation to human disturbance could result in development of tolerance within a population (Pauli et al. 2017), Bötsch et al. (2018) infer from their findings on the recreation-related disturbance to birds in forests where recreation has occurred for decades that habituation to humans has not outweighed the effects of the disturbance. A long-lived species with low recruitment, such as the golden eagle, may be unable to experience individual learning or population-level evolutionary adaptation at a rate sufficient to compensate for a rapidly shifting anthropogenic landscape (Pauli et al. 2017).[12]

In a study subjecting captive female elk to four types of recreational disturbances (all-terrain vehicles riding, mountain biking, hiking, and horseback riding) over a two-year period, the elk showed no evidence of habituation to mountain biking. Similarly, elk travel time in response to hiking was generally above that of control periods, suggesting elk also did not habituate to hiking disturbance (Naylor et al. 2009).

In a study of how bison, mule deer, and pronghorn responded to hikers and bikers on designated recreational trails, Taylor and Knight (2003) found little evidence of habituation to recreationists among the species at the time of the study (summers of two consecutive years). In fact, the pronghorn at the study site did not habituate to largely predictable recreational use over a three-year period following the opening of trails at the site, and used areas that were significantly farther from trails than they had prior to the start of recreational use.

12 Evolutionary adaptation is the hereditary alteration or adjustment in structure or habits, the process by which a species or individual improves its ability to survive and pass on its genes in relationship to the environment (Ha and Campion 2019); unlike habituation, evolutionary adaptation does not result from learning during an individual's lifetime.

Hennings (2017) asserts that wildlife do not appear to habituate to the presence of dogs; impacts potentially linger after dogs are gone because the scent of dogs repels wildlife. It may be too that wildlife do not habituate to dogs (particularly off-leash dogs) because wildlife perceive dogs as predators and because they are unpredictable (Hennings 2016). Dog-specific disturbance has been studied for birds, with no evidence of habituation even with leashed dogs and even where dog-walking was frequent; the disturbance was much weaker for people without dogs (Hennings 2016).

The challenge of research.—Recreation ecology, similar to other fields of ecology, faces challenges in conducting statistically valid research (Quinn and Chernoff 2010). The degree to which and how the biotic and abiotic resources present in any one location respond directly or indirectly to recreational activities depends on many variables, some of which may be confounding (Figure 2, Table 1). Measuring the effects of human activity on wildlife is difficult because of the variability in the underlying spatial, diurnal, seasonal, and even the type of, indices being measured (Burger 2012). Recreation-related effects on wildlife vary among species (Larson et al. 2016) as different wildlife species respond differentially to visual, auditory, olfactory, and tactile stimuli (Hennings 2017). Wildlife responses to recreationists are likely influenced by a suite of variables that may differ in each field setting (Steidl and Anthony 1996; Taylor and Knight 2003), including level of human presence/activity that evokes a response as well as feedbacks and interactions with other factors (e.g., edge effects, availability of cover, exposure to disturbance, or time since fire; Patten and Burger 2018). Study methodology (i.e., design, sampling, data collection, and data analysis) itself encompasses many variables that dictate how other variables will influence the study outcomes. Even if methodology is consistent between/among two or more studies, other variables can result in different study results (Taylor and Knight 2003). Methodological issues may limit the inferences that can be made from the results (Pickering et al. 2010c).

Study design and statistical analyses can utilize methods to control for the effects of confounding variables (e.g., by using covariates). Statistical analyses can be used to examine alternative use-impact or use-response relationships between recreational activity and wildlife responses to assess the effects of recreational activity relative to other known drivers (e.g., habitat fragmentation, invasive species) of species occupancy, distribution, physiology, reproduction and survival (Monz et al. 2013; Reed et al. 2014).

Differences among study results.—Differences among studies' results can be due more to differences in variables not accounted for (e.g., space, diet, competition; Markovchick-Nicholls et al. 2008), study design, and/or analytical methodologies than to actual differences among species' responses to recreational disturbance. As to methodology, for instance, some studies may not include sufficiently high levels of human activity to detect responses from species that can tolerate lower levels of disturbance (Reed et al. 2019).

Reilly et al.'s (2017) study using camera trap data to quantify how hiking, mountain biking, horseback riding, and dog-walking affect habitat use/occupancy and diel shifts in activity patterns of ten mammalian species is illustrative for this discussion because some of its results differ markedly from those of other studies. For example, the authors found no negative association between recreation and habitat use by bobcats (*Lynx rufus*) and coyotes (*Canis latrans*), whereas Reed and Merenlender (2008) documented (in the same study area as Reilly et al.) densities of these two species more than five times lower in protected areas that permitted recreation versus those that did not. Dertien et al. (2018) identify differences in the following aspects of the two studies: field study methods, statistical analyses,

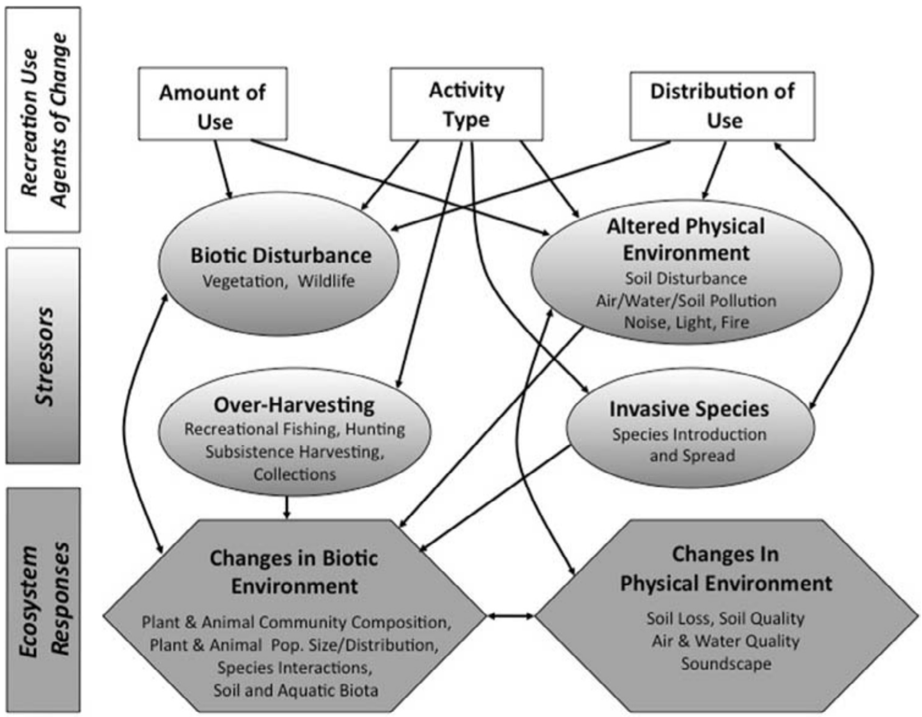

Figure 2. A conceptual model of ecological effects of outdoor recreation (Credit: Monz et al. 2010).

and research design – namely, types of study sites selected, treatment of data sources as replicates or independent of one another, and duration of data collection (one versus three years). These differences may have contributed to the greater variability observed in Reilly et al.'s (2017) study compared to Reed and Merenlender (2008).

Strong variability in other factors that are well known to influence mammalian distributions (e.g., habitat type, human development, or seasonal effects) make it difficult to conclude whether the potential effects of recreation on the target species were truly absent or simply undetected (Dertien et al. 2018). In addition, studies that use abundance, relative abundance, or species richness generally observe stronger effects of recreation than do studies such as Reilly et al.'s (2017) that use occupancy as a response variable (or occupancy interpreted as habitat use; Reed et al. 2019).

Reilly et al. (2017) acknowledge that: species vary widely in their responses to human activities; recreation-related effects on mammalian species that are rare or declining may be greater than on those that are more common or widely distributed; and birds, reptiles, amphibians, and small mammals may respond differently than the large and medium-sized mammals they studied. Finally, in contrasting their results with those of George and Crooks (2006), Reilly et al. do not acknowledge Gill et al.'s (2001) assertion that proximity to other suitable habitat influences how wildlife will respond to human disturbance; George and Crooks (2006) not only acknowledge but give credence to Gill et al.'s work.

Population-level effects

The foregoing discussion reveals many complexities of recreation ecology and provides a sense of why the population-level effects of human disturbance to wildlife are still poorly known (Burger 2012; Hennings 2017). Parameters used to measure population-level effects include population size, density, age structure, fecundity (birth rates), mortality (death rates), and sex ratio (Tarsi and Tuff 2012). Comprehensive assessments of the nonlethal effects on wildlife at the population level are rarely undertaken due to several constraints, including that robust assessment of these effects is challenging (Pirotta et al. 2018). Nonetheless, from a strictly conservation standpoint, human disturbance to wildlife is important only if

Table 1. Variables that influence the outcome of studies designed to assess the ecological effects of recreational activities. Each variable is mentioned in one or more of the cited articles (Taylor and Knight 2003; Beale and Monaghan 2004; Markovchick-Nicholls et al. 2007; Davis et al. 2010; Monz et al. 2010; Pickering 2010a; Quinn and Chernoff 2010; Burger 2012; D'Acunto 2018).

a. regional geophysical traits
b. size(s) of protected area(s) where research occurs
c. type(s) of vegetation present
d. area and density of vegetative cover
e. surrounding environment, including vegetation between the recreational activity and the target species
f. edaphic conditions (e.g., soil type, level of compaction, moisture, composition)
g. weather (temperature, precipitation, wind, shade, sun etc.)
h. timing (day / night / season)
i. time of day x location
j. design of trails (e.g., steepness of trails)
k. placement of trails (orientation to terrain - on flat, along a slope, across a slope)
l. direction of trails (ascending or descending)
m. spatial relationship between trails and target animals
n. trail density
o. wildlife present, target and non-target
p. total # of target wildlife individuals
q. spatial distribution of target wildlife
r. age classes and genders of target wildlife present (adult males/females, subadults, young of year)
s. reproductive status of target wildlife
t. fitness of target wildlife
u. predictability of recreational activity
v. degree of target animals' habituation to tested activities
w. duration of target animals' exposure
x. whether the target animals have the ability to retreat
y. type(s) of recreation
z. duration of recreational activity
aa. # of humans present (e.g., individuals or groups)
bb. # of human disturbances per day
cc. whether recreational activity is on or off an official trail
dd. recreationists' positions
ee. angle / trajectory of recreationists' approach to wildlife
ff. speed and style (e.g., 'aggressive') of recreationists' approach
gg. distance of recreational travel
hh. whether the recreationists apply best practices
ii. recreationists' behavior (e.g., talking or silent, continuous movement or stopping)
jj. encounter distance
kk. perpendicular distance
ll. encounter x perpendicular
mm. researcher bias
nn. study methodology (e.g., is recreationists' approach to wildlife direct or tangential, on or off trail; includes statistical analyses)

it affects survival or fecundity such that a population declines (Gill et al. 2001). Assessing and managing the nonlethal effects on wildlife populations has long been a goal of ecologists, land managers, and decision makers (Pirotta et al. 2018). The management of human activities that cause nonlethal effects on wildlife presents a fundamental ecological problem: how to understand the population-level consequences of changes in the behavior or physiology of individual animals that are caused by external stressors (Pirotta et al. 2018). Given the expansion of recreational activities that can disturb wildlife, quantitatively linking the effects of this disturbance to population dynamics is a major objective for modern conservation (Pirotta et al. 2018).

While behavioral responses, which are studied far more often than other types of responses (e.g., physiological; Larson et al. 2016), have the potential to affect survival or reproductive success, the actual fitness[13] costs of behavioral responses need to be quantified before the responses can be used as reliable estimates of population-level perturbations (Gill et al. 2001).

In most situations when statistical models are used to estimate or forecast the population-level effects of disturbance, selection of a model structure is likely to be driven by data availability (Pirotta et al. 2018). Collecting recreation data in conjunction with ongoing animal population monitoring efforts would be a valuable way to improve the understanding of the effects of human disturbance on demographic trends; and, studies that combine behavioral responses with physiological or demographic metrics would help calibrate the relationships between behavioral responses and population-level effects (Reed et al. 2019). Whichever models are used, uncertainty in the estimated population consequence can be reported as a distribution of potential outcomes, allowing the application of the precautionary principle if the results are used to make management decisions (Pirotta et al. 2018).[14] Application of the precautionary principle is warranted given that any simulation model simplifies reality (D'Acunto et al. 2018).

The dearth of conclusive evidence of recreation-related population-level effects in the literature does not mean that such effects are rare; logic dictates that, if the negative consequences of some observed behaviors or physiological changes in wildlife persist, negative population-level effects will eventually follow. For example, negative population-level effects on desert bighorn sheep (*Ovis canadensis nelsoni*) from recreational disturbance have been documented and are implicated in the bighorn sheep abandonment of habitat (and extirpation of the population) in the Pusch Ridge Wilderness in Arizona, USA (Longshore et al. 2013). And, recreation is one reason cited for the population of bighorn sheep in the Peninsular Ranges of California being listed in 1998 as endangered under the Federal Endangered Species Act (USFWS 2000).

The effects of hikers on elk (*Cervus elaphus*) provide another example of recreation-related population-level effects. Based on a two-year study of the response of female elk to the presence of back-country hikers during the calving season, Shively et al. (2005) recommended that some recreational closures be continued because, despite the evidence that elk reproduction can rebound from depressed levels when hikers are removed or reduced in

13 Fitness refers to reproductive success and reflects how well an organism is adapted to its environment (Hennings 2017).

14 The central tenet of the precautionary principle is that precautionary measures should be taken even if some cause and effect relationships are not fully established scientifically. Generally, the four central components of the principle are: taking preventive action in the face of uncertainty; shifting the burden of proof to the proponents of an activity; exploring a wide range of alternatives to possibly harmful actions; and increasing public participation in decision making (Kriebel et al. 2001).

number, they could not determine if there is a threshold level of reproductive depression from which elk cannot recover. In fact, a 2019 article in *The Guardian* reported that the number of elk in the same herd Shively et al. (2005) studied had dropped precipitously since the early 2010s with the steady increase in recreation; what was once a herd of 1,000 head of elk, had dropped to 53 at last count in February of 2019 (Peterson 2019). The article explains that, for Bill Alldredge, one of the authors of the study, there is no other explanation than the increased levels of trail users in the area that supports this elk herd (Peterson 2019).

In a study to assess the effects of recreational activities on Iberian frogs (*Rana iberica*), an endemic species in decline and listed as vulnerable in the Spanish Red Data Book, Rodríguez-Prieto and Fernández-Juricic (2005) concluded that (1) the decrease in Iberian frog abundance with the proximity to recreational areas suggests that direct human disturbance affects this species at the population level, and (2) overall, the results suggest that direct human disturbance needs to be considered as a potential factor affecting amphibian populations with low tolerance for disturbance.

From the peer-reviewed recreation ecology literature, Steven et al. (2011) compiled 69 journal articles that describe the results of original research examining the effects of non-motorized nature-based recreation on birds. Among the articles were 33 that examined population-level avian responses (i.e., reproductive success including number of nests, number eggs laid, and number of chicks that hatched or fledged). Negative effects were reported in 85% of these 33 articles.

Patten et al.'s (2017) 10-year study of mammalian populations across the County of Orange Central and Coastal NCCP/HCP protected areas coincided with a marked increase of human activity and provides insight to potential population-level effects. Though the authors did not discern a decline in the populations studied, they did discern temporal and spatial shifts by wildlife due to human presence, and they suggested that the associated losses in prey populations are unsustainable in light of additional stressors these populations face, which range from continued loss of habitat to human disturbance in the protected areas. Furthermore, given the avoidance behavior and temporal shifts of the various mammalian species, any further increase in human disturbance may yet drive mammalian populations downward (Patten et al. 2017).

With regard to population-level effects of anthropogenic fragmentation, evolutionary adaptation to such fragmentation has received some attention. Even when adaptation to fragmentation occurs, it may not be enough to fully compensate for the environmental effects from fragmentation, and in some cases may even exacerbate them (Cheptou et al. 2017).

Distinguishing facets of mountain biking

Together with the extent of the above-discussed creation and use of unauthorized trails and TTFs by mountain bikers, the mass-marketing of the sport, and the very large numbers of mountain bikers (Burgin and Hardiman 2012), at least four facets of mountain biking distinguish it from other recreational activities such that it may be of potentially greater concern with respect to its effects on wildlife than yet accounted for in the literature. These facets are distance traveled, speed of travel, biking in the dark, and political lobbying and advocacy.

Distance traveled.—Bikers traveling faster obviously travel farther than hikers per unit time and could therefore disturb more wildlife than hikers per unit time (Taylor and Knight 2003; Burgin and Hardiman 2012); the same applies to bikers and equestrians when bikers travel faster than equestrians. Larson et al. (2016) reasoned that, since motorized activities often cover larger spatial extents than non-motorized activities, it is possible that the effects of motorized activities have been underestimated. The same logic applies to the distances traveled by bikers and hikers. For valid comparisons among recreation-related ecological effects, the comparisons must account for distances traveled and the associated levels of disturbance to wildlife along the entire route traveled.

Speed of travel.—While recreation-related effects on wildlife are generally assumed to be indirect (Dertien et al. 2018), the speed at which mountain bikers travel, combined with their relatively quiet mode of travel, can result in direct disturbance to wildlife. A relatively fast moving, quiet mountain bike may approach an animal undetected until well within the animal's normal flight response zone. The result may be a severe startle response by the animal with significant consequences to the animal and/or the mountain biker (Quinn and Chernoff 2010). The sudden encounter is the most common situation associated with grizzly bear (*Ursus arctos horribillis*) inflicted injury (Quinn and Chernoff 2010). Biking-caused wildlife fatalities likely resulting because of bikers' speed occur with amphibians and reptiles that may be attracted to trails for thermoregulation and are thus exposed to collision with bikes' wheels (Burgin and Hardiman 2012); photo-documentation provides evidence of three such fatalities in CDFW's Del Mar Mesa Ecological Reserve in San Diego where a San Diego horned lizard (*Phrynosoma coronatum blainvillii*, a species of concern under CDFW and the U.S. Fish and Wildlife Service), three western toads (*Anaxyrus boreas*), and two Baja California treefrogs (*Pseudacris hypochondriaca*) were killed by mountain bikes (J. Price, CDFW, personal communication, 2019). The treefrogs appear to have been mating when run over—the photo documentation shows eggs spilling out of the female. Biking is prohibited in this ecological reserve, and two of the run-overs occurred on unauthorized trails (J. Price, CDFW, personal communication, 2019).

Though there are methods (e.g., bells attached to bikes) for mountain bikers to give warning of their approach to other trail users, and these can be effective for this purpose, these methods themselves can introduce additional disturbance to wildlife. And, such warning sounds are ineffective for wildlife whose hearing range does not detect them or who do not hear them soon enough to avoid a collision. Moreover, when recreationists are visible on approach to wildlife, the more threatening (e.g., faster, more direct) the recreationists appear to wildlife (as potential predators), the greater the flight initiation distance from the recreationists (Stankowich 2008). Fleeing from a perceived predator represents potentially needless expenditure of valuable energy.

Biking in the dark.—Mountain biking in the dark (i.e., night riding), which is on the rise in protected areas, can disrupt the natural balance between diurnal and nocturnal wildlife. Consequently, night riding poses a dual threat to wildlife that exhibit diel shifts toward night: night riding can compound the pressure such wildlife experience from daytime recreational activities by increasing encounters with competitors and even further reducing the time available for foraging and breeding (Reilly et al. 2017). Night riding can also startle naturally nocturnal wildlife and wildlife that has become increasingly nocturnal to avoid daytime recreationists and other anthropogenic disturbances. Generally, temporal shifts by wildlife involve disruptions to both the shifting wildlife and to the wildlife naturally active during the time frame the shifting wildlife move into. In this way, such shifts set both groups of wildlife up for conflict and competition, disrupt predator/prey relationships, reduce feeding/hunting time and success, and disrupt breeding and other activities (Gaynor 2018). Temporal shifts can also result in spatial shifts and thus potentially cause further ecological disruptions. Thus, temporal shifts are disruptive not only to individuals, but also to communities, and ultimately, populations (Gaynor 2018).

Political lobbying and advocacy.—In part due to the markedly different motivation driving mountain bikers compared to other recreationists in protected areas, especially in the more extreme forms of mountain biking (Burgin and Hardiman 2012), the mountain biking community has come to wield significant lobbying and advocacy pressure throughout the United States. Networking among members if the mountain biking community has resulted in changes in land managers' decisions (Bergin and Hardiman 2012). In California, a newly formed mountain biking nonprofit aims to gain a voice at the capital with lawmakers to put trail access and trail development front and center (Formosa 2019). And, the community has much experience in planning trail networks, experience that is necessary to negotiate areas appropriate for mountain biking. In San Diego County, the local mountain biking coalition and the United States Forest Service (USFS) work in partnership to build trail networks on national forest lands; because the USFS does not have a budget for recreation, the only way trails will be built on national forest lands within the County is if the coalition pays the USFS for the agency's staff time, studies and environmental review, and project-processing needed to approve the trail networks (SDMBA 2017). While the USFS-biking coalition partnership may be similar to the accepted practice of an applicant (e.g., utility) paying a lead/permitting agency to dedicate personnel to the applicant's project(s) or a certain body of work, conflicts of interest are usually inherent in such collaborations. In addition, much of the USFS-biking coalition partnership's planning process occurs outside of public view, prior to the public knowing anything about it. It is notable that, while not all USFS lands are considered protected areas in the meaning of this paper, the wilderness areas the USFS manages are.[15]

Recommendations and conclusions

Conservation of habitats is critical to the perpetuation of viable populations of sensitive species. California is home to several types of protected areas whose primary or sole purpose is conservation of sensitive species. After conserving these protected areas, the next crucial step in biological conservation is managing how, where, and when humans use the land. However, there is rarely adequate management to control the allowed types and levels of recreation such that they are compatible with conservation, much less prevent the illegal recreation. The following discussion provides recommendations related to the major issues of recreation ecology addressed above. The implementation of most of these recommendations is considered management as the term is used in this paper (footnote #4), and land managers are familiar with most, if not all, of them. Still, it is hoped that the recommendations provide some new insights and even useful guidance for practical application in the management of dual-role protected areas, the wildlife they support, and the recreationists they serve. For simplicity, clarity, and brevity, several of the recommendations are in imperative sentences. For some of the aspects about recreation ecology discussed

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15 The USFS manages approximately 33% of the acreage within the National Wilderness Preservation System (https://wilderness.net/learn-about-wilderness/agencies.php) and describes wilderness areas as places where nature "still calls the shots… They are final holdout refuges for a long list of rare, threatened, and endangered species, forced to the edges by modern development… They are places where law mandates above all else that *wildness* be retained for our current generation, and those who will follow" (https://www.fs.usda.gov/managing-land/wilderness).

above, there are no discrete recommendations.

Continual management is imperative.—Continual management (footnote #4) of recreation is imperative for dual-role protected areas to meet their conservation objectives. The chronic insufficiency of management resources for protected areas is of obvious concern. It is urgent that action be taken to address the chronically underfunded management of protected areas by securing perpetual fiscal support that is sufficient for the management needs in perpetuity; the perpetual fiscal support to be secured includes all costs for personnel and all program costs. The level of management must be commensurate with expanding levels of authorized and unauthorized non-consumptive recreation. Given the upward trajectory of recreational activities in protected areas, garnering broad support for securing the perpetual fiscal support requires a societal course change to a collective perspective of respecting and tending to other species in need of protection. Management that is effective for the biological resources would also improve the often cited economic, educational, and health benefits of protected areas.

Prevent further use and proliferation of unauthorized trails.—Prevent the creation and use of unauthorized trails in the first place. This approach would be far preferable to having to contend with the damage to the ecological resources and cultural ecosystem services (discussed below) from the creation and use of unauthorized trails in protected areas. Here, prevention requires continual management. Consider the lessons learned from the work Greer et al. (2017) describe, as summarized above. Where feasible, gain the trail user community's support for and involvement in proactive efforts to prevent vandalism.

Restore habitat to reverse internal fragmentation.—It is reasonable to assume that the disturbance to wildlife from internal fragmentation associated with authorized trails and from legal recreation on them, occurs at least as much from fragmentation associated with unauthorized trails and recreation on them. The internal trail-related fragmentation and expansion of the effect zone most negatively affects those species for which the fitness costs of disturbance are high but have little or no excess habitat to move to; these species are thus constrained to stay in disturbed areas and to suffer the costs in terms of reduced survival or reproductive success (Gill 2001). For these species, restoring the habitat lost to inappropriate trails (i.e., unauthorized trails, unnecessarily redundant designated trails, and trails to be decommissioned) is critical from the standpoint of the negative recreation-related population-level effects. Using restoration to minimize the effects of recreation within fragmented protected areas in urban areas might enable the fragments to better support the focal species (Reed et al. 2019).

Therefore, though the effects on wildlife from unauthorized trails and recreation, per se, have received comparatively little formal study, the precautionary principle (Kriebel et al. 2001; footnote #14) dictates that there seems no need for further study to justify prioritizing restoration of habitat lost to inappropriate trails. So, for levels or habitat loss and the associated internal fragmentation that meet some yet-to-be-established criteria, the restoration should occur. If there is competition for resources (budget/funding, personnel) between (1) research on recreation-related disturbance to wildlife and (2) restoration of habitat lost to inappropriate trails to stop the disturbance, the latter should take priority to reverse internal fragmentation.

To assess the effects of the restoration on the wildlife communities within the protected area, conduct biological surveys within a year prior to the restoration and three to five years after the completion of the groundwork and planting. For this assessment, valid pre-disturbance wildlife survey data collected prior to the loss of habitat within the footprint of the trails that will be restored and associated effect zone will help. But if there are no pre-disturbance data for the protected area or a nearby undisturbed control area, care must be taken in the interpretation of the results of the survey conducted a year prior to the restoration (i.e., the first survey). This is because the results of the first survey will likely represent wildlife communities altered from the pre-disturbed condition (Hennings 2017). It may be that the level of fragmentation, recreation, and many other factors, have caused conditions in which there are no or very few individuals of the focal species (Hennings 2017). These are reasons to be conservative in estimating the recreation-related effects on wildlife in disturbed protected areas without pre-disturbance data; if wildlife have already vacated the disturbed site before the first survey is done, the results will underestimate disturbance effects on wildlife (Hennings 2017). Here, the purpose of the survey data is to aid in determining how the restoration affects the occurrence and/or density of species (depending on the survey methodology), all other factors being equal. The assessment must account for whether the restoration involves the cessation of recreational activities on and/or in the vicinity of the trails to be restored, especially if no other recreational activities begin elsewhere within the species' effect zone throughout the restoration period. If there is funding available and a desire to monitor human activity and wildlife within the restoration areas, deploy camera traps within the areas; camera traps are the most cost-effective method currently available to monitor wildlife activity (Burger 2012).

Minimally, include the following tasks in the restoration: track the actual and in-kind costs (personnel, capital costs, volunteer hours, etc.) for the entire process; map the inappropriate trails and constructed trail features (some use of aerial imagery may work, but on-the-ground mapping validation is essential; Dertien et. al. 2018); prioritize the order of their restoration; determine the best approach for restoring each trail (e.g., passive, active, or a combination); do the restoration itself;[16] and, monitor for several years. Finally, publicize the costs of the restoration to inform the public (F. Landis, California Native Plant Society, personal communication, 2017); for this, compare the costs of the restoration with the costs of the management (footnote #4) that would have been necessary to prevent the damage requiring the restoration. Reasons for documenting the costs include being able to provide to local and state elected officials comparisons of the costs of reactive and proactive approaches to management, and to inform the public about the costs of repairing ecological vandalism.

If possible and logistically advantageous, it would be prudent and economically beneficial to collaborate with recreationists to volunteer with the restoration. For example, this would be an opportunity to mobilize well-organized volunteer contingents of the mountain biking community that are dedicated to building trails. In fact, in some areas, the mountain biking community provides well-organized volunteer assistance in the designing, building, and/or maintenance of officially designated trails in and outside of protected areas. Such volunteer dedication to the restoration of unauthorized trails is sorely needed.

In addition to the biological benefits, another motivation for this habitat restoration in protected areas is its potential to improve the human experience in protected areas open to public access. California's State Wildlife Action Plan (CDFW 2015) and much of the literature about recreation-related ecological effects point to the economic, educational, and recreational/health benefits (i.e., cultural ecosystem services) of protected areas and the species they support. Regarding the human health benefits, the visible recreation-related

16 Here, restoration encompasses decompacting the soil, building back and stabilizing the damaged or destroyed terrain and soil, and restoring the affected native plant communities.

damage to the terrain requires consideration beyond its ecological effects—it also affects the level of benefit people enjoy while being in nature, as illustrated by a study examining the relationship between recreational impacts in protected areas and human mental/emotional states (Taff et al. 2019). The study's results demonstrate that, as visible recreation-related ecological impacts increased, sense of wellbeing and mental state decreased, especially in response to settings with unauthorized trails. Collectively, the results show that managing tourism in protected areas in a manner that reduces such impacts is essential to optimizing beneficial cultural ecosystem services related to human health and wellbeing (Taff et al. 2019). Also diminishing the human experience is the risk of injury when using unauthorized trails and TTFs (Davies and Newsome 2009), a risk that restoration would remove. The benefits of the cultural ecosystem services from habitat restoration may increase the potential to obtain funding for such restoration.

Use science-based disturbance thresholds and the precautionary approach.—Establish and use science-based disturbance thresholds to guide management, recognizing and accounting for the notion that the imprecision of thresholds applies to all species, even those for which quantitative thresholds for known sources of disturbances under specific conditions have been identified; thresholds may not adequately protect the target focal species under all conditions in which they occur. The determination of disturbance thresholds must consider the influence of trail-related expansion of effect zones, especially with respect to reductions in the proportions of protected areas that are suitable for wildlife.

To compensate for the imprecision of thresholds when using them to guide management, (1) apply a precautionary approach that adopts maximum values of quantitative disturbance thresholds observed for the taxa of concern, while excluding the extreme values of the thresholds (Dertien et al.'s 2018),[17] (2) take into account that the default position should be a precautionary approach that assumes a priori that the functional value of species' abundance is high (Baker et al. 2018), (3) employ continual proactive and adaptive management to protect wildlife from recreational disturbance,[18] and (4) restrict access if the management fails. The need for the precautionary approach stems from the gaps in knowledge about quantitative disturbance thresholds of recreation.

In trail and trail network planning, use the best available science.—When planning new or modifying existing trails and trail networks in protected areas, the best available science ought to guide policy and decision-making about the siting, design, and alignment of the trails, and about the types, levels, and timing of recreation under consideration. To protect the sensitive species, the policy and decision-making should factor in the capacity to manage the existing and planned trails and recreation in perpetuity. No matter how high the pressure from recreationists for more recreational trails and opportunities, it must be recognized that the majority of recreation-related effects on wildlife are negative. The implications of this necessitate thorough consideration as to whether recreational accommodations that are being considered (in conjunction with all other anthropogenic effects) are compatible with

17 The precautionary approach and the precautionary principle (footnote #14) have subtle differences between them, but consideration of the differences is beyond the scope of this paper.

18 Based on section 13.5 of the California Fish and Game Code (FGC) and the Natural Community Conservation Planning Act (i.e., section 2805 of the FGC), adaptive management generally means (1) improving management of biological resources over time by using new information gathered through monitoring, evaluation, and other credible sources as they become available, and (2) adjusting management strategies and practices accordingly to assist in meeting conservation and management goals (e.g., conservation of covered or focal species). Under adaptive management, program actions are viewed as tools for learning and to inform future actions. Adaptive management is a cornerstone of large-scale multiple species conservation (CDFW 2014).

the protected areas' conservation objectives. The planning should incorporate protective disturbance thresholds, allowing for adaptive modifications as needed. In situations where recreation has been assumed to meet the conditions of compatibility (e.g., as negotiated in NCCPs/HCPs), great care is needed to ensure the veracity of this assumption. The outcome of the planning process should be ecologically soundly designed, sited, and aligned trails and trail networks, with science-based restrictions on types, levels, and timing of recreation. In conjunction with new trail/trail network construction, restore the habitat lost to inappropriate trails within the area of the construction.

For future protected areas, plan separate recreational areas.—Planning for future protected areas and associated trail networks and recreational areas holds the greatest potential for successful collaboration among landowners, agencies, recreationists, and other stakeholders that allows for truly protective conditions for sensitive species with respect to recreation. Perhaps it is not too late for California to redirect the trajectory of the recreational juggernaut toward an inspirational conservation success story, where stakeholders come together in the planning process, and apply the prevailing science regarding recreation-related disturbance to wildlife to ensure the perpetuation of viable populations of wildlife in the very protected areas set aside primarily or solely for that purpose. Representatives of the recreation community should sit at the table when planning future protected areas and associated trail networks and recreational areas (Burgin and Hardiman 2012); if the outcome is acceptable to them, it may prevent or minimize the creation of unauthorized trails. For example, without a strong strategic approach to mountain biking that includes community engagement, the outcome will be further degradation of protected areas and, at the least, loss of individuals of wildlife, if not major threats to wildlife populations; it's likely that there will also be on-going conflict between mountain bikers and other recreationists and residents (Burgin and Hardiman 2013).

The limited availability of resources for management suggests that it may be more effective to allocate recreational uses and conservation targets among different sites, which will require a diverse suite of land conservation strategies (Reed and Merenlender 2008). At least until such time that there is management of recreation in protected areas commensurate with recreational pressure, planning for future protected areas should heed what has been commonly known for at least 60 years: if conservation of land occurs without enforcing quotas on visitors, then separate areas need to be provided to accommodate recreational activities elsewhere so that the protected land will not bear the burden of those activities (Wilson 2019). This sentiment applies far more today, principally to protected areas preserved primarily or solely for the perpetuation of sensitive species. While this approach is infeasible for many established protected areas (most protected areas in urban areas), going forward, this ought to be the paradigm of habitat and species conservation in areas of high recreational pressure.

Figure 3 depicts an idealized vision of conservation planning using this approach. For protected areas established pursuant to NCCPs/HCPs negotiated in urban settings within an already fragmented landscape, there is often limited latitude for separate areas for recreation; furthermore, sensitive species are typically distributed more evenly across the urbanized landscape than depicted in Figure 3. Nevertheless, it represents the fundamental approach of separating conservation areas from recreational areas. Even in constrained areas, if planning for recreational access occurs at the regional level, planners and land managers could ensure that protected area networks include some areas that are closed to recreation, thus

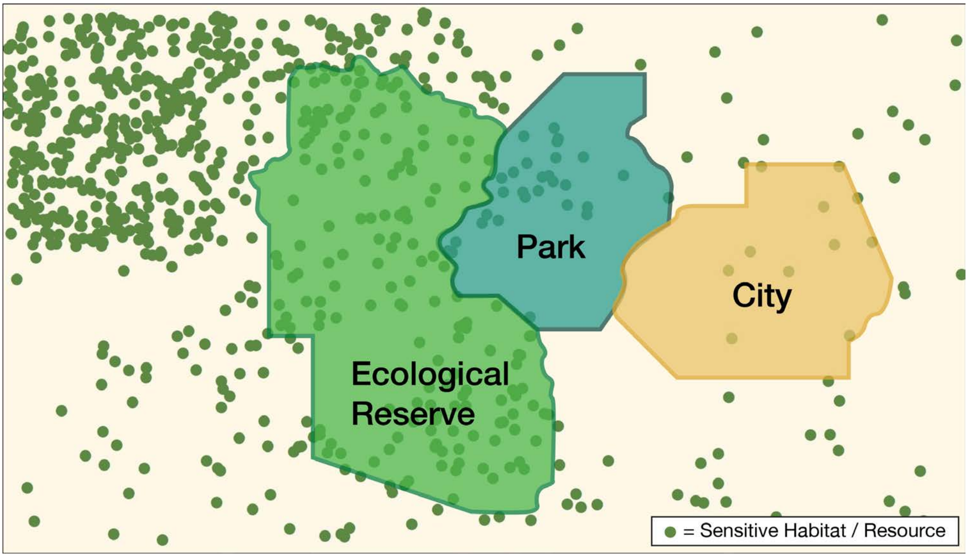

Figure 3. Effective planning for protected areas preserved primarily or solely for the perpetuation of viable populations of sensitive species: provide separate areas for conservation (e.g., ecological reserves) and recreational activities (i.e., parks). (Credit: Landscape Conservation Planning Program, CDFW 2020)

balancing the dual land uses of conservation and recreation at the scale of the protected area network instead of each individual protected area (Reed et al. 2019). Formally incorporating wildlife considerations into the trail planning process from the start is essential to reducing recreation-related disturbance to wildlife; if trail planning is well underway by the time wildlife is considered, it may be too late to gather sufficient wildlife information to inform the planning process (Hennings 2017).

A consideration often not made in conservation planning is the need to address the temporal aspect of human-wildlife interactions. For example, similar to seasonal restrictions, diurnal or nocturnal "temporal zoning" may be necessary to restrict certain human activities during times of the day when sensitive species are most active or when the likelihood of negative human-wildlife encounters is greatest (Gaynor 2018; Whittington 2019). The effectiveness of temporal closures likely depends on the amount and quality of habitat, and levels of human use and fragmentation, within the planned protected areas and in the surrounding landscape. Temporal closures may not benefit wildlife with diurnal activity patterns that differ from the timing of the temporal closures; so, full closures may be required to increase wildlife use in many situations (Whittington 2019). For situations when protected areas and recreational areas are separate but share a boundary, temporal zoning would also apply to the effect zone within the recreational area.

Conclusion.—The most sensible approach for species conservation may be to concentrate research and protection efforts on species whose populations are declining and for which human disturbance is implicated as a possible cause (Gill et al. 2001). The designation of ecological reserves and the conservation of habitat pursuant to NCCPs/HCPs are examples of processes that embody this approach. But, when recreation in such protected areas is not properly planned and adequately managed, their ecological viability and ability to meet their conservation objectives are jeopardized. Implementation of the recommendations provided herein is necessary to ensure the focal species thrive.

Ultimately, for wildlife that avoids human activity, it is unlikely that dual-role protected areas are entirely sufficient or justifiable for meeting conservation objectives; limiting or prohibiting recreation in strategic circumstances and locations within protected areas is necessary to achieve conservation objectives (Bötsch et al. 2018; Dertien et al. 2018; Reed et al. 2019). Enforced closures of inappropriate trails in all protected areas and restoration of those trails would substantially decrease the trail-related disturbance to wildlife across the landscape; waiting until after wildlife detections or estimates of habitat use decrease is too late to implement these measures (Dertien et al. 2018). These approaches require perpetual management commensurate with expanding levels of authorized and unauthorized non-consumptive recreation in protected areas. Action is urgently needed to secure perpetual fiscal support for management sufficient to ensure the perpetuation of viable populations of sensitive species in protected areas.

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